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SOME EFFECTS OF INBREEDING AND RECIPROCAL CROSSING ON THE PERFORMANCE OF LINES OF HOLSTEIN CATTLE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

by

Robert Campbell Beckett, B. Agr., M.S.

* * * * *

The Ohio State University

1974

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INTRODUCTION

For many years the technique of developing inbred lines of maize for subsequent crossing, followed by careful intense selection of those line combinations which performed the best, has been recognized as an extremely useful method of improving grain yields. In view of the tremendous benefits which have been realized from such a procedure in maize, there has been a lot of interest in the possibilities of applying similar methods to other organisms including farm animals. Experiments on maize have indicated that usually those inbred lines which perform best in the inbred state will perform best in linecross combinations. Considerable differences, however, have been found to occur between different cross-combinations of a single line indicating that certain lines tend to blend together better than others.

The normal effect of inbreeding in any naturally crossfertilizing species is a general decline in vigor and overall standard of performance. This is especially true for traits connected with reproduction and livability. As a result any genetic improvements made from such a line development and crossing study must be evaluated in the light of the decreased performance of the line during the line development phase of the program.

The overall rate of genetic improvement in such a hybrid development program as described above is limited by the time required to

develop the inbred lines and the selection intensity which can be practised upon them. The time required to develop the inbred lines is of course largely determined by the generation interval of the particular species involved. Selection intensity is largely determined by reproductive rate, i.e. size of litter and number of litters per year and the fraction of the animals which must be saved in each generation to maintain breeding population size.

For a hybrid development scheme to be economically feasible in animal breeding, it must produce long term genetic gains, significantly greater than those which can be obtained under normal selection methods, in order to more than compensate for the depressed performance of the lines under inbreeding. For this to occur it is essential that nonadditive genetic effects be of significant importance, especially as the selection intensity is usually decreased in the inbred population as a result of their reduced livability and reproductive performance. From a purely theoretical viewpoint it would appear that in the absence of important non-additive genetic effects, selection under a hybrid development scheme would actually be inferior to that practised under normal additive procedures, except of course that inbreeding would allow the true genotype of the individuals to be much more accurately evaluated.

In the realm of farm livestock, hybrid development procedures have been used with a high degree of success with poultry and have also proven valuable for swine. Both these livestock types have the necessary qualifications of a high reproductive rate and short generation interval

to make a reasonably high selection intensity possible. With regard to the larger slower developing farm animals much less investigative work on the feasibility of such a breeding program has been performed. This is especially true for lactational traits in dairy cattle.

One of the main problems in evaluating the importance of hybrid vigor in dairy cattle is the extremely long period required for such a study. The generation interval is long, the reproductive rate is low and the time required to develop the inbred lines prior to crossing is considerable. The low selection potential which must be practised with cattle also limits the rate at which inbreeding can occur. The net result of these factors is that a period of about 15 years is needed for the development of lines inbred to any considerable extent. Because of the large temporary environmental influences on lactational performance it is also necessary that a fairly large number of animals be available for analysis. All of these factors taken together point to the essential requirement of at least several hundred animals available for study over a period of 20-25 years. The financial cost is high especially if the effects of inbreeding are severe and problems with change in personnel and continuous availability of breeding stock are considerable. In consequence the number of studies designed to test the importance of non-additive genetic effects in dairy cattle lactational performance has been small. While the number of studies initiated to test this characteristic has been small, the number which has attained their objectives is even smaller. Only one such investigation has ever been reported as successfully concluded and this investigation at the University of Wisconsin, reported by Mi et al.,

in 1965⁵⁹, was extremely limited both in the size of the cattle population studied, the number of sires represented and the number of different linecross combinations compared. While it did yield much valuable information on the possibility of utilizing heterosis in dairy cattle, it was nevertheless much too small and restricted to provide conclusive answers to all of the questions which invariably arise when the topic of heterosis is being discussed.

The purpose of this study is to evaluate some of the effects of reciprocal crossing of lines of Holstein cattle on production and other traits of economic importance. It is hoped that the interpretation of the data will improve the current concepts of the merits of selection procedures designed to utilize non-additive genetic effects.

REVIEW OF LITERATURE

Historical Background

The practice of mating close relatives is not a new concept as many accounts of it are available in ancient literature. By necessity Cain and Seth must have married and mated with their own sisters as there were no other possible females on the earth at that time. Abraham married his half-sister Sarah and it was also a common practice at that time for brother-sister mating to be practiced among the Pharaohs to prevent dilution of the blood of the gods. While very little information is available on the incidence of inbreeding among domestic animals, it is extremely likely that close matings took place between the small numbers of animals of each original species which survived the Noahic flood, which deluged the earth about 2444 BC. We can also probably assume that a considerable degree of inbreeding did take place in ancient times, due to the tendency for separate communities to exist as isolated units for many generations.

In 1716 the first plant hybrid was identified as such, and in the same year Cotton Mather¹⁰⁵ correctly identified the cause of xenia as being due to a windborne intermixture of varieties on the same ear of maize. In 1766 Josef Gottlieb Koebrenter published his well known dossier and established plant hybridization on a scientific basis.

In 1865 Mendel described hybrid vigor in his pea hybrids, and in 1876 the text "Cross and Self Fertilization in the Vegetable Kingdom", was published by Charles Darwin¹⁵. In it he stated "The first and most important conclusion which may be drawn from the observations given in this volume, is that cross-fertilization is generally beneficial and self-fertilization injurious".

In 1891 Johnson⁴⁷ proposed a pre-mendelian interpretation of hybrid vigor when stating "crossing commonly gives better offspring than inbreeding, and is due to the fact that in the latter, both parents are likely to possess by inheritance the same imperfections, which are thus intensified in the progeny, while in crossbreeding the parents more usually have different imperfections, which often more or less compensate each other in the immediate descendants".

In 1892 G. W. McClure⁵⁷ published his famous paper in which he cited observations on the characteristics of heterosis in corn. He noted: (a) Sterility and deformity often follow selfing. (b) Crossing imparts vigor. (c) That it is impossible to tell in advance what varieties will produce corn of increased size when crossed. (d) That what appears to be the best ear does not always produce the largest crops. (e) Most of the hybrid corn grown the second year is smaller than that grown the first year although most of it is yet larger than the average size of the parent varieties.

In 1893 Morrow & Cardiner⁶⁰ noted that "It seems that crossbred corn gives larger yields, at least for the first and second years after crossing, than an average of the parent varieties, but how much longer this greater fruitfulness will last is undetermined."

In the early nineteenth century the first attempts at production and maintenance of purebred animal species were recorded. The most common procedure seemed to be one of linebreeding to exceptional animals, usually sires, until performance began to decline after which linecrossing was initiated, followed again by more inbreeding. This policy combined with careful selection did actually result in great advances in animal performance and was the basis of the outstanding work done by Robert Bakewell⁶⁶.

One of the earliest examples of the maintenance of homozygosity of cattle was the Duchess family of Shorthorns developed by Bates¹⁰² in the nineteenth century. He started with Colling-bred stock already inbred by about 40% and kept the inbreeding level essentially constant for about 40 years even though fertility was very low. During this time the coefficient of relationship of Duchess cows remained at about 60%.

In 1918 and 1919 the results of King's famous experiments with Albino Norway rats were published 19 , 50 , 51 , in which she showed that selection was seemingly effective in checking any tendency that inbreeding might have had to bring out the undesirable latent effects inherent in the strain.

In 1922 Wright¹⁰⁰ reported that 20 years of continuous brothersister mating with guinea pigs produced no obvious specific degenerations, but on the average a decline in all elements of vigor. There were however, significant differences in the effects of inbreeding on different traits, indicating that each was inherited independently of

each other with each family being characterized by a particular combination of traits usually involving strength in some respects and weakness in others.

General Aspects of Heterosis Theory

The fundamental theoretical principles of quantitative genetics involved in the occurrence of the phenomena of inbreeding and its complement hybrid vigor have been clearly discussed by Falconer²⁵. He pointed out that in the absence of selection, inbreeding in a population alters the genotype frequencies but not the gene frequencies. For a change of mean value to occur in a population under inbreeding there must be present directional dominance at the loci concerned with the character being investigated. The dominance may be partial or complete, or overdominance may be present. He showed that the magnitude of the change in mean value depended on the individual gene frequencies, with genes at intermediate frequencies contributing more than those of high or low frequencies. He stated that when loci combined additively, the change of mean on inbreeding was directly proportional to the coefficient of inbreeding and that epistatic effects depending on interactions between dominance combinations tended to have a curvilinear depressing effect on performance. The direction of the change in mean with inbreeding was shown to be towards the value of the more recessive allele. He also pointed out that the amount of heterosis following a cross between two particular lines depended on the square of the difference in gene frequency between the populations. He observed that heterosis was exactly the opposite of inbreeding in a large closed population in which

no selection had taken place and that no overall long term genetic improvement in such a large population could be achieved through a system of inbreeding followed by linecrossing unless selection forces accompanied it.

Whaley⁹⁴ distinguished between the term hybrid vigor--which he stated as referring to the developed superiority of hybrids, and heterosis--which referred to the mechanism by which this superiority was developed. He also pointed out that hybrid vigor needed to be defined relative to a specific environment.

In 1942 Sprague & Tatum⁸⁶ published their famous paper in which they developed and defined the concepts of General and Specific Combining Ability. The term General Combining Ability (GCA) of a line was used to designate the average performance of a line in hybrid combinations and provided an indication of the importance of genes which were largely additive in their effect. Specific Combining Ability (SCA) was used to refer to those cases in which certain line combinations did relatively better or worse than would be expected on the basis of the average performance of the lines involved. They postulated that SCA may result from several causes such as mendelian segregation and recombination, incorrect genotype classification and various types of factor interactions. Their definitions at that time were being used in the realm of plant breeding, but they did state that "nicking" in farm animals was identical with their concept of specific combining ability.

Two main theories have been put forward in an attempt to explain hybrid vigor and the deleterious effects of inbreeding in mendelian

terms. The first hypothesis, commonly called the "favorable dominance" theory, is based on the observed correlation between dominance and beneficial effects (or recessiveness and detrimental effects). Inbreeding uncovers deleterious recessives and usually results in a deterioration of level of performance. When a hybrid is formed, some of the detrimental recessives brought into the hybrid zygote by one parent are rendered ineffective by their dominant alleles from the other, and an increase in vigor is the result. This theory was put forward by Keeble & Pellew in 1910¹⁴⁸ and more generally developed in mathematical terms by Bruce⁹ in the same year when he showed that the number of homozygous recessive loci would always be less in the hybrid population than the mean number in the two parent populations.

The second hypothesis usually referred to as the "overdominance" theory, is based on the assumption that heterozygosity <u>per se</u>, is a virtue. It depends on the idea that at certain loci the heterozygote is superior to either homozygote and that there is increased vigor in proportion to the amount of heterozygosis. This concept of a stimulating effect of hybridization began in 1908 independently with Shull⁷⁹ and East²⁰ at a time when there was no direct evidence of any locus at which the heterozygote exceeded either homozygote. Hull⁴³ suggested the term "overdominance" to describe this effect in 1945, when, on noting cases where hybrids between two inbred maize lines had a greater yield than the sum of the two inbreds, he realized that such an effect as this would not be possible with dominant genes acting in a completely additive manner. He ignored the possibility of important epistatic effects in formulating this conclusion. Work by Dobzhansky and his co-workers on the reproductive mechanisms of various species supported the "favorable dominance" theory, e.g. heterosis in corn which is cross-pollinated is much higher than for tomatoes which are 90% self-pollinated since deleterious recessives tend to be more quickly eliminated in the latter. In 1948 Crow¹⁴ showed that the best crosses between inbred lines of maize produce yields which are too high to be accounted for without overdominance at some loci. His reasoning, however, was based on several questionable assumptions including the premise that the behavior of linecrosses originating from different varieties was similar to lines originating from the same base population.

Both of these theories have had fluctuating levels of popularity but have managed to survive to the present time. They are not mutually exclusive and in relation to the multiple factor interactions known to exist in the determination of quantitative traits, are also not collectively exhaustive.

With regard to the phenomenon of "nicking" which has been observed in cattle, Seath & Lush in 1940⁸² brought to attention some aspects of the role of epistatic interactions in the control of animal performance. They stated that genes in certain specific combinations may have effects very different from their average effects. They speculated that because of the large amount of segregation and recombination of genes between generations, selection had probably taken place against gene factors which only had good effects when present in specific combinations. If epistatic effects were of major importance, then hybridization would be expected to cause a break-up of some of the desirable gene combinations and result in a reduction of overall performance.

In recent years attempts have been made to investigate the phenomenon of heterosis at the molecular and biochemical levels. Schwartz & Laughner⁸¹ have investigated the polymorphic forms of the enzyme alcohol dehydrogenase in maize. This enzyme is a dimer, and four alleles have been detected. specifying three different isoenzymes in the heterozygote. The isoenzymes differed in their stability over a wide range of pH values and in their activity. They showed that in germinating maize seedlings the combination of two isocnzyme sub-units. one with the characteristic of stability, the other that of high activity, resulted in a heterozygote better than either of the homozygotes. They proposed that in some or many cases the properties of high stability and high activity cannot be combined in the same primary structure and that hybrid vigor may in part result from combining in heterozygotes, alleles for active but relatively unstable enzyme forms with alleles which specify stable but relatively inactive enzymes. These gene products then interact to confer both stability and activity on the hybrid enzyme molecule. This theory was supported by a study of Warner et al.93, which showed that for nitrate reductase in maize, the F1 hybrid resembled one parent in rate of enzyme synthesis and the other parent in the rate of in vivo decay. They postulated also that if these alleles were closely linked and inherited as one unit on a single chromosome, their effects would correspond to those ascribed to additive genetic effects.

The review given above outlines the paucity of the understanding of the mechanisms involved in inbreeding depression and hybrid vigor. Both theories have their strong and weak points, with our present day understanding of the chemical nature of enzymes tending to favor the "overdominance" hypothesis.

The relative importance of additive and non-additive genetic effects in dairy cattle herds was investigated by Freeman & Henderson in 1959²⁷. They defined the genetic covariance between relatives as $COV_{x_ix_j} = a_{ij}V_{10} + d_{,j}V_{01} + a_{,j}d_{ij}V_{11} + a_{ij}^2V_{20} + d_{ij}^2V_{02}$ etc. where V, $a_{,j}$ and $d_{,j}$ were respectively the variance, additive and dominance relationships between animals i and j. Since the dominance relationships would be zero unless the animals were related through at least one common ancestor, they were normally expected to be small, except in the case of full-sibs or where there had been considerable inbreeding. Theoretically, the additive effects (a_{ij}) could have been as large as 0.5 even without inbreeding. They found to support their theoretical genetic theory, that the dominance relationships among animals in a herd were essentially zero, and that the mean additive relationship of all animal pairs was only 0.04. The average additive relationship of related animals was calculated to be 0.13.

Cross-Breeding Work Among Dairy Breeds

If the history of the cattle breeds²⁴ is traced back for several thousand years it reveals the presence of two fairly distinct species, <u>Bos taurus</u>--which refers to the European type of cattle, and <u>Bos</u> <u>indicus</u>--which describes the zebu type, as well as many intermediate

varieties between these two species types. Evidence seems to suggest a single common origin for these two cattle species, with development over long periods of time in distinctly different environments, resulting in natural selection forces leading to ever increasing differentiation within an original single species type. It is generally believed that the Friesian breed, of which the Holstein is only one particular type, originated from a long horned sub-species of European cattle known as Bos primigenius. Jerseys, Guernseys and Brown Swiss cattle are believed to have been developed from the Bos longifrons subspecies which were short horned, while Ayrshires are believed to have come from selection within crosses of these two original subspecies. Looked at in this perspective, crossbreeding is essentially the same basic type of procedure as linecrossing. However, in crossbreeding the stock which are being combined have a greater degree of genetic diversity between them, than do the separate lines within a breed, which have been kept as distinctly separate breeding units for a much shorter period of time. Breed registry societies first were formed around the beginning of the nineteenth century, and Robert Bakewell is given the credit as the founder of pedigree breeding. However, geographical isolation and different objectives in selection had long before this time led to the development of many different types of cattle, and many of the breeds which are still in existence today can rightfully claim their origin to a period far in advance of that of Bakewell.

One of the most extensive of the early American crossbreeding experiments was begun in 1911 by T. L. Bowlker, who made reciprocal

crosses between Guernseys and Holsteins, to test the possibility of having characters for high milk yield and butterfat percentage combined in some of the animals in the F_2 crossbred generation. After his death the cattle were transferred to the Illinois Agricultural Experiment Station where the experiment was continued. In a report by Castle¹³, the F_1 crossbred cows exceeded a mean between the Guernsey and Holstein records by 7.6 percent for the first lactation and 15 percent for the second lactation. Several subsequent reports by Gaines et al.29, and Yapp¹⁰³ supported this finding, and disclosed also that F_2 cows produced from the mating of crossbred parents were inferior in milk production to the F₁ individuals, but still were slightly better than the mean of the original purebred parents. No hybrid vigor was detected for butterfat percentage. The validity of these comparisons must be questioned, because no account was taken of possible environmental changes which could have influenced the production results. Prior to this time, a crossbreeding experiment was started in 1906 at Tranekjaer, Denmark involving Red Danish and Jersey cows. Jersey bulls were used on both purebred Jersey and Red Danish cows, backcrosses were also made to both breeds and an F₂ was developed. Results published 22, 98, indicated that while the F1 crossbreds exceeded the intermediate of the parent breeds in both milk and butterfat yield measured over the first 70 days of lactation, the difference was not of a great enough magnitude to confirm the presence of hybrid vigor. No definite indications of hybrid vigor were obtained from any of the other crossbred types. However, it was highly questionable if production records estimated only over a 70 day period, were of sufficient accuracy to detect small differences in

production which may have existed. Reports⁶³, ⁶⁴ from a very limited number of Jersey and Holstein crosses made at the S. Dakota Agricultural Experimental Station revealed the F_2 crossbred cows to be somewhat lower than the F_1 crossbred cows in milk and butterfat yields.

A study⁷⁸ involving the crossing of Friesian and Jersey cattle was begun in Germany in 1940, but was interrupted by World War II in 1945. A one way cross was made using four highly selected Jersey bulls. Again numbers were small since only 43 animals were distributed in the two purebred and one crossbred classes, but evidence of significant hybrid vigor was present in large enough magnitude to be striking. The crossbred cows exceeded the mean of the parent breeds by 12.2 percent in milk, 15.2 percent in butterfat test, and 36.6 percent in butterfat yield. The average butterfat yield of the crossbred cows was higher than that for either parent breed. Byckov¹² reported that in comparisons of reciprocal crosses of Ayrshires and East Friesians with the parent breeds, the crossbreds exceeded the best of the parent breeds in 300 day butterfat yield by almost 10%. Rostovcev⁷⁶ reported that when Gorbatov Red bulls were mated to East Friesian cows, the milk and butterfat yields of the crossbreds exceeded that of either parent for each of the first three lactations. The crossbreds also exceeded both parent breeds in persistency of milk yield.

Probably the most extensive crossbreeding experiment ever performed was conducted by the U.S.D.A. at Beltsville²⁶. The project began in 1939, and both males and females of the Holstein, Jersey and Red Dane breeds were used for foundation stock, as well as females of the Guernsey breed. The plan of crossbreeding was to make two-breed crosses (reciprocal where possible) of the available breeds using progenyproduction proved sires in all matings. The resulting two-breed females were mated to a proven sire of the third breed, and all succeeding generations of crossbred females were mated to proven sires of the Holstein, Jersey or Red Dane breed on a breed-rotation basis. Direct comparisons of crossbred and of purebred daughters from the same dam were made; 37 pairs being available for comparison. The average production performance of the crossbred daughters exceeded that of their purebred sibs by 1518 pounds of milk, 122 pounds of fat and by 0.30% in butterfat test. Twenty-four of the crossbred daughters produced more milk than their pure sibs, 24 had a higher butterfat test, and 31 produced more butterfat. The three-breed cows averaged higher than the two-breed cows in each of their first five lactation records. Overall, they produced about 600 pounds more milk and 13 pounds more butterfat. The persistency of both groups of crossbreds was superior to that of the purebred foundation animals, and the order of breeds in a cycle did not seem to be particularly important. The conclusion was that when production-proved sires were used for crossbreeding in a 3or h-breed rotation, a big increase in milk and butterfat production over parent stock could be expected in the first cross, and slight increases in subsequent crosses.

Brandt & Brannon⁸ compared purebred Holsteins and Brown Swiss, and their crosses. While the average milk production of the two crossbred means were higher than the averages of the two purebred means (4,085 V's 3,922 Kg. F.C.M.), the only significant interaction constant was that for percent fat, indicating heterosis only for this trait. They found

the effect of breed of dam to be non-significant for all of the production traits studied. In a similar type of study the same researchers bred Brown Swiss bulls to Guernsey and Holstein reciprocal cross cows. A rotational crossbreeding system using Guernsey or Holstein bulls or both was followed, to obtain third and fourth generation crosses. Data analysed were deviations of a crossbred record from records of a contemporary purebred. They concluded that, in general, non-additive effects were not important for production traits in crosses among the various breeds.

Beal & Martin⁵ analysed three two-breed crossbred groups and three three-breed crossbred groups of Red Dane, Red Poll and Milking Shorthorn cattle. All cows were recorded and a total of 246 records were available. Significance was noted at the one percent level for effects due to breed of sire, breed of dam, and breed of dam by breed of sirc interaction. Sires within breed were also found to be significant at the one percent level. The effect of type of dam, i.e. purebred or crossbred, was not significant. A later report on this study by Fan⁶⁵ concluded that for both growth and lactation traits the degree of heterosis was small, with non-additive effects being much smaller than additive effects existing between and within breeds.

McDowell & McDaniel⁵⁸ examined all possible two-breed and threebreed crosses of Holsteins, Brown Swiss and Ayrshires. Ayrshire \bar{x} Holstein and Holstein \bar{x} Swiss crosses were 8-10% above the parental mean for production traits, while no heterosis was observed in the Ayrshire \bar{x} Swiss cross. In general, estimates of heterosis for the three-breed crosses were higher than for two-breed crosses, and ranged

from 9.2 to 13.8% above the parental breed means for milk, fat, solidsnot-fat and protein yield. The average heterosis for fat converted milk in two-breed crosses was about 6%, while that for three-breed crosses was about 14%. The higher degree of heterosis estimated for the three-breed crosses could have been related to a higher percentage of Holstein blood in these crosses. The variability in performance of the crossbreds was similar to that of the purebreds, but all crossbreds averaged fewer days open during lactation than the purebreds, and the degree of heterosis for this trait for the various two-breed crosses ranged from 2-15%. Heterosis for level of feed efficiency was 4-5% for Ayrshire X Holstein and Swiss X Holstein crosses, but was close to zero for Ayrshire \bar{x} Swiss crosses. Little or no heterosis was observed for type traits or milking rate. However, since purebred Holsteins consistently outyielded all crossbred groups, they concluded that this purebreed was superior, except in specific cost-price situations where greater economic emphasis was being given to milk composition and efficiency of feed utilization.

Hollon et al.³⁹, in Louisiana compared 64 Holstein sired crossbreds, 64 Brown Swiss sired crossbreds and 20 daughters of crossbred sires to contemporary sires. Purebred-sired crosses were significantly superior to daughters of crossbred sires, and Holstein-sired crosses were superior to Brown Swiss-sired crosses. Purebred-sired crosses had from 4-16% positive heterosis for milk yield, 0-7% for milk fat, and 1-10% for fat converted milk, but ranged from 1-8% below the weighted parental mean for percentage milk fat. Addition of a third breed nearly doubled the magnitude of heterosis for milk, irrespective of the breed of the third sire, and estimates of heterosis for the other production traits were also higher. It was not clear how much of this increased heterosis was due to heterosis in the two-breed dam for maternal effects. Holstein-sired crossbreds were superior to purebred Holsteins in all traits except milk yield and length of lactation. Breed group differences were not significant for persistency or length of lactation. Deviations from the weighted parental means for daughters of crossbred sires were negative for all production traits, but this may have been related to the fact that the crossbred sires were relatively unselected.

Okumu & Berry⁶² in 1966 published the results of a Canadian study mainly investigating the effects of increasing the use of Holstein sires on production traits. They studied the performances of purebreds, crossbreds and backcrosses among the Holstein, Ayrshire, Jersey and Guernsey breeds, and found evidence of positive heterotic effects among all crosses except Holstein x Ayrshire, when compared with their parental means. No crosses or backcrosses exceeded the purebred Holsteins. Estimates of heterosis ranged from -2.2% to +8.5% for twobreed crosses. A polyallel analysis revealed significant mean squares for General Combining Ability, Specific Combining Ability, and Reciprocal Effects (which included maternal effects). They also looked at 10 artificial insemination sires with a reasonable number of both purebred and crossbred daughters, and showed that differences in ranking occurred, depending on whether they were used to produce purebred or crossbred daughters. They concluded that the best sire for purebreeding was not necessarily best for crossbreeding. Crossbred

daughters tended to have a higher degree of persistency of lactation than purebred daughters. The highly significant reciprocal effects suggested the presence of important maternal or sex-linked effects influencing milk production of the offspring.

One of the most complete accounts of a crossbreeding study was that reported by Touchberry⁸⁹, on the results of four generations of crossbreeding between Holsteins and Guernseys, conducted at the University of Illinois. This experiment was carefully designed in order to avoid the confounding of the comparison of purebreds and crossbreds with sires and years, which occurred at least partially in the previous U.S.D.A. four-breed study at Beltsville²⁶. Twenty cows from each of the Guernsey and Holstein breeds were chosen as the foundation stock for the study, half of them being cross-mated, and the other half bred pure to produce the first generation; the breeding policy of each of the animals was reversed in the next year. A succeeding series of carefully planned cross and pure breed matings was continued for four more generations, to produce contemporary purebred progeny and crossbred progeny, with a wide variety of proportions of genetic components from each of the two foundation breeds. Attempts were made to use a large number of both Guernsey and Holstein sires believed to be representative of the breeds as a whole, to eliminate effects due to differences in the transmitting ability of the various sires. Crossbreeding resulted in 6.4, 7.5, 4.7 and 7.5 percent heterosis for milk. fat, solids-not-fat and protein respectively. There was 18% heterosis for the fraction that lived to calving age (approximately two years). 17% for the fraction that calved once, and 17% for the fraction that

calved twice. Heterosis for birth and growth rate was approximately five percent. By incorporating these measures of viability, growth and production into a measure of total performance in terms of dollars, crossbreeding resulted in 21.7% heterosis. However, when the means for the breed groups included in the study were considered, the Holsteins exceeded the crossbreds by about 10 percent. In a previous report on the same project, Bereskin & Touchberry⁶ concluded that while there was no evidence of specific combining ability between the two breeds, some evidence did exist to support the presence of specific combining ability between certain bulls and cow-breed groups.

In 1971 Donald¹⁹ reported on a crossbreeding study involving British Friesian \bar{x} Jersey crosses conducted in England. Milk yield showed 5% heterosis, but none was observed for milk fat, or solids-notfat percentage. He looked at many different traits and found the degree of heterosis to vary from 0-20%. The amount of heterosis appeared to be inversely related to the heritability of the particular trait being considered.

At present a study is just being concluded by the U.S.D.A. at Beltsville comparing outcrosses, linebreds and crossbreds of the Holstein (H), Brown Swiss (S) and Ayrshire (A) breeds. Several progress reports have been presented by Pearson <u>et al.</u>^{67, 68} and Hooven <u>et al.</u>^{11, 12}. Animals resulting from the use of outcross sires have consistently ranked highest for all of the yield traits. The only cross which offered a favorable comparison to the Holstein outcrosses was the Holstein backcross on S(A x H), which was the best producing group in the three mating systems. However, the poor performance of the
preceeding two and three-way crosses seemed to be important enough to tend to discourage crossbreeding in this direction. The investigators reported a high positive correlation between yield and feed efficiency, indicating that the highest producing cows were the most efficient, regardless of mating system. There were no differences among mating systems for gross feed efficiency. They concluded that "Unless vastly superior fitness and reproductive efficiency of linebreds and crossbreds can be demonstrated, it would seem that the reduced selection pressure that can be applied in linebreeding, and the lack of other breeds of near equal additive genetic merit in systematic crossbreeding, limit the usefulness of these two systems of breeding under present environmental and economic conditions.".

Two breeds of cattle, the Swedish Red & White and the Swedish Friesian, which had been developed as separate breeds for 35 years but were still very similar phenotypically, were merged in 1928, and the effects of inbreeding during the separation, and heterosis during the merging were carefully analysed by Hansson <u>et al.</u>³². In both breeds, inbreeding had a significant depressing effect on yield of fat converted milk, but nicking did not appear to have any significant effect on the genetic improvement of milk yield. This report is in some conflict with one published in 1939 by Johannson¹¹⁴, in which he concluded that the average production of milk and butterfat was five percent higher for the crossbreds than for their contemporaries in the two original breeds. Contemporaries were defined as cows of the same age making their records in the same herd.

In a report given in 1964, Johnson et al.⁴⁵, published results of a comparison between 124 crossbred and 189 purebred cows sired by 24 Holstein, 13 Brown Swiss and 20 Jersey bulls. Nearly all sires had both purebred and crossbred daughters. Comparisons of each crossbred animal with the weighted mean of its contemporary purebred herdmates on a within year-season mature equivalent basis were made, and each parental purebred group was tested with groups of crossbreds to which that group contributed. The average production of the crossbreds $(\frac{1}{2}$ Swiss- $\frac{1}{2}$ Jersey, 1 Swiss-1 Holstein-1 Jersey, 1 Holstein-1 Jersey, 1 Holstein-1 Swiss- $\frac{1}{4}$ Jersey) was significantly greater than the mean production of the parental purebreds. Increases for some crossbred groups were as large as 20% for pounds of milk, 21% for pounds of fat, and 15% for pounds of 1% fat converted milk. The performance of the crossbreds having Jersey and Brown Swiss parentage surpassed that of the purebred Jerseys or Brown Swiss. Performance of crossbreds having Holstein parentage essentially equalled or surpassed that of the purebred Holsteins. This last finding is quite an exception to what has been normally reported in the literature.

Linecrossing Studies in Dairy Cattle

Several reports have appeared in the literature indicating the presence of heterosis when inbred lines of cattle are outcrossed to animals of the same breed. Ralston <u>et al.</u>⁷⁰ in 1948 reported that when an unrelated inbred sire ($F_x=23.0$) was mated to a highly inbred line of Holsteins (av. $F_x=29.8$) produced at the University of California by a system of sire-daughter matings, the offspring produced 203 pounds more

butterfat than their inbred dams and 52 pounds more than the mean of the foundation cows used in the line development. No attempt was made to adjust the data for effects due to environmental changes, or to differences in the transmitting abilities of the sires involved.

An interesting study was performed by Soller & Bar-Anan⁶⁴ in 196k, when they compared the contemporary comparisons computed by crossing bulls of both American and Dutch Friesian origin with (a) full bred or 3/4 Dutch cows (b) full bred or 3/4 American cows. The strain of sire by strain of dam interaction was highly significant, and the average contemporary comparison in each case of the daughters of a sire out of a dam of the opposite strain was greater than the average contemporary comparison of his daughters out of the same strain of dam. The average effect of crossing the two strains was of the order of 1.5 kg of milk per day, or 450 kg over the course of a 300 day lactation. They concluded their report by stating that if heterosis were a cause of superiority of imported bulls, then the widespread use of imported sires, selected because of such superiority, would not contribute to the long term improvement of the cattle population.

Heizer et al.³⁷ in 1938 reported that several sires when crossed on the daughters of another particular sire, and the reciprocal cross, showed significant differences (at the one percent level) in the estimates of their transmitting abilities, compared with those estimated on all their daughters chosen at random. The estimated transmitting ability of a sire seemed to depend in some cases on the identity of the sire of the cow to which he was mated. Heizer and his colleagues seemed to think that there was enough evidence to support the explanation that nicking had indeed taken place between certain of the cow lines. These observations were made in a study designed to test the effect of mating system on the proof of a sire. They also found that one bull, when mated to 15 of his daughters, appeared to have a much lower transmitting ability than when he was outcrossed to other cows.

A study of appreciable magnitude, which has involved the planned development of inbred lines and their subsequent crossing, was undertaken in Wisconsin as a cooperative venture between the Wisconsin Agricultural Experiment Station and the U.S.D.A. An analysis on the early preliminary data on production was published by Kraemer et al.53 in 1958 and a subsequent report by Mi et al.⁵⁹, summarized the main effects of the linecrossing experiment. The foundation animals consisted of six Holstein proven sires, one or two outbred sons of each and 20 open outbred daughters by each sire. Each of these six groups was designated as a sire-line, and matings were planned to produce inbred daughters within each sire-line and linecross daughters for each sire-line sired by bulls of two other lines. For the first-generation offspring, inbreeding was continued within each sire-line by mating the foundation sire or his inbred son to inbred females of the same line. Matings were also made of inbred females of one sire-line to inbred bulls of two other lines to produce linecross offspring. The mating systems used in the third and later generations were similar to those outlined above, namely close inbreeding within each sire-line and linecrossing (2-line, 3-line, etc.). There were 12 reciprocal crosses in addition to the six inbred groups during the 12 years of the experiment. The linecross heifers born in the herd were mated to as many different

bulls as possible, chosen at random from two artificial breeding associations in Wisconsin to produce outbred offspring. These outbred females and their offspring then were used as a control group to check trends in the herd environment. Analyses of 174 first lactations of these outbreds and their outbred progeny did not reveal any significant effects of year, season or their interaction, and these variables were omitted from the main analyses. All animals which had made records of 150 days or greater were included in the study, incomplete records being extended to 305 days using D.H.I.A. conversion factors. Both actual 305 day 2x records of milk and fat, and those adjusted to a mature equivalent basis were analysed. Examination of the disposal records of animals having a lactation of length less than 150 days did not show any evidence of intentional selection of animals. There were, however, more disposals in inbred groups due to infections at early ages, and reproductive difficulties at later ages, indicating some natural selection through lack of reproductive fitness and thriftiness. Overall there were a total of 760 production records, made by 310 inbred and linecross females sired by 31 herd bulls out of six sire lines. The average degree of inbreeding varied between lines, ranging from 15.7 to 27.2%, with an overall average of 25.3%.

Only first lactation records were used. The average differences in production between the inbreds and linecrosses were 2,455 pounds of milk and 97 pounds of butterfat on a mature equivalent basis. This was in contrast to differences of only 1,761 pounds of milk and 49 pounds of butterfat on a mature equivalent basis when the inbreds were compared with the outbreds. Inbreeding brought a significant increase of 0.125

in fat test in relation to outcrosses, this being consistent with the inverse relationship of fat test with production. When compared with linecrosses, the inbreds produced milk which was 0.1% lower in butterfat. Differences in general combining ability among lines measured from both the inbred and linecross progeny were found to be highly significant in most cases. These effects were estimated under the assumption that the sire lines were random, and the specific combining effects of lines in crossing were nonexistent. A highly significant sire line by mating system interaction was found for all production traits of the first lactation. This indicated that different mating systems, i.e. outcrossing, inbreeding and linecrossing would not be expected to produce similar results in different sire lines.

Effects of Inbreeding on Production of Dairy Cattle

While inbreeding had been known for a long time to result in a deterioration in the level of animal performance, it was not until after Wright⁹⁹ had developed his method of path coefficients in 1922 that the exact effects of inbreeding could be precisely quantified. Several early studies in the U.S.A. on the effects of inbreeding on milk production in dairy cattle were conducted by Hays³⁶, Woodward & Graves²⁶, Plum⁶⁹, Regan <u>et al.⁷¹</u> and Bartlett et al.^{3, 4}. These experiments involved generally only small numbers of animals.

Studies involving inbred Jersey cattle at the University of California were reported by Ralston <u>et al.⁷⁰</u> in 1948. The herd had been inbred for 11 years by a system of sire-daughter matings. Butterfat production decreased with each successive generation of sire-

daughter mating, until females with an inbreeding coefficient of 0.375 or above produced 149 pounds less fat than the first generation daughters and 206 pounds less than the foundation females. A later report by Rollins et al.⁷⁵ involving fat-converted-milk yield records on 171 cows, indicated a regression value of -50 pounds with a standard error of 15 pounds. Laben et al.⁵⁵ analyzed 164 first lactation records standardized for length, times milked daily, and age, in the inbred Holstein herd at the University of California in 1955. The average coefficient of inbreeding was just under 13 percent and 22 sires were involved. The intrasire regression coefficients of lactation milk yield, fat yield and butterfat percent on percent inbreeding were -209.8 pounds, -4.88 pounds and +0.008%, respectively. A significant negative regression on maximum daily yield was also reported. No significant effects of inbreeding on persistency or number of days prior to maximum daily production were found. Significant differences were found among three sires in the responses of their daughters to inbreeding. The effects of inbreeding also appeared to increase considerably in magnitude at levels above 20-25%.

The results of the breeding experiment in Wisconsin designed to evaluate the effects of inbreeding, outbreeding and crossing of inbred lines on quantitative traits in Holstein cattle were reported by Tyler <u>et al.⁹⁰ in 1949</u>, Kraemer <u>et al.⁵³ in 1958</u>, and an overall summary of the entire project was given by Mi <u>et al.⁵⁹ in 1965</u>. First lactation records of 111 animals with an average degree of inbreeding of 25.3 percent were analyzed. No curvilinearity of inbreeding effects were detected within sire lines, and simple linear regressions of production on percent inbreeding were -70 pounds, -1.9 pounds and 0.03 percent for mature equivalent milk, fat and fat test, respectively. Inbreeding had significantly different effects within the six different lines which were developed, with regression coefficients ranging from -1 to -133 pounds for actual milk, +0.3 to -4.6 for actual milk fat and -0.006 to +0.014 for fat test. On the average inbreds produced 1,313 pounds less of actual milk and 35 pounds less of actual fat than the outbreds. Inbred cows tended to be older at each calving than the outbreds and linebreds, the actual age differences varying from sire-line to sireline. There was no evidence that increase of production with age was more rapid in inbreds than in outbreds.

In 1930 a project involving inbreeding combined with intense selection was initiated in the Iowa State University Holstein herd. In 1958 Von Krosigh & Lush⁹¹ reported the results of regression analyses involving 534 cows, daughters of 69 sires with 1350 production records. Records were on a 305 day 2x mature equivalent basis, and the coefficients of inbreeding ranged from 0 to 35 percent with a mean of 7.4 and a standard deviation of 6.4. The simple regressions on one percent of inbreeding were $-5h \pm 17$, $-1.7h \pm 0.57$ and $+0.003 \pm 0.003$ for pounds of milk, pounds of butterfat and butterfat percentage, respectively. There was no evidence of curvilinearity in the effects of inbreeding or fat production. Adjustments for body size only removed about 25 percent of the depressing effect of inbreeding on production. These figures were in close agreement with those published by Nelson & Lush⁶¹ and by Thompson & Freeman⁸⁸ in additional analyses of the same herd. Laben & Herman⁵⁴ analyzed the records of 299 Holstein cows expressed on a 305 day 2x mature equivalent basis at Missouri. They obtained intra-sire regressions of -66.1 pounds, -2.07 pounds and +0.003 percent for lactation milk, fat and fat test, respectively, on 1 percent of inbreeding. Using similar production records Davis <u>et al.</u>¹⁶ reported the effects of inbreeding observed in the Holstein herd owned by the duPont family in Nebraska. The study included 630 daughters of 20 major herd sires, and the intra-sire regressions were -30.8 pounds, -0.66 pounds and +0.003 percent, respectively, for milk, fat and fat test. Regressions for individual sires with 20 or more daughters varied irom -235 to +2h0 pounds for milk yield, -10.2 to +9.5 pounds for fat yield and -0.091 to +0.015 for fat percentage. None of the pooled regressions differed significantly from zero.

Gaalas et al.²⁸ analyzed the records of 111 inbred cows having four lactation records. The effect of inbreeding of the cows was significant for first lactation milk and fat only (P<0.05). The effect of inbreeding of the dam on milk production of the cow was not significant. Intra-sire regressions on each one percent of inbreeding were:

	MILK (105.)	Fat (los.)
lst Lactation	-105.3	-3.62
2nd Lactation	-41.9	-1.06
3rd Lactation	-18.0	-1.32
4th Lactation	-26.2	-0.86

Average of L Lactations

Dayton¹⁷ at Michigan State University analyzed the records of 211 inbred Jersey cows from 29 different sires. The intra-sire regressions on inbreeding were -21 pounds, -0.8 pounds and +0.005 percent for milk

-47.9

-1.69

and fat yields, and fat test, respectively. The mean degree of inbreeding was 18 percent. Analysis of results of a study at S. Dakota¹⁰⁴ investigating the effects of rapid inbreeding on production traits in Holstein cattle, revealed that when lactation records were expressed on a mature equivalent basis adjusted for sire effects, the 57 outbred control animals produced 1953 pounds more milk and 59 pounds more fat than the 35 inbreds. Inbreds were superior to outbreds for fat test and protein-lactose-mineral percentage.

Allaire & Henderson at Cornell² estimated the intra-sire regression on inbreeding in a group of 999 Holstein cattle with mean $F_x = 4.9$, to be -33.7 and -0.9 pounds, respectively, for milk and fat yields. Including age and body weight as additional variables in the model had a negligible effect on the regression values. Response to increasing levels of inbreeding was found to more closely resemble a linear response than a higher order expression. Their results appeared to indicate that the rate of depression was greater for the mean yield records than for first lactation records.

Robertson⁷⁴ in 1954 analyzed the effects of inbreeding from the production records of 82 British Friesian heifers resulting from siredaughter matings. He observed no effect on age at first calving or on fat percentage. When records were corrected for the genetic merit of the sire the average decline in milk yield was 740 \pm 240 pounds, which was equivalent to a decline of 0.32 percent for each one percent increase in inbreeding. Hansson <u>et al.³²</u> in 1961 reported the intra-sire regression within herds and years for first lactation 305 day milk yield to be -31.5 pounds in Swedish Red & White cattle, and -24.3 pounds in

Swedish Friesian cattle. On the average, sire-daughter matings resulted in a decrease of 788 pounds in milk yield of the former and 568 pounds of the latter breed.

Brum¹⁰ in 1963 did an extensive analysis of the effects of inbreeding on performance of the Holstein cattle populations which are being examined in this thesis. He looked at actual 305 day 2x records independent of age at calving, for first through fourth lactations, and obtained the following intra-sire regression coefficients on percent inbreeding.

	Number of <u>Animals</u>	Mean 	Milk	Fat		
First Lactation	123Ц	3.3	-41.3 ± 9.2	$\begin{array}{r} -1.2 \ \pm \ 0.33 \\ -1.19 \ \pm \ 0.54 \\ -0.54 \ \pm \ 1.00 \\ +1.01 \ \pm \ 1.48 \end{array}$		
Second Lactation	785	2.8	-42.9 ± 19.33			
Third Lactation	481	2.5	-25.6 ± 24.8			
Fourth Lactation	26Ц	2.1	+4.9 ± 40.0			

Nested analyses of covariance were used to remove the effects of herd, year-season and sire. The linearity of regression on degree of inbreeding for first lactation milk yield was upheld. Inclusion in the model of heart girth measurement at three months after calving had very little effect on the estimated first lactation regression values. He estimated that an animal resulting from a sire-daughter mating, would on the average be only 2.5 percent smaller in heart girth than a noninbred, but would produce 10 percent less milk. Regression values for milk and fat yield were significant at the one percent level for first lactation production, and at the 5% level for second lactation production even though the standard error of the second lactation estimate had greatly increased. For third lactations, regression estimates were much lower and standard errors had so increased as to almost equal the regression coefficients. In the fourth lactation the regression coefficient was approximately zero. He postulated that the decreasing regression values with increasing age could be due partially to the effects of inbreeding on size decreasing as the animal approaches mature size. It could also have been a result of selection pressures tending to favor the retention of animals with a more heterozygous genetic makeup than would be expected from their pedigree. This last proposal was supported by the observation that first lactation regression estimates of animals which had four or more records yielded values of 0.00 ± 26.5 and 0.55 ± 0.97 for milk and fat yields, respectively. Sire differences with respect to the effect of inbreeding on first lactation milk production were present beyond the one percent level of probability.

Results of the studies discussed above are summarized in Table 1 to facilitate their comparison.

In all of these reports there was good agreement that inbreeding results in a significant reduction in level of production. The exact effects of inbreeding varied from study to study, and this was to be expected because of variations in the additive genetic merit of the animals used, especially the sires. The general conclusion would be that inbreeding tends to reduce milk production measured on a mature equivalent basis by about 50 pounds and fat by about 1.5 pounds per each one percent increase in the inbreeding coefficient.

One additional effect of inbreeding is to uncover undesirable homozygous recessive factors. Robertson⁷³ in 1949 reported on 13 inbred lines, in 10 of which harmful recessives appeared. Other effects of inbreeding summarized by Young et al.¹⁰⁴ include depression of birth

Location	Authors	Type of Record	No. Cows	Fr	Milk (1bs)	Fat (1bs)	Fat 🖇
California	Rollins, et al.	Actual FCM	171		-50.0	•	
Ħ	Laben, et al.	305 2x JRE	164	13.0	-209.8	-4.88	+0.008
Wisconsin	Mi, <u>et al</u> .	305 2x ME	111	25.3	-70.0	-1.9	+0.03
Iowa State	Van Krosigk & Lush	305 2x ME	534	7 •L	-54.0	-1.74	+0.003
Missouri	Laben & Herman	305 2x ME	29 9	6 6 7	-66.1	-2.07	+0.003
Nebraska	Davis, et al.	305 2x ME	630		-30.8	-0.66	+0.003
Beltsville	Gaalas, et al.	First Lactation	111		-105.3	-3.62	-
17	11	Second Lactation	111		-41.9	-1.06	-
88	**	Third Lactation	111		-18.0	-1.32	-
11	H	Fourth Lactation	111	•••	-26.2	-0.86	
tt	11	4 Lactation Mean	111		-47.9	-1.69	
Michigan State	Dayton	305 2x ME	211	18.0	-21.0	-0.8	+0.005
Cornell	Allaire & Henderson	Mean Herdmate Deviations	999	4•9	-33.7	-0.9	.
Britain	Robertson	305 2 yr. 10 mo.	82	25.0	-29.6		+0.00
Sweden	Hansson, et al.	Actual FCM	12,897		-31.5		
tt	łł	Actual FCM	10,927		-24.3		
Ohio	Brum	lst Lact-305 2x	1,234	3.3	-41.3	-1.24	
n	87	2nd Lact-305 2x	785	2.8	-42.9	-1.19	
81	11	3rd Lact-305 2x	481	2.5	-25.6	-0.54	
ŧ)	11	4th Lact-305 2x	26h	2.1	+4.9	+1.01	

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Table 1. Average Change In Production For Each Increase of 1% In Inbreeding

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weight, growth, liveability and reproductive performance, and a small increase in solids-not-fat percentage believed to be at least partially a result of the inverse relationship between milk yield and percentage composition.

The Importance of Nicking and Maternal Effects on Production of Dairy Cattle

Johnson <u>et al</u>.⁴⁶ in 1940, in a study of Jersey cattle concluded that while some matings of one bull did show a pronounced difference that could be called nicking, this phenomenon was not a prevailing factor among Jersey cattle. They also stated that "Far too often effects described as nicking may be only a reflection of the superior transmitting ability of the sire being used."

In 1965 Allaire & Henderson¹ investigated the importance of specific combining ability among sires by estimating the magnitude of the sire x maternal grandsire interaction component. By restricting the sire x maternal grandsire subclasses to those having > 10 animals, a total of 359 subclasses involving 4,816 animals were available for study. The interaction component only accounted for 1.4 percent of the total first lactation variance, and non-additive genetic effects were concluded to be of minimal importance in a general breeding program.

Van Vleck & Bradford⁹² compared estimates of heritability of production traits using the daughter-dam regression and the paternal half-sib correlation. Heritability estimates for first and second lactations were much higher for daughter-dam regressions than for paternal half-sib correlations.

Heritability Estimates

	1st Lactation	2nd Lactation	3rd Lactation
Daughter-dam regression	0.37	0.30	0.24
Pat H.S. correlation	0.24	0.21	0.23

These comparisons suggested a large maternal effect in the first, a small influence in the second and a negligible influence in the third lactation.

Holtman⁴⁰ at Wisconsin, in a study of linecrossing in Holstein cattle, reported that there appeared to be a negative genetic correlation between maternal effects and the general combining abilities of the lines.

Lee & Henderson⁵⁶ in 1969 analyzed first lactation records taken from the New York Dairy Records Processing Laboratory. They concluded that genetic maternal effects were of little or no importance, and the estimate of non-additive genetic variance computed as the sire xmaternal grandsire interaction was near zero.

Numerous investigations summarized by Koch⁵² in 1972, found evidence of a negative genetic correlation between the maternal environment provided by a beef cow dam and the subsequent production performance of her daughter. This was concluded to be due to differences in nutritional regimes under which the heifer calf was reared under single suckling management practices. Several studies summarized by Schultz⁸⁰ in 1969, found a similar negative correlation between level of nutrition during rearing and subsequent production of dairy cattle. Under normal dairy herd replacement rearing conditions, calves are reared on a fairly well standardized level of nutrition within each herd.

MATERIALS AND METHODS

Mating Plan and Data Collection

In 1948 a project designed to investigate some of the effects of inbreeding and reciprocal crossing among lines of Holstein cattle on dairy cattle performance was initiated in the state of Ohio. The study was performed by the Dairy Science Department of the Ohio State University in co-operation with the United States Department of Agriculture Research Center at Beltsville, Maryland, and the Ohio Department of Mental Hygiene and Mental Retardation and was part of an overall breeding research scheme involving several of the North Central States in the U.S.A., known as the NC-2 Breeding Project.

Six inbred lines of purebred Holstein cattle were developed involving about 600 cows. Three of these lines were in three separate herds; one large herd was divided into two lines, and one line was developed within two smaller herds. During the 25 years of the study, the breeding program, production testing and records collection were all under the direction and supervision of Dr. Tom Ludwick of the Dairy Science Department at Ohio State University assisted by Earl Rader, with various graduate students aiding in the data collection and field work.

Two or three related bulls were introduced as the basic foundation sires for each line. The pedigrees of the sires used in the development

of the different lines were inspected through seven generations to ensure that no two sire lines would have any close common ancestors. For each line the sires introduced at its formation were at least as closely related as half-brothers and were selected on the basis of a superior production pedigree. Since the herds were owned by the Department of Mental Hygiene and Correction in Ohio, and onc of the stipulations was that the program should not cause a significant decrease in level of production, relationship among the females within a line was increased as rapidly as possible while attempting to keep the degree of inbreeding as uniformly low as possible. For ease of computation, specific crosses were designated as basic reference points and the subsequent mating plan was arranged to build up an average degree of relationship of 25 to 30 percent among the females within each line. The average degree of inbreeding within each cow population varied from zero to five percent prior to the initiation of the project. and the herds were closed when the breeding scheme began.

The rate of line development varied from herd to herd, and in 1961 four of the lines were well enough developed to allow linecrossing to begin (for this study, a line of cattle was a group of females which had an average relationship to one another of 25% with some animals having a relationship of only 12%.). At this time the average inbreeding of the four earliest developed lines was approximately 12 percent and the average relationship among the females was about 28%. Sixty percent of the qualified animals in each line were selected at random within age groups to be used in a linecrossing scheme, the remaining h0 percent were continued to be linebred in order to maintain contemporary

linebred stock. Linecrossing began in the remaining two herds in 1962 and in 1965, respectively. Semen was frozen from sires used to develop the female groups and by the use of artificial insemination reciprocal crosses between all lines were made. All reciprocal crosses were represented in the initial four lines used in linecrossing, but some were missing when all six lines were considered. Contemporary linecrosses and linebreds were growing and producing in the same herd at the same time.

The coefficients of Inbreeding (F_x) were calculated using the method of path coefficients developed by Wright⁹⁹. Five generations including the following ancestors were used in calculating inbreeding values for the first generation of linebred animals born: sire, dam, maternal grandsire, maternal great grandsire, and maternal great-great grandsire.

In subsequent generations the inbreeding coefficients of the sire and dam were also used in calculating F_x for each individual. The coefficient of relationship between animals was calculated by the method of Wright⁹⁹. Matings were planned on the basis of the calculated inbreeding and degree of relationship of the expected progeny.

Young sires for line development were chosen on the basis of the production records of their dams and also on the contribution which they could make towards achieving the desired degree of genetic relationship within each line. These young sires which had to be free from serious physical defects were chosen from the highest producing cows in the line which could be fitted satisfactorily into the mating plan. Most sires chosen performed as planned, with a few having to be replaced because of infertility problems. For a sire's daughter to be included in the analysis, he had to have at least one linebred and one linecross daughter with the required production and other data.

No animals were culled for production levels until they had made at least one normal or extendable production record. A few heifers were unavoidably lost due to accidents, severe illness and calving complications etc., but their distribution was expected to be random. Complete records were kept on all animals from birth to slaughter, with date and reason for disposal being recorded. Heifer calves were all blood typed by the O.S.U. Cattle Blood Typing Laboratory. These blood types provided a basis for the verification of parentage records, and in most cases enabled any parentage disputes to be resolved. If the parentage of any animal could not be exactly determined, she was excluded from the study.

Degree of homozygosity as indicated by blood and milk polymorphic systems was used for checking the calculated degree of inbreeding. In 1966 Hines <u>et al.</u>³³ reporting on four of the six lines concluded, that despite considerable variation not accounted for by any linear relationship between homozygosity of blood and milk loci and inbreeding coefficients, the degree of homozygosity of seven blood and milk polymorphic systems appeared to behave generally as predicted by inbreeding . theory, with no good evidence for deviation from the expected linear relationship.

All of the milk analysis work was performed by NC-2 personnel. Initially the following tests were performed monthly on milk samples from all lactating cows.

1. Milk Fat Percentage by the Tesa Reagent Procedure.

2. Total Solids Percentage by the Golding Density Beads Method.

3. Milk Protein Percentage using the Buffalo Black Dye Absorption Method.

4. Solids-not-fat (SNF) Percentage was found from the difference between tests 1 and 2 described above.

Because of the high repeatibility of protein and SNF percentages for various lactations, first lactation data were used as an indication of the genetic ability of an individual for these traits.

All records of duration 90-304 days, and not terminating with a dry date were extended to a 305 day-2x basis. The one exception was a first lactation animal slaughtered for low production before she had produced for 90 days. She milked for 86 days, and her record was extended and included in the study. All records were expressed on a mature equivalent (ME) basis. Records interrupted by an abortion on or after 152 days of production were extended from the time of the abortion. An abortion occurring before the 152nd day of lactation was usually ignored, except in a few specific instances where our detailed records clearly showed that it did have a drastic effect on the subsequent performance of the animal during the remainder of that lactation. A few obviously abnormal records were also discarded because the health reports revealed serious influences of chronic diseases or accidents upon the animals making them. Milk and fat production were recorded through the Dairy Herd Improvement Association; SNF and Protein records were kept by project personnel. Total solids analyses were used only to compute SNF values and were not recorded

per se. All data are available for inspection in the files of the O.S.U. Department of Dairy Science.

The distribution of animals by lines and linecrosses of the six lines is given in Table 2 along with the number of sires represented in the crossing of the various lines. As indicated previously a line of cattle included a group of closely related females, however, for purposes of clarity in tables and discussion, when lines were crossed the males which represented a specific group were designated as a "sire line". The females used for a specific cross were labeled "female line".

Methods of Analysis

Effects of Inbreeding

The effects of inbreeding on the following traits were examined for each inbred line separately, the analyses being performed on the first lactation linebred animals only.

1. 1. Mature Equivalent (ME) 305 day Milk yield.

- 2. ME 305 day Butterfat Yield.
- 3. ME 305 day Solids-not-Fat yield.
- 4. ME 305 day Protein yield.
- 5. Age at Calving in months.
- 6. Days in milk during lactation--305 days or less.
- 7. Days open during lactation.

The following fixed model (Model I) was used for five of the lines.

 $Y_{ijkl} = \mu + S_i + Y_j + S_k + b_{Y/F_x} + e_{ijkl}$

where μ is the mean, Y_{ijkl} is a measure of the performance of the 1th daughter of the ith sire freshening in the kth season of the jth year,

Line of Sire	No. of Sires]	Line d	of Dam		
		<u>1</u>	2	3	<u> </u>	5	6
1	7 ^a	85 ^a	17	11	11	21	0
2	7	18	102	9	4	8	14
3	5	19	14	77	6	0	l
4	7	17	17	13	112	12	נו
5	6	15	3	0	0	65	2
6	7	0	38	0	0	10	85

Table 2. Distribution of Linebred and Linecross Animals By Line of Sire and Line of Dam

^aOnly 6 sires with 79 linebred progeny were included in the l_1 line analysis-one sire did not have linecross progeny in lines 2- l_1 .

The number of sires, and linecross and linebred animals involved in each of the four line and six line studies can be summarized as follows:

Four Line Study - 25 sires, 370 linebred and 156 linecross progeny

Six Line Study - 39 sires, 526 linebred and 291 linecross progeny

 e_{ijkl} represents the random error associated with this lth individual and b_{Y/F_X} represents the linear regression on inbreeding of the trait being studied. In line 1, sires were confounded with years, and the regression coefficients for this line were estimated with a similar model from which sire effects were deleted. An additional analysis on line 1 fitting Year-Sire subclasses, gave almost identical estimates of the regression coefficients and their standard deviations.

Estimation of Heterotic Effects

Least Squares Analysis of Variance procedures were used to test for the presence of heterotic effects. Separate analyses were conducted on a population made up of lines 1-4 which developed very closely together with respect to time and which had all possible diallel crosses available, with most of the sires having progeny in all 4 lines. The procedures of analysis used for both the four and six line groups were very similar.

The plan of the analysis to test for the presence of heterotic effects was arranged to follow closely that described as Analysis II by Gardner & Eberhart³⁰, and the following mixed model (Model II) was initially employed.

 $Y_{ijklmno} = \mu + L_{i} + S_{ij} + T_{k} + H_{l} + Y_{m} + SE_{n} + (LT)_{ik} + (ST)_{ijk} + (HY)_{lm} + (HSE)_{ln} + (YSE)_{mn} + b_{Y/DO} + e_{ijklmno}$

where $Y_{ijklmno}$ is a measure of the performance of the oth daughter of the jth sire within the ith sire line born to the lth dam line (or herd) and beginning production in the mth year and nth season, μ is the mean and T_k refers to the type of breeding involved with each animal being either a linebred or a linecross. The regression of Y on the number of days each animal was open during the lactation $(b_{Y/DO})$ was included in the analysis as an independent random variable, being fitted as both a linear and quadratic partial regression. The term $e_{ijklmno}$ is an estimate of the random error associated with this oth individual. In the four lines used in the first analysis, herd of birth and production, and line were identical and were therefore completely confounded. The year of calving was defined as beginning with October and running through the succeeding September, with, for example, November 1968 being classified as 1969. Each year was divided into two seasons with season one running from October through May and season two running from May through September. These divisions were decided upon, on the basis of investigative work which had been performed by researchers¹¹ several years earlier on these same herds.

In this model the mean square and constant estimates for lines L_i were equivalent to that for the General Combining Ability (GCA) of these lines estimated on the basis of both the linebred and linecross progeny of the sires of each line. The mean square and constant estimates for T_k , the type of breeding, i.e. either linebred or linecross, measured the importance of heterosis computed as an average effect over all lines (Av. Het.). The line x type of breeding interaction components (LT)_{ik} were a measure of what Gardner & Eberhart referred to as line heterosis (L. Het.), and were an indication of the individual differences between lines in their heterotic effects. The sire within line x type of breeding interaction (ST)_{ijk} components indicated if sires within lines tended to rank differently depending on whether they were evaluated on the basis of their linebred or linecross progeny, and was an indication of the importance of individual differences in heterotic effects between sires within the same line.

This analysis was performed using a Mixed Model Least Squares Analysis Program as described by Harvey^{3h}, ³⁵ under Model Type 07, sires within lines were considered as being random with all other effects being considered as fixed. Since the results of the Least Squares Analysis of Variance revealed the interactions $(ST)_{ijk}$, $(HSE)_{ln}$ and $(YSE)_{mn}$ to be non-significant, these effects were deleted from the model and the analysis was repeated as Model Type 03, as described by Harvey³⁵.

The linear and quadratic regressions on days open during lactation were originally included in the model, in an attempt to increase the accuracy of evaluation of the genetic merit of the various lines and linecrosses for the traits being considered. Schaeffer et al. 77, analysing the effects of days open on lactation performance fr-1V Herd Improvement Association Records at Cornell University, concluded that the heritability of days open was essentially zero, and the effect of days open on Holstein milk production was largely environmental. The relationship between days open and milk production was found to be curvilinear, and they concluded that adjustments for days open in sire evaluations would increase accuracy without introducing any genetic biases. Similar conclusions have been reported by Wilton et al.95, Smith & Legates⁸³, and Ripley⁷². Several studies investigating the effects of days open on milk production have been undertaken in the herds being considered in this analysis. Etgen²³ in 1958 examined the effects of days open on 1508 ME production records of cows that had a

previous 40-90 day dry period. He found that as days open increased, milk and butterfat production also increased, the effect being of least significance in 2 year old cows (which appeared to be most persistent), somewhat larger in three and four year olds and largest in older cows. Overall he found a difference in production of 1263-2685 pounds of milk and from 35-92 pounds of fat per 305 day lactation due to the effect of carrying a calf 220 days or being open all the lactation. Spalding⁸⁵ in a later study in 1961, concluded that holding days dry constant, a difference in successful service period of 64 to 164 days resulted in an average difference in 305 day milk yield of about 1170 pounds in favor of the larger period.

However, in this study the initial analyses revealed that type of breeding, i.e. linebred or linecross, had a vory large effect on "days open" and it was decided that including a regression on "days open" in the model was undesirable, because of the significant correlation between these two effects. The analyses were then repeated including "days open" as an additional dependent variable. The same model and procedure was later used including the linear regression on inbreeding as a continuous independent variable.

Including the linear regression on inbreeding in the model, resulted in the adjustment of levels of performance of both linebreds and linecrosses to a base level equal to the average inbreeding of the combined population of linebreds and linecrosses. The mean F_X for the linebreds and linecrosses combined was 8.44 ± 3.30 while the linebreds alone averaged 12.49 ± 2.04. Since all of the linecrosses had an inbreeding coefficient assumed to equal zero, and most of the linebred

animals on inspection, were found to have F_x values greater than 8.50, adjustment of both linebred and linecross animals records to a base F_x value of 8.44 was almost as efficient a procedure as adjusting the records of the linebreds only to an inbreeding level of zero. This allowed a comparison to be made between linecrosses and linebreds free from inbreeding effects and gave some indication whether or not the superior performance of the linecrosses was the result of the recovery of vigor lost during inbreeding.

These two analytical procedures were repeated on the data involving the six lines, the herd by season interaction now being included in the model, as preliminary analyses revealed it to account for a significant amount of the total variation.

Estimation of Specific Combining Ability and Residual Reciprocal Effects

The data from the four line crosses which had all 16 subclasses filled were used to obtain estimates of Specific Combining Ability (SCA) and Residual Reciprocal (RR) effects. These effects were estimated according to the method of Harvey³³ and the following model (Model III) was utilized:

 $Y_{ijklmn} = \mu + LD_{ij} + S_{ijk} + Y_1 + SE_m + e_{ijklmn}$

where Y_{ijklmn} is a measure of the performance of the nth individual bred from the kth sire in the ijth sire line-dam line subclass freshening in the lth year and mth season, μ is the mean and e_{ijklmn} is the random error associated with this mth individual. Sires were considered as being random with all other effects being considered as fixed. The mean square for sire line-dam line subclasses was tested using the mean square obtained for sires. All other effects were tested by the error term. remaining after absorbing sires and sire line-dam line subclasses into all other effects in the model.

Maternal effects could not be estimated as they were completely confounded with herd environmental effects.

The degrees of freedom for heterosis were partitioned as described by Harvey³³ and were as follows, (p representing the number of lines being crossed = 4):

Scurce of Variation	Degrees of Fr	eed	om
Mean	l	=	1
Average Heterosis	l	Ŧ	1
Sire Lines	(p - 1)	E	3
Dam Lines	(p - 1)	Ŧ	3
Line Heterosis	(p - 1)	£	3
Specific Combining Ability Effects	$\frac{p(p-3)}{2}$	=	2
Residual Reciprocal Effects	$\frac{p(p-3)}{2}+1$	E	3

The equations were solved after imposing the following restrictions:

 $\Sigma_{i}\hat{c}_{ij} = \Sigma_{j}\hat{c}_{ij} = \Sigma_{i}\hat{c}_{ij} = \Sigma_{i}\hat{c}_{ij} = \Sigma_{i}\hat{r}_{ij} = \Sigma_{j}\hat{r}_{ij} = \hat{r}_{ij} + \hat{r}_{ji} = 0$

where c_{ij} and r_{ij} refer to the estimates of specific combining ability and residual reciprocal effects, respectively, for crosses between the i^{th} sire and j^{th} dam line.

These restrictions were applied and the equations solved using the transformation matrix in Table 3 given by Harvey³³. Premultiplying the column vector of subclass estimates by this transformation matrix

								Linec	ross	Combi	natio	n					
E	ffect	SD11ª	SD12	SD13	ՏԵլլ	SD21	SD22	SD23	SD2L	SD31	SD32	SD33	SD34	SD41	SD42	SD43	SDLLp
Average	Heterosis	3	-1	-1	-1	-1	3	-1	 1	-1	-1	3	-1	-1	-1	-1	3]
GCA	Sire Line 1 Sire Line 2 Sire Line 3	0 0 0	6 0 -3	6 -3 0	6 -3 -3	0 6 -3	0 0	-3 6 0	-3 6 -3	0 -3 6	3 0 6	0 0 0	-3 -3 6	0 -3 -3	-3 0 -3	-3 -3 0	0 C 0
<u>SCA</u>	1 S ₁₂ S ₁₃	0	կ -2	-2 Ц	-2 -2	4 -2	0 0	-2 -2	-2 4	-2 4	-2 -2	0 0	4 -2	2 -2	-2 L	ان 2-2	0 0
Residua	l Reciprocal RR ₁₂ RR ₁₃ RR ₂₃	0 0 0	6 -3 3	-3 6 -3	-3 -3 0	-6 3 -3	0 0 0	3 -3 6	3 0 -3	3 -6 3	-3 3 -6	0 0 0	0 3 3	3 3 0	-3 0 3	0 -3 -3	0 0 0

Table 3. Transformation Matrix Used To Estimate Average Heterosis, General Combining Ability, Specific Combining Ability and Residual Reciprocal Effects From Model III For the Four-Line Crosses

^aFirst letter and digit indicates line of sire, second letter and digit indicates line of dam.

^bThe coefficients of the last column of each row were subtracted from the other coefficients in that row to impose the restriction $\Sigma_i \Sigma_j SD_{ij} = 0$.

was accomplished using the linear contrasts option available on the computer program. This procedure also allowed tests of significance to be made for these effects, utilizing the error term remaining after absorbing the sire and sire line-dam line subclasses into the other fixed effects in the model. Simultaneously in this analysis estimations of overall average heterosis (Av. Het.) and the General Combining Ability (GCA) of each line based on the performance of its linecross progeny only, were also made by a similar procedure, applying the restrictions on the equations that $\sum_k h_k = \sum_{i \in i} = 0$ where h_k refers to the average heterosis measured on linebreds (k = 1) and line-crosses (k = 2), and e_i refers to the general combining ability of the ith line measured on the performance of its linecross progeny only.

RESULTS

Effects of Inbreeding on the Six Lines

Preliminary analyses revealed the effects of inbreeding on the traits being studied to be most fully explained by a linear regression. Analyses were performed only on linebred animals included in the study on a within-line basis. Mi et al.⁵⁹ have estimated the effects of inbreeding on populations including both linebred and outbred animals, assuming that the degree of inbreeding (F_x) of the linecross animals was equal to zero. This was a questionable assumption in view of the fact that if a positive heterotic effect was present, these animals should in fairness to their linebred associates have been assessed a negative inbreeding coefficient value. The effects of inbreeding varied little among sires within lines and the mean squares for sires were generally not significant except for milk yield in line 5 (Tables 7-13). Mean Squares for the Linear Regression of Inbreeding were only significant for milk and fat production in line 5, days in milk for line 3, and "days open" for line 1. The high level of uniformity of sircs within each inbred line for all traits agreed with the results expected from quantitative genetic theory on the basis of their close relationship to one another. The number of inbred animals represented in each line, their mean F_X and degree of within-line variation are given in Table 4.

The results of the regression analysis on the average effects of inbreeding on each line are given in Table 5.

The average effects of inbreeding on the six lines combined together as a single population are given in Table 6.

It was evident that while the overall trend of effects of the inbreeding program was to cause a decreased level of performance, the specific effects of such a mating scheme on any particular line were very difficult, if not impossible, to accurately forecast. While the standard deviations of the linear regressions were fairly large the differences in regression values between lines were of a large enough magnitude to demonstrate clearly the differences in effects that inbreeding had upon them.

The effects of inbreeding on level of milk production varied very markedly between lines with regression coefficients ranging from +86 to -160 pounds of milk per unit increase in inbreeding level. While the standard errors of regression coefficient were large, the differences between estimates for several of the lines were of a large enough magnitude to be significant at the 5% level of probability. Significant differences were also found for yields of fat and SNF, and for days in milk during lactation. In four of the lines inbreeding had a depressing effect on milk production while in the other two lines the effects of inbreeding were of a positive nature. The observed regression coefficients for fat, SNF and protein yield were in close agreement with those expected on the basis of the values observed for milk yield, and there was no evidence of a marked change in milk composition associated with changes in level of production. The small number of animals represented in each line resulted in the standard errors for the regression coefficients of inbreeding on milk compositional quality being rather large. This factor in combination with the known high correlations between yield of milk and yields of fat, SNF and protein had the effect of making the comparison between observed regression values for milk components and those estimated from yields of milk of very low sensitivity.

There was no real evidence to support the hypothesis that the significant changes in level of milk production resulting from an inbreeding program are accompanied by an inverse change in milk compositional quality.

Analysis of the Four-Line Diallel Crosses

Lines 1-h were chosen as a suitable group for analysis because all possible combinations between lines were present, and the mating arrangements for each line were parallel on the basis of time. The availability of all possible line combinations allowed the estimation of Specific Combining Ability, Residual Reciprocal Effects, Average Heterosis and General Combining Ability based on the performance of linecross progeny only, using Model III. The method of estimation was such that herd effects, though not specifically adjusted for in this model, automatically cancelled out of the equations. The estimates were therefore unbiased with regard to herd environmental influences. Analyses under Model II yielded estimates of Average Heterosis, Line Heterosis and General Combining Ability effects based on the performance of both linebred and linecross progeny. Model II was repeated with the inclusion of the linear regression on inbreeding in the model as a continuous independent variable.

Results From Model II

The Analyses of Variance for the effects of interest resulting from the two analyses under Model II for the seven traits being examined are given in Tables 14-20. Constant Estimates, Least Squares Means and Standard Errors are found in Tables 21-27. The mean square for Sires/ Lines was used to compute F for Lines, the remainder mean square being used as the denominator to compute the remainder of the F values.

Average Heterosis. The importance of average heterotic effects was estimated on the basis of the average differences between the linebreds and linecrosses, fitted in the model as "type of breeding". The mean squares attributable to the linear regression on inbreeding were not significant for any of the traits except for days in milk during lactation (P < 0.10).

When the analysis was performed excluding the linear regression on inbreeding from the model, the mean square for type of breeding or average heterosis was significant at the 1% level for fat yield. Mean squares for yield of SNF and protein were significant at the 5% level and there was evidence of a heterotic effect for milk yield at the 10% level of significance. While including the linear regression on inbreeding in the model did cause a reduction in the magnitude of the proportion of the total variance attributable to type of breeding, the F values for several traits were still large enough to indicate the presence of heterotic effects in excess of those expected on the basis of a simple recovery of the performance levels lost during inbreeding. Mean squares for average heterosis were still significant at the 5% level for yields of fat and protein, and at the 10% level for SNF yield. The F value for milk was almost large enough to reach the 10% level of significance (P = 0.11).

On the average the linecrosses produced 555, 27.5, 48.0 and 19.6 pounds more of milk, fat, SNF and protein, respectively, than the linebreds. The regression of inbreeding on these four yield traits was positive due largely to the exceptional performance of line 1 linebred animals, and when this regression was included in the model it had the effect of increasing the superiority of the linecrosses over the linebreds.

Fitting the model excluding the linear regression on inbreeding provided no evidence for the presence of average heterctic effects for age at calving or for days in milk during the lactation. However, average heterotic effects for days open during lactation were highly significant (P < 0.01) with the linebreds being open an average of 27.40 days longer than the linecrosses. Adjusting the data for level of inbreeding caused the difference in days open to decline to 14.80 days which was not significant. The adjustment of the data for degree of inbreeding resulted in the mean square for average heterosis for days in milk becoming significant at the 5% level of probability, with the linecrosses on the average milking 13.63 \pm 5.77 days longer than the linebreds. The simple correlation between days open and days in milk was +0.11.

Line Heterosis. The mean square for line heterosis computed as the line x type of breeding interaction component was significant at the 10% level for yield of milk, fat and SNF regardless of whether the data were adjusted for the effects of inbreeding or not. It was not significant for any of the other four traits. Lines 2 and 3 behaved very similarly with regard to the level of superiority of the linecrosses over the linebreds for yields of milk, fat and SNF. In line 4 the linebreds produced considerably less milk, SNF and protein than the linecrosses but were almost equal to them in yield of fat. The effects of inbreeding on line 1 were strikingly unique. The linebreds produced 1225, 19, 92 and 31 pounds more of milk, fat, SNF and protein, respectively, than the linecrosses; the use of linear functions and "t" tests revealing the differences to be significant at the 5% level for milk, and at the 10% level for SNF and protein yields (Table 28). These differences still remained at the same level of significance when the regression on inbreeding was included in the model. Regardless of whether the regression on inbreeding was included in the model or not the reproductive performance of line 1 linebreds, as indicated by days open during the first lactation, was significantly better than that of the linecrosses (P = 0.025). Linebreds from line 1 on the average were open for 28 days less than linecrosses when the data were adjusted for effects of inbreeding. The only traits for which inbreeding appeared to have a possibly depressing effect on the performance of line 1 were age at calving and days in milk. However, the differences between linecrosses and linebreds for these two characteristics were not quite large enough to be significant at the 10% level.
Linecrosses milked consistently longer than linebreds in each of the four lines when the data were adjusted for inbreeding effects, despite the fact that in three out of the four herds, the linecrosses became pregnant from 10-43 days before the linebreds. This trend provided evidence for the existence of heterotic effects for milking persistency. Apart from line 1 the reproductive performance of the linecrosses was substantially better than that of the linebreds, even though adjustments for the effects of inbreeding were made to the data.

General Combining Ability. Under Model II, general combining ability effects for each line were estimated on the basis of both linebred and linecross progeny. The mean square for lines was tested against the mean square for sires/lines to detect differences between lines in their general combining abilities. Differences between sires nested within lines were observed at the 5% level for yields of milk and fat, and at the 10% level for yields of SNF and protein.

Regardless of whether the data were adjusted for effects of inbreeding or not, differences between lines were significant at the 5% level for yields of milk and SNF, and at the 10% level for yield of fat. Distinct differences were not found for protein yield, days in milk or days open during the lactation. Adjusting for the level of inbreeding increased slightly the proportion of the variance of age at calving accounted for by line differences, causing the mean square for lines to be significant at the 10% level of probability.

Examination of the constant estimates for the four lines for the four components of yield indicated that three of the lines were of approximately equal genetic merit, while line 2 was substantially

inferior to all of them. Despite the uniquely superior performance of the linebred progeny from line 1, this line only ranked third of the h lines for yields of milk and fat. This was due to the poorer than average performance of its linecross progeny. The overall reproductive performance of line 1 was considerably better than that of the other lines, its linebred progeny performing much better than the linebreds of the other three lines; its linecross progeny performing slightly worse. The difference in general combining ability for days open between line 1 and the mean of the rest of the lines, was significant at the 0.025% level regardless of whether the data were adjusted for the effects of inbreeding or not.

Results From Model III

Under Model III each sire line-dam line combination was considered a separate subclass. Because all linebred animals from a single line were only located within a single herd it was not possible to estimate herd effects from this analysis. Using the transformation matrix described earlier, the linear functions being fitted were of such a nature that herd effects were automatically cancelled out in the computation of average heterosis, general combining ability, specific combining ability and residual reciprocal effects. Maternal effects were totally confounded with herd effects and could not be estimated in this manner. The remainder mean squares from Models II and III were similar in magnitude indicating that both models accounted for an approximately equal proportion of the total variance. Computing constant estimates for heterotic effects by the use of linear functions allowed them to be tested for significance against the error term remaining when sires and sire line-dam line subclasses were absorbed into all other effects in the model, utilizing the "t" test by a subroutine built into the statistical computer program.

Average Heterosis. The constant estimates, least-squares means and standard errors for average heterosis effects were calculated for the seven variables being examined and are given in Table 29. When Model III was used omitting the linear regression on inbreeding, average heterosis effects were significant at the 1% level for all four yield traits. When the data were adjusted for the effects of inbreeding, average heterosis effects were still significant at the 5% level for fat and protein yields but did not reach significance at the 10% level for yields of milk and SNF. The "t" values in the latter two traits were 1.40h and 1.522 representing probability values of 0.17 and 0.13, respectively.

Evidence for the presence of average heterosis effects existed at the 1% level for reproductive performance when no adjustment for the effects of inbreeding was made to the data. This significant difference between linebreds and linecrosses, as under Model II, disappeared when the linear regression on inbreeding was included in the analysis. Similar results occurred for days in milk as under Model II with adjustment for inbreeding effects causing a marked increase in the "t" value for average heterosis, raising it from the level of non significance to that of significance at the 5% level of probability. No evidence was found for heterosis effects relating to age at calving. All of the constant estimates for average heterosis obtained from Model III were

smaller than those found from Model II, but the differences between the two sets of estimates were not significant. The standard errors of the estimates under Model III were smaller, indicating that the estimates under this model were more accurate than those obtained from Model II (Table 30).

General Combining Ability. General combining abilities of the four lines were estimated on the performance of their linecross progeny alone. This method provided a more reliable estimate of the additive genetic merit of a line than if linebreds were also included in the evaluation. It is possible in linebreds for certain gene combinations to be fixed with inbreeding, which due to epistatic interactions may make a particular set of linebreds perform better or worse than would be expected on the basis of their additive genetic merit alone. If such a line is crossed, sets of genes acting epistatically either extremely favorably or unfavorably are broken up, and a clearer view of the relative additive genetic potential of the different lines can be obtained.

A comparison of the estimates of general combining ability under Models II and III for the seven traits being examined is given in Table 29. Under Model III it was of interest to note that line 1 ranked last of the four lines for five of the seven traits. This indicated that the apparent genetic superiority which linebreds from line 1 had over all the other linebreds was not transmitted to its linecross progeny. Line 3 had improved the strength of its position as being the best of the h lines for additive genetic ability for yields of milk and SNF, and had improved substantially its estimated relative merit for yields of fat and protein. The performance of line 2 for components of yield evaluated under Model III was much better relative to that of the other lines than under Model II, due largely to the fact that the poor performance of the linebreds had now been removed. The relative merit of line 4 declined when estimated under Model III for all four yield traits.

Specific Combining Ability (SCA). The imposition of the restrictions required to enable the equations for specific combining ability effects to be solved, resulted in only two degrees of freedom being left for these effects, one for the estimate of SCA for the cross between lines 1 and 2 (S_{12}), the other for the cross between lines 1 and 3 (S_{13}). Estimates for SCA for other linebred combinations were then calculated on the basis of the restrictions that had been imposed. The relationship between SCA estimates for the various line combinations is illustrated figuratively below, the letter 'a' representing the estimate for S_{12} , 'b' representing the estimate for S_{13} .

Line of		Line c	of Sire	
Dam	1	2	3	4
1	0	a	b	-(a+b)
2	a	0	-(a+b)	ď
3	ъ	-(a+b)	0	a
<u> </u>	-(a+b)	Ъ	а	0.

The estimates of specific combining ability effects compared the observed performance of specific reciprocal line crosses with their expected performance levels based on the general combining abilities of the lines from which they were derived. Estimates of the computed specific combining ability effects, their standard errors and "t" values used in estimating their significance for each of the seven traits are given in Table 32. The estimates of SCA for the remainder of the linecross combinations calculated as described above are presented in a matrix-like form in Tables 33 and 34.

One trait for which there appeared to be a significant specific heterosis effect between lines was for reproduction. This involved the progeny resulting from crossing line 1 and line 3, line 1 and line 4, line 2 and line 3, and line 2 and line 4. Animals resulting from this first cross showed very poor reproductive performance and were open 17.36 days longer than the average of all crosses. This difference was significant at the 10% level (P = 0.07). Examination of the estimates of specific combining ability for age at calving revealed that they calved on the average 0.65 months older than the average of all other crosses. This difference was not quite significant at the 10% level (P = 0.13), but the trend seemed to support the significant SCA effects for days open which had been observed. Progeny from the cross between line 1 and line 4 showed much better than average reproductive performance being open 16.14 days less than would be expected on the basis of the general combining abilities of their parental lines.

The 23 animals from the cross between lines 2 and 3 were only open for approximately 107 days. This was 23 days less than would have been expected from the average performance of the linecrosses from these two lines estimated from Model II and the difference was significant at the 10% level. The 21 linecross animals from mating lines 2 and 4 also performed significantly better on the average than expected, and were

open approximately 20 days less than expected from the average performance of linecrosses from these two lines. However, the difference between the reciprocal crosses was approximately 90 days and this tended to complicate the conclusions drawn from this observation. Taken as the simple average of the two reciprocal crosses this linecross had a poorer reproductive performance than average.

Residual Reciprocal Effects (RR). Residual reciprocal effects in this analysis involved differences between reciprocal crosses which were caused by sex-linked genes. Because maternal effects were completely confounded with herds, they cancelled out along with the herd effects when the linear contrasts for estimating reciprocal effects given in Table 3 were applied. Three degrees of freedom for reciprocal effects remained after the restrictions required to solve the equations had been imposed. This allowed estimates of the residual reciprocal effects for the crosses between line 1 and line 2 (RR12), line 1 and line 3 (RR_{13}) and line 2 and line 3 (RR_{23}). By the nature of the restrictions involved the estimate of these effects in a reciprocal cross were equal and opposite in sign. The method of utilizing the restrictions imposed to compute the remainder of the residual reciprocal effects for other linecrosses is illustrated figuratively below, the letter 'a' representing the effect for the RR₁₂ cross, 'b' the RR₁₃ cross reciprocal effect and 'c' the RR23 residual reciprocal effect.

Line of		Line of Sire				
Dam	1	2	3	4		
1	0	-a	-b	(a+b)		
2	a	0	-C	-(a-c)		
3	ď	С	C	-(b+c)		
<u> </u>	-(a+b)	(a-c)	(b+c)	0		

Estimates of the computed residual reciprocal effects, their standard errors and "t" values computed against the remainder mean square from the analysis of variance are given in Table 35. The remainder of the residual reciprocal effects estimated on the basis of the restrictions which had been imposed, are given in Tables 36 and 37.

Significant reciprocal differences for reproductive performance were observed in crosses between line 1 and line 3 at the 1C% level, and in crosses between lines 1 and line 4 at the 5% level of probability. The progeny resulting from the mating of dams from line 1 with sires from line 3 had a much poorer reproductive performance than the reciprocal crosses. The difference in environmental influences from Model II for reproduction for lines 1 and 3 was 17 days in favor of line 1, the actual difference in days open between the crosses was however 42 days. The environmental difference for days open between dams from lines 1 and 4 was 27 days in favor of line 4, the actual observed differences between the reciprocal crosses was 20 days in favor of the crosses performing under the environment of line 1, indicating a 47 day difference in days open between the reciprocal crosses. The difference in days open between the reciprocal crosses of lines 2 and 4 was 87 days in favor of the females from line 2. When this difference was adjusted for herd environmental effects the difference in days open decreased to 16 days still in favor of the offspring whose dams came from line 2. A close examination of the 4 animals whose dams came from line 4 revealed two of them to be open for less than 100 days while the other two were each open for about 270 days, the reliability of the average reproductive performance estimate of this side of the reciprocal cross had therefore

to be seriously questioned, and valid conclusions could not be made on the relative reproducing abilities of these reciprocal crosses.

Comparison of Linebreds With the Mean of the Reciprocal Linecrosses. There existed the possibility that the sires chosen to represent each line were not truly representative of the genetic merit of that line. In order to detect the presence of such an occurrence the genetic merits of the lines were also estimated on the basis of the performance of the reciprocal linecrosses of that line i.e. the means of six groups of animals were used to assess the level of performance of the linecrosses from each line. Sub-class means estimated from Model III were adjusted for herd environmental effects using the estimates of herd effects found from Model II. The mean values for all of the reciprocal crosses of each line were averaged to determine the average performance of the linecrosses for each line. The mean values of the linebreds and reciprocal linecrosses for each line are compared in Table 38.

This analysis revealed that lines 1, 3 and 4 were very similar in genetic merit for milk production, the linecrosses in each case yielding a little more than the linebreds. The difference between linecrosses and linebreds for these three lines ranged from 70 to 270 pounds. The linebred animals of line 2 produced 2100 pounds less milk than the mean of the other three lines, its linecross progeny also producing 1100 pounds less milk. On the average over all four lines the linecrosses produced 410 pounds more milk than the linebreds. Based on the performance of their linecrosses, all lines were approximately equal in genetic merit for yields of fat, SNF and protein. The linebred animals from line 2 performed at a lower level than the linebreds from the other three lines

in yield of milk constituents. Crossbreds from line 2 produced milk of higher fat, SNF and protein content than the remainder of the linecrosses. A comparison of the milk compositional quality of the linebreds and linecrosses from line 2 indicated the linecrosses exceeded the linebreds for fat (3.92 vs. 3.63), SNF (9.37 vs. 8.86) and protein percentages (3.72 vs. 3.58). Over all lines the linecrosses produced 30 pounds more each of fat and protein, and 71 pounds more of SNF.

In three out of four of the lines the linecrosses calved at an earlier age than the linebreds. The mean difference between all linebreds and linecrosses was 0.26 months. Apart from line 1, the linecrosses had a better reproductive performance than the linebreds, the difference in days open for each line ranging from 18.6 to 42.5 days. In line 1 the linebreds were open 12.8 days less than the linecrosses. There was a tendency for the linecrosses to be more persistent than the linebreds, but the clarity of this feature was somewhat obscured by the effects of inbreeding and linecrossing on the related factor of reproduction. In lines 3 and 4 the linebreds actually milked longer than the linecrosses, but the difference was smaller than would have been expected on the basis of their much poorer reproductive performance.

Analysis of the Six-Line Crosses

The progeny of all six lines were combined and analysed as a single population. The linebreds from lines 1-4 were the same as used for the four-line analyses except for the progeny of sire seven from line 1 which were omitted from the earlier analyses because this sire did not have any linecross progeny in lines 2, 3 or 4. Because all linecross combinations were not available it was not possible to perform an analysis utilizing Model III on these data. The method of analysis performed under Model II was exactly the same as described for the fourline cross. The model was initially fitted omitting the linear regression on inbreeding, and was then repeated including the adjustment for the effects of inbreeding. The analyses of variance for the seven traits being examined are given in Tables 39-45, the constant estimates, leastsquares means and standard errors are found in Tables 46-52. F values for making tests of significance were computed in the same way as for the four-line cross analysis.

Average Heterosis. Results from the Analyses of Variance revealed that when the data were unadjusted for the level of inbreeding, the mean square for average heterosis, as indicated by type of breeding, was significant at the 1% level for all four yield traits. The average yield of the linecrosses exceeded that of the purebreds by 723, 33, 63 and 26 pounds of milk, fat, SNF and protein, respectively. When the linear regression on inbreeding was included in the model the regression coefficients were of small magnitude and negative in nature for yields of milk, fat and SNF, but the coefficient for yield of protein equalled +0.20. However, in all four cases the standard errors for the regression coefficients were substantially larger than the actual estimates. Adjusting the data for level of inbreeding increased the size of the standard errors for all of the constant estimates. As a result, though little change was observed in the relative yields of linebreds and linecrosses for all four yield traits the F values were decreased considerably in size. When the data were adjusted for

inbreeding the mean square for milk yield was no longer significant at the 10% level (P = 0.15). The mean square for average heterosis for yield of SNF just failed to be large enough to meet the 10% level of significance requirements (P = 0.11). However, the mean squares for yields of fat and protein though considerably reduced in si_ze were still significant at the 5% level of probability.

When the data were uncorrected for level of inbreeding the mean square for average heterosis for age at calving was significant at the 5% level. Adjustment of the data for level of inbreeding caused this mean square to decline to an extremely low level and it would appear that the older age at calving (+0.5 Mo.) of the linebreds when compared with the linecrosses could be explained on the basis of the effects of inbreeding alone. The observations from the analyses of variance for days open during lactation were very similar in nature to those made from the analyses on age at calving. Using the model excluding the adjustment for level of inbreeding revealed that the linebreds were open for 21 days longer than the linecrosses. Adjusting for the level of inbreeding caused this difference to be reduced to 12 days, which while not significant, did indicate the possible presence of some small heterotic effects for reproductive performance. No evidence was found for significant average heterosis for days in milk using both analyses. However, even though the linecrosses on the average were open for 12 days less than the linebreds, their length of lactation was five days greater.

When linear contrasts were used to compare the linecrosses with the linebreds the results given in Table 53 indicated significantly superior performances of the linecrosses for six out of the seven traits when the data were unadjusted for level of inbreeding. After adjustments for level of inbreeding, the linecrosses were still significantly superior to the linebreds for yields of fat and protein and age at first calving.

Line Heterosis. The adjustment of the data for effects of inbreeding by including in the model the linear regression on level of inbreeding did not cause any appreciable change in the size of the mean square for line heterosis, as indicated by sire-line x type of breeding interaction, for any of the seven traits.

The mean squares for line heterosis were significant at the 5% level for yields of milk and fat, and at the 10% level for yields of SNF and protein. No evidence was found for line heterosis for the three other traits. An examination of the least-squares means and standard errors revealed that for all of the lines except line 1 the linecrosses exceeded the linebreds in production of milk, SNF and protein. The yields of fat for the linebred and linecross progeny from line 4 were almost equal. In all the other lines except line 1 the linecrosses consistently outperformed the linebreds for yield of fat. The reproductive performance of the linecrosses was superior to that of the linebreds in all 6 lines. Differences between linecrosses and linebreds in days open during lactation ranged from 6-41 days. No uniform pattern of differences between linecrosses and linebreds was observed for age at first calving or days in milk during lactation.

General Combining Ability. The mean square for lines for all traits was not significantly changed by including the linear regression on inbreeding in the model. For each of the four yeild traits it was highly significant at the 1% level of probability. This confirmed, as expected from the results of the four-line cross data, that significant differences in breeding values for production traits existed between lines. The order of ranking of lines 1-4 was essentially the same as that found from the four-line analysis except that line 1 was now ranked above line 4. Line 2 was still computed to be much lower in general combining ability than the lines 1, 3 or 4. Lines 5 and 6 were even lower in breeding value than line 2 and were ranked in that order. Little differences in general combining ability were found to exist between lines 1, 3 and 4, when their breeding values were estimated on the basis of the performance of both their linebred and linecross daughters.

The mean squares for lines were not significant for age at first calving or for days in milk during first lactation. The mean square for lines was significant at the 5% level of probability for days open during lactation indicating significant differences in breeding value for reproductive performance between lines. The average number of days open during lactation ranged from 115 days for progeny of line 5 to 154 days for progeny of line 4.

DISCUSSION

The results which have been presented in the previous section revealed extensive genetic differences between lines. The effects of an inbreeding program differed widely between lines. The relationship between the performance of linebred and linecross progeny within a line differed widely between lines. Within a single line the effects of inbreeding on different traits tended to be fairly uniform, however in certain of the lines exceptions to this were observed. The observation of these differing and sometimes even conflicting results would lead to the suggestion that the types of gene action most important for some of the traits were different in different lines.

The overall effect of inbreeding on yields of milk, fat, SNF and protein was to depress slightly their levels of production. However, in lines 1 and 4 significant improvement in level of production was observed. These increases in yield were of a large enough nature to refute the commonly expressed view that inbreeding always results in a decreased level of performance. The extent to which inbreeding depressed milk production in the other four lines varied widely. The effect on line 3 was reasonably small in magnitude, the regression coefficient equalling -ll pounds per one percent increase in level of inbreeding. The regression coefficients of milk yield on percent

inbreeding level for lines 2 and 6 of -38 and -24 pounds, respectively, agreed fairly closely with the results of previous inbreeding experiments reported in the review of literature. These two lines were developed within the same herd. The constant estimates and leastsquares means for herd effects revealed that this herd had the best environment of all the herds included in the study. In line 5, inbreeding had a drastic effect on level of milk production as the regression coefficient of -160 pounds clearly suggested.

The breeding program used in an inbreeding scheme has the effect of increasing homozygosity of lines. If there were a number of genes present in the homozygous state which acted in an epistatic manner with each other, then inbreeding could result in the fixing of specific gene combinations. If epistatic gene interactions were important in determining the performance of an individual for a trait, then the fixing of either favorable or unfavorable combinations of genes by inbreeding could cause extreme deviations in level of performance of the linebreds from the mean of their linecross contemporaries. When those lines in which epistatic gene effects were important would be crossed with lines having different gene frequencies and gene combinations, their specific gene combinations would be broken up and the resulting progeny would be expected to perform at a level reflecting only the additive genetic merit of their parents. The favorable effects which inbreeding had on the milk production of lines 1 and 4 could in theory be due to either (a) The sires chosen to start these lines being of outstanding genetic merit, the inbreeding program causing their offspring to receive an increasing proportion of their superior genes.

or (b) An accumulation and fixation of a set or sets of genes rendered homozygous by inbreeding and acting favorably together as a unit in epistatic combination. If each of these gene pairs were homozygous within a line then crossing-over would not cause a change in the epistatic combinations.

If the first circumstance were correct we would expect the line to transmit its superior additive genetic merit to its linecross offspring, resulting in an extremely high general combining ability estimate for this line. If the good performance of the linebreds was due largely to epistatic gene interactions then we would expect line crossing to cause a disruption of the gene combinations and the resulting linecross progeny to perform poorer than expected from the production levels of the parents.

When favorable dominance effects play an important part in determining the level of milk production, the increasing degree of homozygosity resulting from an inbreeding program would be expected to result in a depression of level of performance. If different alleles were homozygous in different lines, linecrossing would be expected to cause a sudden increase in degree of heterozygosity and an improvement in level of production should result.

The mean squares for average heterosis for milk yield indicated that the linecrosses significantly outyielded the linebreds. When the data were corrected for level of inbreeding, the F values for average heterosis were still quite large but did not quite attain the 10% level of significance. This indicated that while dominance effects were of

significance in determining milk yield, the importance of situations in which the heterozygous gene pair was superior to either of the homozygotes was rather low.

When the milk yield of each of the lines was considered separately there appeared to be evidence for different types of gene effects being important for the same trait. The results from Model II indicated that the linebred progeny from line 1 performed much better than the other linebreds, even outyielding its own linecrosses. This analysis examined only the linecross animals on a within sire and line basis and ignored the performance of the reciprocal cross. When the reciprocal crosses were included in the comparison, no difference in milk yield was found between the linecross and linebred progeny of line 1, with the linebreds producing at a similar level to those of lines 3 and 4. These two methods of estimation of the mean yield of the linebreds produced values differing by 700 pounds for milk yield. This change was mainly responsible for the yields of the linebreds and linecrosses being no longer significantly different. No significant reciprocal differences for any of the production traits were found for any of the linecrosses. Line 1 also had a highly significant positive regression for milk yield on degree of inbreeding. The difference between the results of the two analyses for line 1 are not easy to explain. In the analysis which included the reciprocal linecrosses no adjustment was made for herd x year interactions which Model II revealed to be of significant importance. However, this was likely to account only for a small portion of the difference as a close examination of the data revealed that both the linebreds and linecrosses were fairly uniformly distributed across

herds and years. The failure of inbreeding to cause a decrease in milk yield would indicate that favorable dominance alleles were of minor importance in relation to additive genetic effects in determining milk production for line 1. Line 1 appeared to be of approximately equal additive genetic merit to lines 3 and 4.

Line 4 performed fairly similarly to line 1 for production traits during inbreeding. The level of milk production of its linebred progeny increased slightly with increasing degree of inbreeding. The superiority of its linecrosses to its linebreds was about the average for all lines as indicated by the constant estimates for line heterosis. The small though non-significant superiority of the linecrosses over the linebreds suggested that dominance effects for milk yield were present in this line but were of relatively minor importance in relation to additive effects.

Line 3 showed a small depression in milk yield during inbreeding, but its linecross progeny performed similarly to the linecrosses from lines 1 and 4. The evidence for a depression in milk production with inbreeding would imply that dominance gene effects had a small but important role in controlling its level of production.

Line 2 suffered a significant depression in milk yield with inbreeding, indicating that dominance or epistatic gene effects were of importance in controlling this trait in this particular line. The performance of both its linebred and linecross progeny were below the average of the linebred and linecross progeny from the other five lines, indicating it to be of low additive genetic merit for milk production. It ranked fourth of the six lines studied. There appeared to be no evidence of over-dominance occurring in the crosses of this line, and the improved performance of the linecrosses over the linebreds appeared to be largely due to the recovery of the vigor lost during inbreeding and to favorable additive genes it received from other lines.

The milk yield of the progeny of line 5 was very severely depressed under inbreeding as the regression coefficient of -160 pounds per degree of inbreeding suggested. The extent of this depression could indicate the presence of important deleterious recessives, the very large importance of dominance gene effects in determining this trait, or the development of the line from sires of extremely low additive genetic merit. The development and fixing of unfavorable combinations of genes acting in an epistatic way together could also cause this depression. The performance of the linecross progeny from line 5 relative to the linebreds was not as greatly superior as anticipated, had the inbreeding depression been due to the fixing of unfavorable gene combinations, the removal of favorable dominance in mean yield being only about 500 pounds. This would support the theory that the foundation sires for line 5 were of extremely low additive genetic merit and that the large linear reduction in milk production with inbreeding was mainly due to an increasing level of relationship to them.

The effect of inbreeding on the milk yield of line 6 was not quite as detrimental as on line 2 linebred individuals. However, the general combining ability of line 2 estimated on the basis of both linebred and linecross progeny performances was very significantly better. Line 6 was clearly much inferior to all of the other lines in additive genetic merit for milk production. The milk yield of its linecross progeny was

below that of both the linecross and linebred progeny of all lines except for the linebreds from line 5. The moderate depression in milk yield that occurred with inbreeding would indicate that dominance effects were important, but the relative extent by which the superiority of the line 6 linecrosses over the linebreds was due to the recovery of the heterozygous condition or to the reception of superior additive genes from the lines on which it was being crossed was difficult to ascertain.

The significant mean squares for average heterosis for yields of fat and protein remaining after the data had been adjusted for level of inbreeding, indicated that over-dominance effects were of importance for these traits. The mean square for yield of SNF when the data were corrected for level of inbreeding did not quite reach the 10% level of significance but was large enough in magnitude to indicate that overdominance gene effects may have played a minor role in controlling this trait. It was interesting to note in the analysis comparing the linebreds with the reciprocal linecrosses that in only one case did the yield of a linecross fail to exceed the yield of the best linebred for fat, SNF and protein. This exception was due to the extremely high fat yield of line 4 linebred animals which exceeded all of the linecrosses.

The mean squares for line heterosis for yields of fat and SNF were significant in both the analysis of the four-line crosses and the analysis of the six-line crosses. The mean square for line heterosis for yield of protein was only significant for the analysis of the sixline crosses.

No definite patterns of change in percentage of milk constituents were observed, but over all lines the linecross animals besides producing about 720 more pounds of milk than the linebreds also produced milk which averaged slightly higher (0.05%) in fat content. Percentages of SNF and protein for the linebred and linecross animals appeared to be essentially the same. It would appear therefore that there is evidence to support the concept of heterosis for fat percentage in milk, but that the difference in levels of yield of the linecross and linebred animals for SNF and protein was largely due to the high correlation between the yield of milk and that of its constituents. There is in general an inverse relationship between milk yield and milk compositional quality which tends to cause the variance of milk constituent yields to be relatively smaller than that of milk yield itself. The observation that the linecrosses produced considerably more milk, of equal SNF and protein quality, than the linebreds would suggest that there was present a small amount of heterotic effects for SNF and protein percentage which overcame their usually negative correlations with milk yield.

Inbreeding, on the average, appeared to slightly increase the age at calving of the linebreds, the difference being approximately 0.5 months when estimated under Model II, however, the relative effects of inbreeding varied with different lines. It was impossible to say whether the delayed age of the linebreds at calving was due to poorer reproductive performance, or perhaps to their somewhat smaller size than the linecrosses at breeding time. The observation that the linecrosses had a better reproductive performance than the linebreds during their first lactation would lend support to the first proposal. In four out of the six lines the linecrosses calved at a younger age than the linebreds, in one other line the ages were almost identical while in line 3 the linebreds freshened 0.4 months before the linecrosses. The differences in age at calving only exceeded one month for linebred and linecross progeny of lines 1 and 5. Since there was no evidence for significant line heterosis effects it would appear that the influence of inbreeding and linecrossing on age at calving was essentially the same for each of the six lines.

One of the main guidelines which the dairy farmer uses to terminate the lactation of a cow is her expected freshening date. Advancing pregnancy also has an inhibitory physiological action on milk yield. The time at which the dairyman actually terminates the lactation of a cow is usually decided by a simultaneous consideration of these two factors of daily yield and expected freshening date. The length of lactation and the number of days a cow is open during this period should therefore be considered together as interrelated torics. The linecrosses on the average milked 3 days longer than the linebreds yet were open for 21 days less. This would suggest that there was definite evidence for heterosis for lactation length in the linecrosses. A closer comparison of days open and days in milk for the linebreds and linecrosses of each line revealed that except in the case of line 5 the linecrosses appeared to be more persistent than the linebreds. In lines 3 and L the linebreds were open 36 and 51 days, respectively, more than their linecross contemporaries yet they only milked about 2-3 days longer, and it would appear that their persistency was relatively lower

than that of the linecrosses. It is perhaps of interest to note the unique performance of the linebred animals from line 1 which under Model II were open for 6 days longer and milked for 11 days less than their linecross contemporaries, yet still managed to produce a substantially greater volume of milk.

A comparison of the performance of the linebred and linecross progeny from lines 5 and 6 for milk yield and reproductive performance indicated that inbreeding did not have uniform effects for all traits. Inbreeding of line 5 had a very drastic effect on milk production, yet fertility did not appear to have been altered. A similar though less striking comparison was seen for line 6. From the point of view of line 4 the situation was reversed with the effect of inbreeding on milk yield being essentially zero to slightly positive in nature and the effect on reproduction being clearly adverse.

There was no definite statistical evidence for nicking among lines, for any of the L lines evaluated in this respect, for yields of milk, fat, SNF and protein. However, this did not rule out the possibility of a nicking effect occurring due to epistatic effects among other line combinations. There was evidence for significant specific combining ability effects for reproductive performance for four of the linecross combinations, and for residual reciprocal effects for reproduction in two of the crosses. The data available did not provide definite explanations of the observed reciprocal cross differences in reproduction to be made with any appreciable degree of reliability, however, it is possible that genotype x environment interactions may have been involved. In view of the known contribution of several different hormones to the reproductive process, and the requirement for them to be present in correct ratios to each other, it would seem feasible that the significantly poorer or better than average reproductive performance os some of the linecross combinations could have been due to the presence of sets of genes whose gene products acted in a (favorable or unfavorable) synchronous manner to control the whole reproductive process.

Sire Line	No. of Cows	Mean F _x	S. Deviation
1	85	11.47	3.22
2	102	14.00	4.50
3	77	10.52	3.86
4	112	11.40	3.78
5	65	10.78	4.16
6	85	16.21	5.11
All Herds	526	12.49	2.04

Table 4. Degree of Inbreeding Within Each Line

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Variable	Sire Line					
	1	2	3	4	5	6
Milk ^a	86.00±86.80	-38.40±51.70	-11.CO±82.LO	55.60±102.30	-160.10±85.60	-24.30±60.00
B. Fat ^a	3.11± 3.22	-1.13± 1.91	0.93± 2.63	3.20± 3.33	-6.03± 2.93	-0.72± 2.20
S.N.F. ^a	7.66± 7.63	-2.82± 4.26	0.65± 6.68	1.85± 8.21	-12.03± 7.60	-0.83± 4.90
Protein ^a	3.08± 3.06	-0.78± 1.69	0.70± 2.50	0.56± 3.22	-3.78± 3.08	0.20± 1.94
Age at Calving ^b	0.02 <u>±</u> 0.10	-0.02± 0.03	0.02± 0.10	-0.17± 0.11	0.01± 0.09	0.00± 0.04
Days in Milk	1.99 <u>+</u> 1.25	0.41± 1.18	1.81± 0.97	-0.07± 0.83	-1.37± 1.62	-1.24± 1.39
Days Open	6.05± 2.66	-1.01± 1.31	2.46± 3.37	-3.90± 3.35	1.58± 2.65	0.20± 1.32

Table 5. Regression Coefficients and Standard Errors For Effects of Inbreeding on Individual Lines

^aUnits are in pounds.

^bAge at calving is expressed in months.

Variable	Linear Regression Coefficient	S. Error
Milk ^a	-7.03	26.41
Fat ^a	0.29	0.95
S.N.F.ª	-0.44	2.23
Protein ^a	0.27	0.89
Age at Calving ^b	-0.05	0.03
Days in Milk	0.28	0.41
Days Open	0 . 7L	0.84

Table 6. Mean Effects of Inbreeding Over All Herds

^aUnits are in pounds.

bAge at calving is expressed in months.

Sire Line	Source	df	Mean Squares	<u> </u>
1	Rgrsn Inbreeding-Linear Remainder	1 74	60720.20 61784.32	0.983
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	49234.38 26028.98 47247.44	1.042 0.551
3	Sires Rgrsn Inbreeding-Linear Remainder	4 1 62	23786.90 1179.62 65891.82	0.361 0.018
4	Sires Rgrsn Inbreeding-Linear Remainder	6 1 94	109391.04 21041.97 71229.61	1.536 0.295
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 48	106068 .17 3510 .88 17 2887 .35 49410 .21	2.147* 0.071 3.499**
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	36067 •88 6548 •97 39815 •23	0.904 0.164

Table 7.	Analysis of Variance For Effects of Inbreeding On
	Milk Yield (10 lbs) For Individual Sire Lines

*Significant at 10% level.

**Significant at 5% level.

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Sire Line	Source	df	Mean Squares	F
1	Rgrsn Inbreeding-Linear Remainder	1 74	9536.85 8480.89	1,125
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	4858.33 2272.06 6403.92	0.759 0.355
3	Sires Rgrsn Inbreeding-Linear Remainder	և 1 62	226.04 830.68 6714.42	0.034 0.124
<u>ь</u>	Sires Rgrsn Ińbreeding-Linear Remainder	6 1 94	13001.46 6953.71 7524.70	1.728 C.924
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 18	7789.72 138.10 24499.37 5807.85	1.341 0.024 4.218**
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	5182.34 580.65 5385.06	0.962 0.108

Table 8. Analysis of Variance For Effects of Inbreeding On Fat Yield (lbs) In Individual Herds

**Significant at 5% level.

Sire Line	Source	df	Mean Squares	F
1	Rgrsn Inbreeding-Linear Remainder	1 74	48103.58 47704.31	1.008
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	33279.56 14054.76 32065.81	1.038 0.438
3	Sires Rgrsn Inbreeding-Linear Remainder	4 1 62	14134.88 413.99 43297.02	0.326 0.010
4	Sires Rgrsn Inbreeding-Linear Remainder	և 1 62	77646.07 2324.44 45823.32	1.694 0.051
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 48	59809.19 22.92 97612.57 39007.13	1.533 0.001 2.502
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	20312.20 770.09 26597.30	0.764 0.029

Table 9. Analysis of Variance For Effects of Inbreeding On Solids-Not-Fat Yield (lbs) In Individual Herds

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Sire Line	Source	df	Mean Squares	F
1	Rgrsn Inbreeding-Linear Remainder	1 74	7792.67 7682.21	1.014
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	6029.90 1076.92 5018.27	1.202 0.215
3	Sires Rgrsn Inbreeding-Linear Remainder	4 1 62	1519.35 469.93 6069.39	0.250 0.077
Ц	Sires Rgrsn Inbreeding-Linear Remainder	6 1 94	10861.54 215.42 7047.86	1.541 0.031
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 48	7258.90 218.04 9628.78 6387.20	1.136 0.034 1.508
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	3602.98 42.37 4194.67	0.859 0.010

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Table 10. Analysis of Variance For Effects of Inbreeding On Protein Yield (lbs) In Individual Herds

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Sire Line	Source	df	Mean Squares	F
1	Rgrsn Inbreeding-Linear Remainder	1 74	0.30 7.50	0.040
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	1.45 1.10 176.32	0.692 0.524
3	Sires Rgrsn Inbreeding-Linear Remainder	ц 1 62	4.23 0.39 9.15	0.462 0.042
4	Sires Rgrsn Inbreeding-Linear Remainder	6 1 94	13.30 19.48 7.61	1.748 2.560
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 48	9.86 2.01 0.12 5.51	1.790 0.365 0.021
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	1.15 0.00 1.85	0.623 0.000

Tablell. Analysis of Variance For Effects of Inbreeding On Age At Calving (Mo.) In Individual Herds

Sire Line	Source	df	Mean Squares	F
1	Rgrsn Inbreeding-Linear Remainder	1 74	3252.41 1280.08	2.541
2	Sires Rgrsn Inbreeding-Linear Remainder	6 1 84	1995.40 289.49 2472.57	0.807 0.117
3	Sires Rgrsn Inbreeding-Linear Remainder	4 1 62	255.88 3166.06 909.35	0.281 3.482*
4	Sires Rgrsn Inbreeding-Linear Remainder	6 1 94	184.92 3.46 466.31	0.396 0.007
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 40	3278.38 3064.94 1274.58 1762.23	1.860 1.739 0.723
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	2568.03 1697.68 2154.43	1.192 0.788

Table 12. Analysis of Variance For Effects of Inbreeding On Days In Milk For Individual Herds

*Significant at10% level.

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Sire Line	Source	df	Mean Squares	F
l	Rgrsn Inbreeding-Linear Remainder	1 74	30110 . 211 5808 . 18	5.184***
2	Sires Rgran Inbreeding-Linear Remainder	6 1 84	1867.41 1789.90 3017.21	0.619 0.593
3	Sires Rgrsn Inbreeding-Linear Remainder	4 1 62	1608.20 5858.08 11021.31	0.146 0.532
4	Sires Rgrsn Inbreeding -Li near Remainder	6 1 94	1544.58 10328.33 7628.42	0.202 1.354
5	Sires Herds Rgrsn Inbreeding-Linear Remainder	5 1 1 48	3447.35 290.97 1682.84 4744.65	0.727 0.061 0.355
6	Sires Rgrsn Inbreeding-Linear Remainder	6 1 69	983.92 45.15 1930.16	0.510 0.023

Table 13. Analysis of Variance For Effects of Inbreeding On "Days Open" For Individual Herds

***Significant at 1% level.

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Table 14.	Analysis of Variance For Milk Yield (]	LO 1bs)
	of the Four-Line Diallel Crosses	

Source	df	Mean Squares	F
a. Excluding the Linear Regr	ession or	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder	3 21 1 3 457	337246.17 86457.51 205833.95 135727.70 55507.73	3.901** 1.558** 3.708* 2.445*
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	3 21 1 3 1 456	344007.98 86527.86 146167.89 137798.52 22109.74	3.976** 1.557** 2.630 2.479* 0.398

*Significant at 10% level.

**Significant at 5% level.
Table 15. Analysis of Variance For Fat Yield (1bs) of the Four-Line Diallel Crosses

Source	df	Mean Squares	F
a. Excluding the Linear Regr	ession or	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder b. Including the Linear Regre	3 21 1 3 457 ession or	28397.84 11050.98 50642.18 15872.60 6881.99	2.570* 1.606** 7.359*** 2.306*
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	3 21 1 3 1 456	30619.74 11012.23 42334.76 16550.53 8731.74 6877.93	2.781* 1.601** 6.155** 2.406* 1.270

*Significant at 10% level.

**Significant at 5% level.

***Significant at 1% level.

Table 16. Analysis of Variance For Solids-Not-Fat Yield (1bs) of the Four-Line Diallel Crosses

Source	df	Mean Squares	F	
a. Excluding the Linear Regr	ession or	Inbreeding.		
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder	3 21 1 3 457	179596.50 58722.08 154316.27 81023.99 38240.08	3.058** 1.536* 4.035** 2.119*	
b. Including the Linear Regr Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	ession or 3 21 1 3 1 456	186020.81 58643.59 112877.07 82336.14 18165.43 38284.10	3.172** 1.532* 2.948* 2.151* 0.474	

*Significant at 10% level.

**Significant at 5% level.

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Table 17. Analysis of Variance For Protein Yield (1bs) of the Four-Line Diallel Crosses

Source	df	F	
a. Excluding the Linear Regr	ression or	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder	3 21 1 3 457	13632.87 8556.02 25803.06 9563.38 5917.43	1.593 1.446* 4.361** 1.616
b. Including the Linear Regr	ression or	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	3 21 1 3 1 456	14829.54 8503.82 22708.51 9887.38 5094.19 5919.23	1.744 1.437* 3.836** 1.670 0.861

*Significant at 10% level.

**Significant at 5% level.

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Source	df	Mean Squares	ন্
a. Excluding the Linear Regi	ression on	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder b. Including the Linear Regi	3 21 1 3 457 ression on	11.51 5.74 5.47 4.02 6.00 Inbreeding.	2.005 0.957 0.913 0.671
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	3 21 1 3 1 456	11.84 5.61 9.69 4.24 4.67 6.00	2.109* 0.936 1.615 0.706 0.779

Table 18. Analysis of Variance of Age at Calving (Mo.) For the Four-Line Diallel Crosses

*Significant at 10% level.

Table 19.	Analysis of	Variance	For Days	in Milk	During
	Lactation of	f the Four	r-Line Dia	allel Cr	osses

Source	df	Mean Squares	F	
a. Excluding the Linear Regr	ession or	Inbreeding.		
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder	3 21 1 3 457	783.90 775.25 7山.32 696.山 1052.12	1.011 0.737 0.707 0.662	
 b. Including the Linear Regr Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder 	ession on 3 21 1 3 1 456	1035.45 805.08 4102.56 826.54 3493.20 1046.76	1.286 0.769 3.919** 0.790 3.337*	

*Significant at 10% level.

**Significant at 5% level.

Table	20.	Analysis of Variance For Days Open During Lactation
		of the Four-Line Diallel Crosses

Source	df	Mean Squares	F
a. Excluding the Linear Regr	ession or	Inbreeding.	
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Remainder b. Including the Linear Regr	3 21 3 457 ession or	2279.16 3126.54 50221.60 7881.80 6300.19	0.729 0.496 7.971*** 1.251
Sire Lines Sires/Lines Type of Breeding S. Lines x Type of Breeding Regression on Inbreeding Remainder	3 21 1 3 1 156	2372.77 3155.27 4831.22 8121.52 5233.78 6302.52	0.752 0.501 0.767 1.289 0.830

***Significant at 1% level.

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		^b Y/F,	Excluded Fro	om Model	b_{Y/F_X} Included in M		n Model	
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean	526	1551.52	1551.52	19.51	1556.97	1556.97	22.93	
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4	118 133 116 159	26.08 -111.40 49.66 35.66	1577 .59 11:10.12 1601.17 1587 .18	42.79 45.62 43.35 38.43	26.45 -113.90 51.26 36.19	1583.42 1443.07 1608.23 1593.16	ЦЦ.70 Ц6.09 Ц6.1Ц Ц0.63	
Average Heterosis Lineb Linec	reds 370 rosses 156	-27.74 27.74	1523.77 1579.26	21.34 26.86	-40.70 40.70	1516.27 1597.67	26.07 40.39	
Line Heterosis								
S. Line 1. Lineb Linec S. Line 2. Lineb	reds 79 rosses 39 reds 102	90.08 -90.08 -18.72	1639.93 1515.26 1363.65	65.39 52.34 59.61	90.42 -90.42 -51.56	1633 .1 4 1533.70 1350.80	66.81 63.40 65.19	
Linec S. Line 3. Lineb	rosses 31 reds 77	48.72 -41.42	1516.59 1532.01 1670.34	64.15 65.02	51.56 -39.51 39.51	1535.33 1528.01 1688.00	73.96 65.50	
S. Line 4. Lineb Linec	reds 112 rosses 47	0.07	1559.50 1614.85	64.34 50.71	0.65 -0.65	1553.11 1633.20	65.64 61.87	
^b Y/F _x					2.19		3. <u>1</u> 8 ല	

Table 21. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Milk Yield (10 lbs) From the Four-Line Diallel Crosses

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		by/Fx	Excluded Fro	om Model	^b Y/F _x	Included in	Model
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean	526	560.49	560.L9	7.02	563.91	563.91	8.23
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4	118 133 116 159	1.58 -30.94 9.59 19.77	562.07 529.54 570.08 580.26	15.39 16.43 15.60 13.82	1.84 -32.65 10.68 20.13	565.75 531.27 574.60 584.04	16.04 16.56 16.56 14.58
Average Heterosis Linebr Linecr	eds 370 osses 156	-13.76 13.76	546 .73 574 . 25	7.65 9.57	-21.90 21.90	542.01 585.82	9.32 14.30
Line Heterosis							
S. Line 1. Linebr Linecr	eds 79 osses 39	23.45 -23.45	571.76 552.38	23.36 18.70	23.67 -23.67	567.52 563.99	23.82 22.60
S. Line 2. Linebr Linecr	eds 102 osses 31	-21.13 21.13	494.65 564.13	21.32 22.94	-22.92 22.92	486.45 576.09	23.27 26.40
S. Line 3. Linebr Linecr	eds 77 osses 39	-15.18 15.18	541 . 14 599 . 02	23.23 19.44	-13.98 13.98	538.72 610.48	23 . 35 23 . 13
S. Line 4. Linebr Linecr	eds 112 Posses 47	12.85 -12.85	579 . 35 581.16	22.98 18.11	13.22 -13.22	575 . 36 592 . 72	23.40 22.05
^b Y/F _x					1.38		1.22

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Table 22. Listing of Constant Estimates, Least-Squares Means and Standard ErrorsFor Fat Yield (lbs) From the Four-Line Diallel Crosses

			by/F _x E	xcluded Fro	m Model	b_{Y/F_X} Included in 1		in Model	
Va	riable	No . of Obse rvations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean		526	1340.60	1340.60	16.03	1345.55	1345.55	18.81	
GCA S. L S. L S. L S. L S. L	ine l ine 2 ine 3 ine 4	118 133 116 159	27.62 -81.31 33.77 19.92	1368.22 1259.29 1374.37 1360.52	35.16 37.46 35.61 31.58	27.99 -83.76 35.34 20.44	1373.53 1261.78 1380.89 1365.98	36.67 37.79 37.85 33.34	
Average H	eterosis Linebreds Linecrosses	370 156	-24.02 24.02	1316.58 1364.62	17.56 22.17	-35.77 35.77	1309.78 1381.31	21.44 33.40	
Line Hete	rosis								
S. Line 1 S. Line 2 S. Line 3 S. Line 4	 Linebreds Linecrosses Linebreds Linebreds Linebreds Linebreds Linebreds Linebreds Linebreds Linebreds 	79 39 102 31 77 39 112 47	70.29 -70.29 -35.41 35.41 -33.22 33.22 -1.66 1.66	1414.50 1321.95 1199.86 1318.73 1317.13 1431.61 1334.84 1386.20	53.91 43.15 49.12 52.86 53.60 44.85 53.05 41.81	70.61 -70.61 -37.99 37.99 -31.49 31.49 -1.13 1.13	1408.37 1338.69 1188.03 1335.54 1313.63 1448.14 1329.08 1402.88	55.02 52.22 53.66 60.88 53.94 53.43 54.07 50.96	
by/F _x						1.99		2.89	

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Table 23. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Solids-Not-Fat Yield (1bs) From the Four-Line Diallel Crosses

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				by/Fx E	xcluded Fro	om Model	b_{Y/F_X} Included in 1		ed in Model	
	Vari	able	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Moan			526	531.04	531.0h	6.03	533.60	533.66	7.05	
CCA S	5. Lin 5. Lin 5. Lin 5. Lin	не 1 не 2 не 3 не 11	118 133 116 156	10.01 -21.59 0.կկ 11.14	541.05 509.44 531.47 542.18	13.24 14.07 13.41 11.90	10.22 -22.97 1.32 11.43	543.87 510.69 534.97 545.09	13.76 14.14 14.20 12.52	
Averag	ge Het	erosis Linebreds	370	-9.82	521.21	6.66	-16.04	517.61	8.13	
		Linecrosses	156	9.82	540.86	3.53	16.04	549.70	12.94	
Line H	ietero	sis								
S. Lir	ne l.	Linebreds Linecrosses	79 39	25.26 -25.26	556.49 525.61	20.61 16.49	25.42 -25.42	553.26 534.49	20.99 19.92	
S. Lir	ne 2.	Linebreds Linecrosses	102 31	-12.46 12.66	487 . 16 531 . 73	18.73 20.16	-13.83 13.83	480.82 540.56	20.41 23.16	
S. Lir	ne 3.	Linebreds Linecrosses	77 39	-6.97 6.97	514.68 548.27	20.49 17.14	-6.06 -6.06	512.87 557.07	20.57 20.38	
S. Lir	ne 4.	Linebreds Linecrosses	112 47	-5.82 5.82	526.54 557.82	20.29 15.99	-5.54 5.54	523.51 566.67	20.63 19.45	
by/Fx							1.05		1.13	

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Table 24. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Protein Yield (1bs) From the Four-Line Diallel Crosses

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		^b Y/F _x E	b_{Y/F_X} Excluded From Model			b_{Y/F_X} Included in Model			
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error		
Mean	526	27.35	27.35	0.14	27.27	27.27	0.17		
GCA S. Line 1	118	0.61	27.96	0.31	0.60	27.87	0.33		
	133	-0.04	27.31	0.32	0.00	27.28	0.33		
S. Line 3	116	-0.40	26.95	0.32	-0.43	26.84	0.34		
S. Line 4	159	-0.16	27.19	0.28	-0.17	27.10	0.30		
Average Heterosis									
Linebreds	370	0.14	27.49	0.17	0.33	27.60	0.21		
Linecrosses	156	-0.14	27.21	0.24	-0.33	26.94	0.38		
Line Heterosis									
S. Line 1. Linebreds	79	0.48	28.58	0.55	0.17	28.68	0.56		
Linecrosses	39	-0.48	27.33	0.44	-0.47	27.06	0.53		
S. Line 2. Linebreds	102	0.00	27.46	0.49	-0.05	27.65	0.54		
Linecrosses	31	0.00	27.16	0.53	0.05	26.90	0.61		
S. Line 3. Linebreds	77	-0.35	26.74	0.55	-0.37	26.80	0.55		
Linecrosses	39	0.35	27.15	0.46	0.37	26.88	0.55		
S. Line 4. Linebreds	112	-0,14	27.20	0.55	-0.15	27.29	0.56		
Linecrosses	Li7	0.14	27.18	0.43	0.15	26.92	0.52		
^b Y/F _x					-0.03		0.04		

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Table 25. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Age At Calving (Mo.) From the Four-Line Diallel Crosses

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					^b Y/F _x ^F	Excluded Fro	om Model	by/Fx	Included in	Model
	T	Vari	able	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean			<u> Ang ang Prington dakan</u>	526	292.98	292.98	1.87	295.15	295.15	2.19
<u>CCA</u>	s. s. s.	Line Line Lin Lin	e 1 e 2 e 3 me 4	118 133 116 159	-0.32 -4.92 1.66 3.58	292.66 288.06 294.64 296.56	4.13 4.27 4.18 3.73	-0.18 -5.85 2.26 3.78	294.96 289.29 297.41 298.92	4.30 4.30 4.43 3.93
<u>Aver</u>	age	Het	erosis Linebreds Linecrosses	370 156	-1.67 1.67	291 .3 1 294.65	2.21 3.16	-6.82 6.82	288.33 301.96	2.78 5.06
Line	He	tero	sis							
S.L	ine	1.	Linebreds Linecrosses	79 39	-5.70 5.70	285.28 300.03	7.31 5.85	-5.57 5.57	282.58 307.34	7.44 7.06
S.L	ine	2.	Linebreds Linecrosses	102 31	-1.91 1.91	284.49 291.64	6.53 7.03	-3.03 3.03	279.44 299.15	7.12 8.07
S.L	ine	3.	Linebreds Linecrosses	77 39	3.50 -3.50	296.47 292.81	7.26 6.07	4.26 -4.26	294.84 299.97	7.29 7.22
S.L	ine	4.	Linebreds Linecrosses	112 47	4.11 -4.11	299.00 294.12	4.34 5.69	4․34 -4․34	296.45 301.40	7•34 6•92
by/F	x							0.67		0.48

Table 26. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Days In Milk During Lactation For the Four-Line Diallel Crosses

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			^b Y/F _x ^E	xcluded Fro	m Model	b_{Y/F_X} Included in Model			
Variable		No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean		526	146.77	146.77	4.58	149.42	149.42	5.38	
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4		118 133 116 159	-8.44 0.25 2.69 5.50	138.33 147.02 149.46 152.27	10.11 10.46 10.22 9.13	-8.26 -0.94 3.45 5.75	141.16 148.48 152.87 155.17	10.56 10.56 10.87 9.65	
Average Heterosi Line Line	is ebreds ecrosses	370 156	13.70 -13.70	160.47 133.07	5.42 7.72	-7.40 7.40	156 .82 142 . 02	6.81 12.42	
Line Heterosis			oz 50			07 (7		20.07	
S. Line I. Line Line	ebreds ecrosses	79 39	-21.78	130.26 146.40	17.89 14.32	-21.51 21.61	120.95 155.37	18.27 17.34	
S. Line 2. Line Line	crosses	31 77	-0.96 0.96	134.28	17.19 17.19	-2.35 2.35	143.43	19.81	
S. Line J. Line Line	Crosses	- 39 2112	-8.85	126.90	14.86	-9.78	135.69	17.71	
Line	crosses	47	-13.88	124.68	13.92	-14.17	133.60	16.98	
bi/Fx						1.07		1.17	

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Table 27. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Days Open During Lactation For the Four-Line Diallel Crosses

Table 28. List of t Values For the Comparison of Sire Line 1 Linebred Progeny With Linebred Progeny From Sire Lines 2-4

Trait	t Values
Milk Yield	2.010**
Fat Yield	1.464
S.N.F. Yield	1.903*
Protein Yield	1.792*
Age at Calving	1.312
Days in Milk	1.344
Days Open	2.550**

*Sire Line 1 linebreds superior at 10% level.

**Sire Line 1 linebreds superior at 5% level.

	by/Fx Exc	luded From	n Model	b_{Y/F_X} Included in Model			
Variable	Constant Estimate	Standard Error	t	Constant Estimate	Standard Error	t	
Milk (10 lbs)	41.51	14.68	2.828***	37.77	26.91	1.404	
Fat (lbs)	14.91	4.88	3.054***	19.77	8.98	2.202**	
S.N.F. (1bs)	34.66	12.22	2.836***	34.11	22.42	1.522	
Protein (lbs)	14.78	4.83	3.060***	18.24	8.87	2.057**	
Age at Calving (Mo.)	-0.133	0.17	0.774	-0.17	0.32	0.547	
Days in Milk	2.00	1.46	1.369	6.66	2.69	2.474**	
Days Open	-14.60	3.87	2.699***	-5.07	7.10	0.714	

Table 29. Estimates of Average Heterosis^a From Model III For the Four-Line Diallel Crosses

^aEstimated as difference between Least-Squares Means for Linecrosses and Linebreds.

**Significant at 5% level.

***Significant at 1% level.

	Statistical	Statistical Model III	
Variable	Six-Line Crosses	Four-Line Crosses	Four-Line Crosses
Milk (10 lbs)	72.30 ± 25.98	55.48 ± 24.10	41.51 ± 14.68
Fat (1bs)	32.96 ± 8.113	27.52 ± 8.61	14.91 ± 4.88
S.N.F. (lbs)	63.18 ± 21.24	48.04 ± 19.87	34.66 ± 12.22
Protein (lbs)	25.94 ± 7.77	19.64 ± 7.60	14.78 ± 4.83
Calving Age (Mo.)	-0.54 ± 0.24	-0.29 ± 0.20	-0.13 ± 0.17
Days in Milk	3.16 ± 3.15	3.34 ± 2.69	2.00 ± 1.46
Days Open	-20.60 ± 6.44	-27.40 ± 6.57	-14.60 ± 3.87

Table	30.	A Comparison of Estimates of Average
		Heterosis From Three Analyses

^aMean difference between linecrosses and linebreds.

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Table 31.	A Comparison of Estimates of General Combining
	Ability From the Four-Line Diallel Crosses
	Based on the Performance of (a.) Linecross
	Progeny Only (b.) Linebred & Linecross Progeny

		a. From	Linecross	b. From	Linebred &
		Progen	y Only	Linecros	s Progeny
Variable	hy /m a	Constant	Standard	Constant	Standard
		Estimate	Error	Estimate	Error
	``				
WILK (10 105)	10 (1	10.01	0(0)	10.70
S. Line I	+0.00	-49.04	43.04	20.00	42.19
S. Line 2	-3.84	-38-32	49.99	-111.40	45.02
S. Line 3	-1.10	67.97	44.52	49.66	43.35
S. Line 4	+5.56	19.99	49.33	35.66	38.43
Fat (1bs)					
S. Line 1	+3.41	-19.09	14.58	1.58	15.39
S. Line 2	-1.13	-7.90	16.62	-30.94	16.43
S. Line 3	+0.93	22.27	14.80	9•59	15.60
S. Line 4	+3.20	4.72	16.L2	19.77	13.82
S.N.F. (1bs)			·		
S. Line 1	+7.66	-27.66	36.51	27.62	35.16
S. Line 2	-2.82	-26.72	41.63	-81.31	37.46
S. Line 3	+0.65	51.01	37.07	33.77	35.61
S. Line h	+1.85	3.37	11.13	19.92	31,58
Protein (1bs)				2
S. Line 1	⁻ +3.08	-8,54	14.42	10.01	13.24
S. Line 2	-0.78	-5.04	16.11	-21.59	14.07
S. Line 3	+0.70	6.51	11,61	0.11	13.11
S. Line h	+0.56	7.07	16.21	11,1),	11.90
Age at Calvi	ng (No.)	1001			22070
S. Line 1	+0-02	0.018	0.51	0.61	0.31
S. Line 2	-0.02	0.36	0.58	-0.01	0.32
S. Line 3	+0.02	-0.17	0.52	-0.1.0	0.32
S. Line h	-0.17	-0.07	0.57	-0.16	0.28
Davs in Milk	~ • • = •			-0.10	0.20
S. Line 1	+1.99	8.02	1.36	-0.32	. 1.13
S. Line 2	+0.11	5.1.1	1. 07	_1, 02	1. 27
S Time 3	+1 81	-2 75	1.1.5	-4.JZ J 66	1. 18
S I ino li		0 17	5.05	2 58	2 72
Dave Open	-0.01	U.II		J•J0	2.10
S Line 1	+6 06	00 FF	יו ככ	_8 1.1.	10 11
S line 2	.1 01	-0 03 	12 17	-0•44 0 25	10.17
S IIIC 2	-10 PV	_3 KI.	エン・エ/ ココ ワワ	0.27	TO 00
	-3 00	-7 Kg	12 22	2.09	10.22
D. TTHE T	-2.70	-1.02	20.02	2.20	ブ・エブ

^aInbreeding regression coefficients estimated from linebred animals in each sire line. ı.

Variable	Specific Linecross	Constant Estimate	Standard <u>Error</u>	t
Milk (10 lbs)	S ₁₂ ^a	-17.30	33.46	0.517
	S ₁₃	36.38	35.99	1.019
Fat (lbs)	S12	0.91	11.13	0.081
	S13	5.49	11.97	0.458
S.N.F. (lbs)	5 ₁₂	-18.92	27 . 86	0.679
	S ₁₃	22.50	29.97	0.751
Protein (1bs)	S12	-1.87	11.01	0.170
	S13	0.96	11.81:	0.081
Age at Calving (Mo.)	S ₁₂	-0.29	0.39	0.746
	S ₁₃	0.65	0.42	1.553
Days in Milk	s ₁₂	0.61	3.32	0.184
	s ₁₃	-0.16	3.58	0.044
Days Open	s ₁₂	-1.22	8.81	0.138
	s ₁₃	17.36	9.48	1.832*

Table 32. Specific Combining Ability Effects and Their Level of Significance

^aFirst digit refers to line of sire, second digit to line of dam.

*Significant at 0.07% level, all other effects were not significant.

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:	Milk Yi	ield (10) 1bs)		Fat Yield (1bs)						
Line of Dam	<u> </u>	Line of 2	Sire 3	<u></u>	Line of Dam	<u> </u>	Line o: 2	f Sire 3	<u> </u>		
1	0	-17	+37	-20	1	0	+0.9	+5.5	-6.4		
2	-17	0	-20	+37	2	+0.9	0	-6.4	+5.5		
3	+37	-20	0	-17	3	+5.5	-6.4	0	+0.9		
4	-20	+37	-17	0	կ	-6.4	+5.5	+0•9	0		

Table 33. Specific Combining Ability Estimates For Four Yield Traits For All Crosses Between Four Lines

S.N.F. (1bs)

Protein (1bs)

Line of		Line of	Sire		Line of	Line of Sire			
Dam	1	2	3	4	Dam	1	2	3	4
l	0	- 19	+23	-4	l	0	-2	+1	+1
2	-19	0	-4	+23	2	-2	0	+1	+1
3	+23	-4	0	-19	3	+1	+1	0	-2
4	-4	+23	-19	0	4	+1	+1	-2	0

Table 34.	Specific Combining Ability Effects For Age At Calving,
	Days in Milk and Days Open During Lactation Fcr All
	Crosses Between Four Lines

Age At Calving (Mo.)						Day	rs in Mi	<u>lk</u>	
Line of	·	Line o	f Sire		Line of	·	Line o	f Sire	
Dam	1	2	3	<u> </u>	Dam	1	2	3	4
1	0	-0.29	+0.65	-0.36	1	С	+0.61	-0.16	-0.45
2	-0.29	0	-0.36	+0.65	2	+0.61	0	-0.45	-0.16
3	+0.65	-0.36	0	-0.29	3	-0.16	-0.45	0	+0.61
4	-0.36	+0.65	-0.29	<u> </u>	<u> </u>	-0.15	-0.16	+0.61	0

Days Open

Line of	Line of Sire							
Dam	1	2	3	4				
1	0	-1.22	+17.36	-16,14				
2	-1.22	0	-16.14	+17.36				
3	+17.36	-16.14	0	-1.22				
<u> </u>	-16.14	+17.36	-1.22	0				

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Variable	Specific Linecross	Constant Estimate	Standard Error	t
Milk (10 lbs)	RR12 ^a	33.83	37.50	0 .902
	RR13	1.14	37.81	0.030
	RR23	-35.59	41.99	0.848
Fat (lbs)	RR12	16.27	12.47	1.305
	RR13	Ц.28	12.57	0.340
	RR23	- 7.35	13.96	0.527
S.N.F. (1bs)	RR12	25.32	31.23	0.811
	RR13	0.01	31.48	0.000
	RR23	-29.87	34.96	0.854
Protein (lbs)	RR12	9.87	12.34	0.800
	RR13	-3.05	12.44	0.245
	RR23	-6.30	13.81	0.456
Age at Calving (Mo.)	RR12	0.29	0.44	0.658
	RR13	0.12	0.44	0.268
	RR ₂₃	-0.36	0.49	0.731
Da y s in Milk	RR ₁₂	-2.71	3.73	C.728
	RR ₁₃	-2.57	3.76	0.684
	RR ₂₃	4.60	4.17	1.102
Days Open	RR12	-6.14	9.88	0.622
	RR13	18.45	9.96	1.853*
	RR23	-24.09	11.06	2.179**

Table	35.	Residu	al	Reciprocal	Effects	and	Their
		Level	of	Significand	e		

^aFirst digit refers to line of sire, second digit to line of dam.

*Significant at 10% level of significance.

**Significant at 5% level of significance.

Milk Yield (10 lbs) Fat Yield (1bs							.bs)		
Line of <u>Dam</u>	1	Line o: 2	f Sire 3	4	Line of Dam	I	ine of 2	Sire 3	4
1	0	-34	-1	35	1	0	-16	-4	20
2	34	0	36	- 70	2	16	0	7	-23
3	1	-3 6	0	35	3	4	-7	0	3
4	-3 5	70	- 35	0	4	-20	23	-3	0

Table 36.	Residual Reciprocal Effects For Four Yield Traits
	For All Crosses Between Four Lines

S.N.F. Yield (1bs)

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Protein Yield (1bs)

Line of	1	Line of	f Sire		Line of]	Line of	Sire	
Dam	1	2	3	4	Dam	1	2	3	4
1	0	-25	0	25	1	0	-10	3	7
2	25	0	30	-55	2	10	0	6	-16
3	0	-30	0	30	3	-3	- 6	0	9
4	-25	55	-30	0	և	-7	16	-9	0

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1	Age at	Calving	(Mo.)			Day	ys in Mi	ilk	
Line of		Line o	f Sire		Line of		Line o	of Sire	. <u></u>
Dam	<u>لم</u>		3	<u> </u>	Dam		2	3	
1	0	-0.29	-0.12	0.41	1	0	2.7	2.6	-5.3
2	0.29	0	0.36	-0.65	2	-2.7	0	-4.6	7.3
3	0.12	-0.36	0	0.24	3	-2.6	4.6	0	-2.0
4	-0.41	0.65	-0.24	0	4	5.3	-7.3	2.0	0

Table 37. Residual Reciprocal Effects For Age at Calving, Days in Milk and Days Open During Lactation For All Crosses Between Four Lines

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Days Open

Line of		Line of Sire				
Dan		<u>د</u>	<u> </u>	4		
l	0	6.1	-18.4	12.3		
2	-6.1	0	24.1	-18.0		
3	18.4	-24.1	0	5.7		
4	-12.3	18.0	-5.7	0		

		B	reeding Li	ne	Overall
Trait	1	2	3	<u></u> կ	Means
Milk (10 lbs)					
Linebreds	1569.	1356.	1550.	1580.	1514.
Linecrosses	1576.	1472.	1577.	1595.	1555.
Fat (1bs)					
Linebreds	562.	493.	548.	585.	547.
Linecrosses	566.	578.	581.	582.	577.
SNF (1bs)					
Linebreds	1365.	1202.	1325.	1354.	1312.
Linecrosses	1373.	1379.	1396.	1384.	1383.
Protein (1bs)					_*_
Linebreds	5 3 6.	486.	519.	534.	519.
Linecrosses	540.	549.	547•	551.	549.
Age at Calving (Mo.)					
Linebreds	27.98	27.71	27.14	27.42	27.50
Linecrosses	21•21	2(•))	21.00	2(•)1	2[•]0
<u>Days in Milk</u>		0°5 0	00(r	000 0	007 0
Linebreds	203.0	205.2	290.5	299.9	291.2
Linecrosses	290.0	273.7	274.0	274•1	<i>273•2</i>
Days Open	109 C	<u>הרג</u> ה	160 r	ר פר	167.0
Linecrosses	1/1 2	137 C	137 8	TOT •O	138 0
TTHECT 09969	1410)	C+1CT		T) • T	4,0CF

Table 38. Comparison of Linebreds With Reciprocal Linecrosses^a (Four Lines)

^aData estimated from subclass means found using Model III adjusted for herd effects calculated from Model II.

Table 39.	Analysis of Variance of Milk Yield (10 lbs)
	For the Six-Line Crosses	

Source	df	Mean Squares	F	
a. Excluding the Linear Reg	ression of	n Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	631378.27 75006.78 486841.02 120659.87 50719.78	8.42 *** 1.48** 9.60*** 2.38**	
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	611611.34 74953.35 109326.35 115334.04 8192.44 50779.18	8.16*** 1.48** 2.15 2.27** 0.16	

**Significant at 5% level.

***Significant at 1% level.

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Table 40. Analysis of Variance of Fat Yield (1bs) For the Six-Line Crosses

Source	df	Mean Squares	F	
a. Excluding the Linear Reg	ression o	n_Inbreeding	-	
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	90639.79 8254.80 101204.92 19926.93 6560.54	10.98*** 1.26 15.43*** 3.04**	
b. Including the Linear Regi	ression o	n Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	89570.15 8254.81 34382.54 19476.73 1.63 6569.70	10.85*** 1.26 5.23** 2.97** 0.00	

**Significant at 5% level.

***Significant at 1% level.

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Table 41. Analysis of Variance of Solids-Not-Fat Yield (1bs) For the Six-Line Crosses

Source	df	Mean Squares	<u> </u>	
a. Excluding the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	458070.67 50999.84 371948.29 77792.47 36245.03	8.98*** 1.41* 10.26*** 2.15*	
b. Including the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	448405.06 51042.62 97236.79 75531.59 2612.34 36292.00	8.79*** 1.11* 2.68 2.08* 0.07	

*Significant at 10% level.

***Significant at 1% level.

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Table 42. Analysis of Variance of Protein Yield (1bs) For the Six-Line Crosses

Source	df	Mean Squares	F	
a. Excluding the Linear Reg	ression o	n Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	76240.43 7041.80 62676.81 11783.46 5731.93	10.83*** 1.23 10.94*** 2.06*	
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	76115.21 7031.96 25277.67 11784.46 290.39 5739.53	10.82*** 1.23 4.40** 2.05* 0.05	

*Significant at 10% level.

******Significant at 5% level.

***Significant at 1% level.

Table 43.	Analysis of Variance of Age at Calving (Mo.)
	For the Six-Line Crosses

Source	df	Mean Squares	F	
a. Excluding the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	7.45 6.33 27.59 6.93 4.92	1.18 1.29 5.60** 1.41	
b. Including the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	6.98 6.33 5.72 7.14 7.70 4.92	1.10 1.29 0.025 1.45 1.57	

**Significant at 5% level.

Source	df	Mean Squares	F
a. Excluding the Linear Reg	ression on	Inbreeding	
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	1019.09 1196.56 935.68 1007.11 1231.62	0.85 0.97 0.76 0.82
b. Including the Linear Reg	ression on	Inbreeding	
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	997.55 1198.29 572.63 1003.04 57.90 1233.26	0.83 0.97 0.46 0.81 0.05

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Table by. Analysis of Variance of Days in Milk For the Six-Line Crosses

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Source	df	Mean Square	F	
a. Excluding the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Remainder	5 33 1 5 717	7609.34 2768.33 39199.29 4731.56 5159.51	2.75** 0.54 7.66** 0.92	
b. Including the Linear Reg	ression on	Inbreeding		
Sire Lines Sires/Lines Type of Breeding S. Line x Type of Breeding Rgrsn Inbreeding-Linear Remainder	5 33 1 5 1 716	7228.68 2769.98 4549.85 5166.28 3431.71 5161.93	2.61** 0.54 0.88 1.00 0.67	

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Table 45. Analysis of Variance of Days Open For the Six-Line Crosses

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**Significant at 5% level.

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		^b Y/F _x ^E	by/F _x Excluded From Model			$b_{Y/F_{X}}$ Included in Model		
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean	817	1451.45	1451.45	23.32	1449.38	1449.38	24.61	
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4 S. Line 5 S. Line 6 Average Heterosis Linebreds	145 155 117 182 85 133 526	100.70 -48.44 108.49 84.36 -72.34 -172.77 -36.15	1552.15 1403.01 1559.94 1535.81 1379.11 1278.68 1415.31	38.69 42.70 44.99 40.91 51.27 45.50 22.71 23.06	100.00 -1:6.80 107.1:8 81:10 -73.53 -171.26 -29.56 20.56	1549.38 1402.57 1556.86 1533.48 1375.85 1278.12 1419.83	39.77 42.74 46.13 41.67 52.40 45.55 25.88 26.52	
Line Heterosis	291	30.15	T101.00	29.00	29.50	1410.93	30.52	
S. Line 1 Linebreds Linecrosses S. Line 2 Linebreds Linecrosses S. Line 3 Linebreds Linecrosses S. Line 4 Linebreds Linecrosses S. Line 5 Linebreds Linecrosses S. Line 6 Linebreds Linecrosses	05 60 102 53 77 40 112 70 65 20 85 48	-90.29 -90.29 4.27 -4.27 -40.48 40.48 16.76 -16.76 -34.82 34.82 -36.02 36.02	1498.01 1371.13 1434.89 1483.32 1636.57 1516.42 1555.19 1308.15 1450.07 1206.52 1350.84	50.97 1:1.02 1:8.72 1:7.20 63.01: 52.51: 65.08 1:2.20 60.21: 75.82 1:6.21 52.1:6	-89.84 5.17 -5.17 -11.84 16.39 -16.39 -35.99 35.99 -33.57 33.57	1489.09 1378.19 1426.95 1485.47 1628.25 1520.32 1546.65 1310.31 1441.39 1214.99 1341.24	59.85 18.67 53.11 53.40 63.44 57.96 66.18 49.29 60.72 79.99 52.10 59.56	
^b y/F _x					-1.06		2.64	

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Table 16. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Milk Yield (10 lbs) From the Six-Line Crosses

Variable			by/Fx Excluded From Model			$b_{Y/F_{X}}$ Included in Model		
		No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean		817	514.94	514.94	7.42	514.97	514.97	7.77
<u>GCA</u> S. L: S. L: S. L: S. L: S. L: S. L:	ine 1 ine 2 ine 3 ine 4 ine 5 ine 6	145 155 117 182 85 133	27.90 -7.94 32.39 40.60 -20.80	542.84 507.00 547.33 555.55 494.15	12.39 13.41 14.35 13.01 16.32 14.73	27.90 -7.96 32.40 40.61 -20.78 -72.17	542.88 507.01 547.37 555.58 494.19	12.73 13.43 14.72 13.26 16.68
Average He	Linebreds Linecrosses	526 291	-16.18 16.18	498.16 531.42	7.18 9.69	-16.57 16.57	498.40 531.54	8.36 12.49
Line Heter S. Line 1	<u>rosis</u> Linebreds Linecrosses	85 60	26.83 -26.83	553 . 18 532 . 49	19.7կ 13.73	26.83 -26.83	553 . 13 532 . 62	20.04 16.29
S. Line 2	Linebreds Linecrosses Linebrede	102 53 77	1.00 -1.00	491.52 522.48	16.06 15.56	0.99 -0.99	491.42 522.59	17.52 17.61
S. Line 4	Linecrosses Linebreds	۲۱ 40 ۶۲۲	17.53	581.34 557.43	17.54 21.67	17.51 18.37	581.46 557.37	19.35 22.04
S. Line 5	Linecrosses Linebreds Linecrosses	70 65 20	-18.36 -9.21	553.67 168.16	14.05 20.07 25.26	-18.37 -9.19	553.79 468.13	16.42 20.23 26.65
S. Line 6	Linebreds Linecrosses	85 48	-19.45 19.45	406.87 478.72	15.60 17.71	-19.48 19.48	106.75 178.86	17.59 20.11
by/Fx			:			-0.015		0.950

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Table 47. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Fat Yield (1bs) From the Six-Line Crosses

		by/F, Excluded From Model		m Model	by/F _x Included in Model			
Vari	able	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean		δ17	1258.50	1258.50	19.01	1257.36	1257.36	19.92
GCA S. Lin	e l	162	89.09	1347.59	31.59	88.84	1346.20	32.49
S. Lin	e 2	155 -	-28.02	1230.49	34.68	-27 •45	1229.91	34.75
S. Lin	e 3	117	83.16	1341.66	34.69	82.81	1340.17	37.66
S. Lin	le 4	182	60.45	1318.95	33.33	60.36	1317.72	33.99
S. Lin	e 5	85	- <u>1</u> 7.65	1210,86	41.78	-48.06	1209.30	42.75
S. Lin	ie 6	133	-157.03	1101.48	37.26	-156.50	1100.85	37.34
Average Het	erosis							
	Linebreds	526	-31.59	1226.91	18.17	-27 .87	1229.49	21,20
	Linecrosses	291	31.59	1290.10	24.00	27.87	1285.23	30.40
Line Hetero	sis							
S. Line 1	Linebreds	85	73.79	1389.78	48.75	73.54	1391.87	և9.52
	Linecrosses	60	- 73 . 79	1305.40	33.91	-73.54	1300.54	40.26
S. Line 2	Linebreds	102	7.22	1206.12	40.10	7.73	1209.77	43.75
	Linecrosses	53	-7.22	1254.86	38.85	-7.73	1250.05	43.99
S. Line 3	Linebreds	77	-34.31	1275.76	52.08	-35.08	1272.22	52․հկ
	Linecrosses	40	34.31	1407.57	43.41	35.08	1403.11	47.91
S. Line 4	Linebreds	112	12.88	1300.24	53.73	12.67	1302.52	54.67
	Linecrosses	70	-12.88	1337.66	34.83	-12.67	1332.91	40.72
S. Line 5	Linebreds	. 65	-34.25	1145.01	49.73	-34.91	1146.51	50.17
_	Linecrosses	20	34.25	1276.70	62.59	34.91	1272.08	66.08
S. Line 6	Linebreds	85	-25.3և	1Ch4.55	38.30	-23.95	1049.03	43.21
	Linecrosses	48	25.34	1158.41	43.48	23.95	1152.68	49.40
^b Y/F _x	•					-0.599		2.233

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Table 18. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Solids-Not-Fat Yield (1bs) From the Six-Line Crosses

			by/F _x Excluded From Model			by/F _x Included in Model		
Variable	Nc. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean		817	498.48	498.48	6.81	498.88	498.88	7.12
GCA S. L	ine l	145	34.43	532.91	11.37	34.61	533.48	11.68
S. L:	ine 2	155	-0.57	497.91	12.27	-0.97	497.90	12.27
S.L	ine 3	117	20.49	518.97	13.17	20.74	519.61	13.49
S. L:	ine 4	182	28,50	526.98	11.93	28,57	527。山山	12.14
S.L:	ine 5	85.	-16.19	482.29	14.96	-15.90	482.98	15.28
S. L	ine 6	133	-66.67	431.81	13.55	-67.04	431.83	13.56
Average He	eterosis	•						
	Linebreds	526	-12.97	485.51	6.57	-14.21	484.66	7.68
	Linecrosses	291	12.97	511 . li5	8.96	14.21	513.09	11.58
Line Heter	rosis							
S. Line 1	Linebreds	85	26.34	546.28	18.25	26.42	545.70	18,52
	Linecrosses	60	-26.34	519.54	12.70	-26.12	521.27	15.06
S. Line 2	Linebreds	102	5.78	1490.73	14.82	5.61	489.31	16.15
	Linecrosses	53	-5.78	505.10	14.36	-5.61	506.50	16.24
S. Line 3	Linebreds	7 7	-8.26	497.73	19.46	-8.01	497 . 40	19.57
	Linecrosses	40	8.26	540.20	16.22	8.01	541.83	17.88
S. Line 4	Linebreds	112	1.45	515.46	20.03	1.52	456.76	20.36
	Linecrosses	70	-1.45	538.50	12.99	-1.52	509.20	15.16
S. Line 5	Linebreds	. 65	-12.23	457.08	18.55	-12.01	456.76	18.69
	Linecrosses	20	12.23	507.49	23.3և	12.01	509.20	24.62
S. Line 6	Linebreds	85	-13.08	405.77	14.45	-13.54	104.09	16.28
	Linecrosses	79	13. C3	457.86	16.40	13.54	L59 .5 8	18.61
^b Y/F _X						0.200		0.888 129

Table 49. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Protein Yield (1bs) From the Six-Line Crosses

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		^b Y/F _x ^E	by/Fx Excluded From Model			$b_{\mathrm{Y}/\overline{r}_{\mathrm{X}}}$ Included in Model		
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error	
Mean	817	27.04	27.04	0.21	26.98	26.98	0.22	
<u>GCA</u> S. Line 1 S. Line 2 S. Line 3 S. Line 4 S. Line 5	145 155 117 85	0.51 -C.17 -0.12 -0.10	27.55 26.88 26.62 26.95 27.41	0.34 0.37 0.40 0.36 0.45	0.19 -0.12 -0.15 -0.10 0.31	27.17 26.86 26.53 26.88 27.32	0.35 0.38 0.41 0.37 0.47	
S. Line 6 Average Heterosi	182 182	-0.20	26.84	0.11	-0.16	26.82	0.41	
Linet	preds 526 prosses 291	0.27 -0.27	27.31 26.77	0.20 0.27	0.47 -0.47	27.45 26.50	0.23 0.34	
Line Heterosis S. Line 1 Linet Lineo S. Line 2 Linet Lineo	oreds 85 crosses 60 oreds 102 crosses 53	0.59 -0.59 -0.09 0.09	28.1;2 26.68 27.06 26.70	0.55 0.38 0.45 0.43	0.58 -0.58 -0.06 0.06	28.52 26.41 27.27 26.45	0.55 0.45 0.49 0.49	
S. Line 3 Linet Linec	preds 77 prosses 40	-0.49 0.49	26.41 26.84	0.58 0.49	-0.53 0.53	26.1.8 26.59	0.59 0.54	
S. Line 4 Linet Lineo S. Line 5 Linet	preds 112 prosses 70 preds 65 prosses 20	-0.34 0.34 0.26 -0.26	20.00 27.02 27.94 26.89	0.60 0.39 0.56 0.70	-0.35 0.35 0.22 -0.22	27.00 26.76 28.01 26.62	0.61 0.45 0.56 0.71	
S. Line 6 Lines Lines	preds 85 prosses 48	0.07 -0.07	27.19 26.50	0.43 0.49	0.15 -0.15	27.44 26.20	0.49 0.56	
^b Y/F _x					0.033		0.026	

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Table 50. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Age at Calving (Mo.) For the Six-Line Crosses
			by/F _x Excluded From Model			$b_{Y/F_{X}}$ Included in Model		
Variable	00	No. of servations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean		817	287.94	287.94	2.65	288.10	268.10	2.77
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4 S. Line 5 S. Line 6		145 155 117 182 85 133	2.47 -5.06 2.83 5.84 -3.15 -2.92	290.41 282.88 290.77 293.78 284.79 285.01	4.17 4.64 5.14 4.63 5.81 5.44	2.46 -5.04 2.82 5.84 -3.16 -2.91	290.56 283.06 290.92 293.94 284.94 285.19	4.60 4.65 5.28 4.72 5.94 5.45
Average Heteros Line	is breds crosses	526 291	-1.58 1.58	286 .35 289.52	2.51 3.78	-2.14 2.14	285.96 290.24	3.08
Line Heterosis S. Line 1 Line Line S. Line 2 Line Line S. Line 3 Line Line	breds crosses breds crosses breds crosses	85 60 102 53 77 40	-3.85 3.85 -1.68 1.68 2.38 -2.38	284.97 295.84 279.62 286.14 291.56 289.97	7.74 5.38 6.14 5.95 8.22 6.85	-3.81 3.81 -1.75 1.75 2.49 -2.49	284.61 296.52 279.16 286.95 291.27 290.57	7.86 6.39 6.70 6.73 8.27 7.56
S. Line 4 Line Line S. Line 5 Line Line S. Line 6 Line Line	breds crosses breds crosses breds crosses	112 70 65 20 85 48	2.83 -2.83 6.92 -6.92 -6.59 6.59	295.02 292.53 290.12 279.45 276.84 293.19	8.42 5.46 7.81 9.83 6.20 7.04	2.86 -2.86 7.02 -7.02 -6.80 6.80	294.56 293.22 289.82 280.06 276.25 294.13	8.57 6.38 7.87 10.37 6.99 8.00
^b Y/F _x						0.089		0.412

Table 51. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Days in Milk For the Six-Line Crosses

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		b_{Y/F_X} Excluded From Model			b_{Y/F_X} Included in Model		
Variable	No. of Observations	Constant Estimate	Least- Squares Means	Standard Error	Constant Estimate	Least- Squares Means	Standard Error
Mean	817	141.16	141.16	5.42	142.50	142.50	5.67
GCA S. Line 1 S. Line 2 S. Line 3 S. Line 4 S. Line 5 S. Line 6	145 155 117 182 85 133	-3.51 2.01 5.18 12.95 -25.87 9.21	137.65 143.17 146.34 154.11 115.29 150.40	9.15 9.49 10.52 9.47 11.89 11.14	-3.11 1.06 5.77 13.10 -25.18 8.37	139.39 143.55 148.26 155.59 117.31 150.86	9.41 9.50 10.80 9.65 12.16
Average Heterosis Linebreds Linecrosse	526 s 291	10.30 -10.30	151.46 130.87	5.14 7.74	6,03 -6,03	148.52 136.47	6.30 10.35
Line Heterosis S. Line 1 Linebreds Linecrosse	85 s 60	-7.23 7.23	140 .71 134.58	15.84 11.02	-6.94 6.94	138.48 140.30	16.08 13.08
S. Line 2 Linebreds Linecrosse S. Line 3 Linebreds	102 s 53 77	0.10 -0.10 7.90	153.57 132.78 16հ.5հ	12.56 12.17 16.82	-0.48 0.48 8.78	149.10 138.01 163.07	13.70 13.77 16.92
S. Line 4 Linebreds	s 40 112 5 70	-7.90 15.16	128.15 179.57 128.65	14.01 17.24	-8.78 15.41	133.46 177.03	15.46 17.54
S. Line 5 Linebreds Linecrosse	s 70 65 s 20	-7.49 7.49	118.10 112.48	15.98 20.11	-6.73 6.73	116.61 118.01	16.11 21.22
5. Line o Lineoreds Linecrosse	о5 s 48	-0.45 8.115	148.56	14.41	-10.03 10.03	154.86	16.36
Y/F _X					0.007		

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Table 52. Listing of Constant Estimates, Least-Squares Means and Standard Errors For Days Open For the Six-Line Crosses

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Trait For Comparison	t	t ^a
Milk Yield	2.548**	1.208
Fat Yield	3.501***	2.041**
S.N.F. Yield	2.701***	1.380
Protein Yield	2.983***	1.896*
Age at Calving	2.087**	2.108**
Days in Milk	0.884	0.691
Days Open	3.777***	1.282

Table 53. A Comparison of Linecrosses With Linebreds From the Six-Line Crosses Using Linear Contrasts

^aData adjusted for level of inbreeding.

*Linecrosses significantly superior to linebreds at 10% level.

**Linecrosses significantly superior to linebreds at 5% level.

***Linecrosses significantly superior to linebreds at 1% level.

SUMMARY AND CONCLUSIONS

During the period 1948-1974, States of the North Central Region cooperated with the United States Department of Agriculture and other agencies to evaluate some of the effects of systems of breeding on the long range improvement of dairy cattle performance. A portion of the contribution by Ohio, in cooperation with United States Department of Agriculture, Ohio Department of Mental Hygiene and Correction, and Ohio Agricultural Research and Development Center has been concerned with some of the effects of reciprocal crossing among lines of Holstein cattle on production and other traits of economic importance. The current investigation involves a portion of the studies which relates to general and specific combining abilities, and inbreeding.

Over a period of 25 years, six lines of Holstein cattle, involving approximately 800 milking cows, were developed in six large herds owned by Ohio Department of Mental Hygiene and Correction. Three to five closely related, unproved, bulls were selected by pedigree, and performance of their respective sires to develop the lines. The sire groups which were selected to start the development of the various lines, did not have any common ancestors within the first seven generations. Sires within a group were usually half brothers or more closely related. Matings were designed to develop a high relationship among

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the females and yet to hold inbreeding as low as possible. A line of cattle represented a group of females which were, on the average, 25% or more related to one another. After three to four generations of line development, the lines were reciprocally crossed simultaneously by the use of A.I. A percentage of the animals in each line was also continued to be linebred in order to produce contemporary linebred and linecross individuals.

Detailed records of productive and reproductive performance were kept, as well as information on health status and reasons for disposal. Traits examined in this study included mature equivalent yields of milk, fat, solids-not-fat and protein; lactation length, age at first calving and reproductive performance during first lactation. Least-squares mixed model analytical procedures were used to analyze the data. Features studied for the traits included general and specific combining abilities, average and line heterosis and reciprocal effects.

Results of the analyses indicated that different types of gene effects were important in controlling production in Holstein cattle. Additive or additive x additive genetic effects appeared to be of most importance, and the significance of dominance effects appeared low and varied between lines.

The evaluation of the inbreeding data indicated widely differing effects of inbreeding on the different lines, with regression coefficients on degree of inbreeding ranging from +86 to -160, +3.4 to -6.0, +7.7 to -12.0 and +3.1 to -3.8 pounds for yields of milk, fat, SNF and protein, respectively. A linear regression line most fully explained the effects of inbreeding. These findings indicated that it was possible to improve production by linebreeding, and substantiated the claims which had been made by cattle breeders of the past who believed that inbreeding had been a source of genetic improvement in their herds. The results found by many previous researchers indicating the undesirable effects of inbreeding on reproduction were verified. In five out of the six lines the linebreds were open during the first lactation for a longer period of time than the linecrosses. In line 1 the comparison of the reproductive performances was a little unclear with two different methods of analysis giving conflicting results. In some cases the differences between the linebreds and linecrosses within a line were not significant but the trend was uniform. The mean difference between the linebreds and linecrosses of all six lines was 21 days.

Examination of the general combining abilities of the lines revealed distinct differences in additive genetic merit. Three of the lines were of approximately equal genetic merit and were superior to the remaining three lines for production traits.

No evidence was found for the existence of specific combining effects for production traits between the four lines examined for this effect. However, there was definite evidence to suggest the presence of nicking for reproductive performance for four of the linecross groups.

Reciprocal differences for specific linecrosses were observed only for reproductive performance involving two of the line combinations.

When all lines were considered as a whole, there appeared to be definite evidence for heterosis for milk fat percentage. The overall superiority of the linecrosses over the linebreds was small, and in view of the present trend away from milk containing a high fat content it was probably of little real economic value. The higher milk yield of the linecrosses when compared with the linebreds was achieved without a decrease in compositional quality.

When considered in the light of reproductive performance, there appeared to be some heterotic effects influencing persistency of lactation. Over all six lines the linecrosses, on the average, milked for three days longer than the linebreds.

The decrease in level of production of several of the lines during inbreeding appeared to be due largely to an increasing degree of relationship to sires of low additive genetic merit rather than to the loss of favorable dominance allelic effects. The possibility of nicking between cattle lines for production traits, while not excluded, was considered to be of low likelihood.

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