THE EFFECTS OF INBREEDING ON HERITABLE TRAITS IN A HERD OF JERSEY CATTLE

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Major professor

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ABSTRACT

THE EFFECTS OF INBREEDING ON HERITABLE TRAITS IN A HERD OF JERSEY CATTLE

By

Arthur D. Dayton

Inbreeding is a system of mating that the animal breeder may use to change the genetic properties of a population. Inbreeding is defined as the mating of individuals more closely related than the average of the population from which they came.

The purpose of this study was to determine the effects of inbreeding on seven growth characteristics, milk and fat production and body conformation.

Foundation animals, including twenty-one females and five males, were purchased in California and brought to Michigan State University in 1951 to establish an inbred herd.

Data used in this study were collected over a 15-year period with inbreeding ranging from zero to 50 per cent and averaging about 30 per cent. The number of animals used varied but at most, 265 animals were available for birth weight analysis.

The regression coefficients of body measurements on inbreeding were generally negative although only a few were statistically signifi-

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cant indicating that inbreeding has a depressing effect on growth. The rate of growth was slower for inbreds than non-inbreds from birth to 18 months and then tended to increase after 18 months.

Intra-sire regressions, using the average of each cow's records, were -.75±.74 pounds of fat, -21±13 pounds of milk, and .005±.004 per cent milk fat for each increase of 1 per cent in breeding.

Maximum likelihood method was used to estimate simultaneously the effect of years, changes in average real producing ability of the herd, and the effects of inbreeding. The maximum likelihood estimates of inbreeding effects indicated a decline in production up to inbreeding coefficients of 12 and then an increase in production for animals inbred from 16 to 30 per cent and large negative estimates for animals inbred greater than 30 per cent.

THE EFFECTS OF INBREEDING ON HERITABLE TRAITS IN A HERD OF JERSEY CATTLE

By

Arthur D. Dayton

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST O

Title

LIST OF TABLES (Continued)

LIST OF

LIST OF TABLES (Continued)

Figure

LIST OF FIGURES

Figure Page

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INTRODUCTION

For a population there exists a theoretical average level of consaguinity. Inbreeding, one of two mating systems which can be used to change the genetic properties of a population, is defined as the mating of individuals more closely related than the average relationship in the population.

Types of inbreeding include closebreeding (mating between such closely related individuals as full sibs or parent and offspring), linebreeding (mating of related individuals --usually less closely related than with close inbreeding -- to maintain high relationship to a favored ancestor), and inbreeding by isolation of small segments of a population. Pedigree isolation may have had an important role in forming the dairy breeds as we know them today since they have been genetically isolated from the rest of their species for as long as breeding has been strictly pure.

Dairy cattle breeders have long discussed the merits of inbreeding, with extreme and continued inbreeding being described for a century or more by such terms as "breeding in" and "in". A knowledge of the effects of mating systems on economically important characters is important in formulating breeding programs for improvement. Generally, there has been a decline in levels of performance as inbreeding progresses, but the magnitude of these effects differ from one study to another. Although existing information about the effects of mating systems on such economically important traits as milk yield, body weight, and heart girth in dairy cattle is fairly extensive, genetic progress from using this inforration b

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mation has been hindered by several confounding factors. In most cases the level of inbreeding has not been high, different intensities of artificial selection have been operating simultaneously, the environmental conditions under which the experimental data were collected have not been comparable, and the genetics of the foundation animals were unknown. Other factors such as environmental fluctuations cannot be ignored, particularly in experiments with dairy cattle where the generation interval is long.

Some deductive approaches to quantitative inheritance have been developed from the basic assumptions that (1) each trait is a result of a large number of loci which interact with one another and with the environment in complex ways, and (2) that for these traits individual genes or blocks of genes segregate and recombine in a Mendelian pattern. The total phenotypic variation of a character can be partitioned into components of genotypic and environmental differences. Further separation of genotypic differences into variances due to the additive effects of the genes and the cominant and epistatic deviations from the additive scheme can be made on data collected from specially designed experiments. The relative importance can be determined by separating genetic differences into the additive and nonadditive effects of genes. Since inbreeding causes a change in genotypic frequencies in a population, experimental evidence relative to effects of inbreeding on the variance of heritable traits is needed.

The object of this study was to determine the effects of inbreeding on body size and type at different ages and on production in a herd of inbred Jersey cattle.

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REVIEW OF LITERATURE

Introduction. "The primary effect of inbreeding is to make more loci homozygous. This is a result of mates being alike in more of their genes than would two individuals chosen at random from that population. Consequently, the uniting gametes will be alike in more of their genes and the resulting offspring will be homozygous in more loci than if their parents were unrelated. All the other effects of inbreeding, such as uncovering recessive genes, increasing the resemblance between relatives, and splitting the population into distinct families or lines, flow from this primary one of increasing homozygosis.", Lush (1948).

Computing the coefficient of inbreeding (F) is to determine the probable increase in homozygosity caused by mating individuals which are related to each other more closely than the average relationship within that population. The most widely known concept of the coefficient of inbreeding is the result of work by Sewall Wright (1922). Wright proposed to use the coefficient of correlation between uniting gametes to measure the intensity of inbreeding. This correlation measures only the effects of consanguinity between mates and does not include any additional increase or decrease in homozygosis which may result from selection or mutation. This omission is not serious, since the changes which selection and mutation can make in homozygosis within the space of a few generations are nearly always small. For F to express accurately the changes in homozygosis requires that the gene frequency remain constant.

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Method of computing the coefficient of inbreeding. The computation of the inbreeding coefficient for regular systems of inbreeding was known before Wright's method of path coefficient was developed; however, most of the inbreeding which occurred in livestock was irregular, and prior to Wright's method no logical technique was known for comparing the inbreeding from irregular systems of mating.

Wright's proposal for F is based on the relation

$$F = \left[R_{sd}\,(1 + F_s)^{\frac{1}{2}}\,(1 + F_d)^{\frac{1}{2}}\right]/2$$

$$= (\text{Covariance SD})/\,2$$

where S and D refer to the sire and dam, respectively. For computation this equation reduces to:

$$F = \tfrac{1}{2}\sum\left[\tfrac{1}{2}^{\,n+n'}\,(1 + F_a)\right]$$

where the term within the brackets is computed separately for each line of descent through which S and D are related, A is the common ancestor through which they are related in that line, n is the number of generations intervening between S and A in that line, and n' is the corresponding number of generations between D and A. The F thus computed measures the fraction of the heterozygosis in the foundation animals (those of the date to which the pedigree was traced for computing F) which has probably been turned into homozygosis by the inbreeding.

Mean and variability of an inbred population. The effects of inbreeding on the mean and variance of the population are pointed out by Lush (1948). In the main if the effects of the genes are additive, the mean will remain unchanged with increased inbreeding, but the mean will decrease with inbreeding if the effects of the genes are dominant.

So far as epistatic effects are concerned, inbreeding will decrease the mean if the genes are dominant in their epistatic effects but will

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tend to raise the mean of the population if the desireable epistatic effects are recessive. If the epistasis consists of a genetic intermediate being preferred, inbreeding will tend to lower the mean because it will spread the population toward both extremes and will produce a lower frequency of intermediate zygotes and more of the undesirable extremes in both directions.

The genic variance of the population will be increased by inbreeding over what the variance would be, had the population been mating at random. Variance due to dominance tends to decrease as heterozygosis disappears, and epistatic variance is shifted from variance within inbred lines to variance between inbred lines.

Experience from inbreeding dairy cattle. Experiments have been carried out and are underway to explore the possibilities of herd improvement by a combination of mild inbreeding and selection. In addition, analyses have been made of herds and breeds in which inbreeding has been practiced to study the effects it has had on various characters. These analyses were mainly on three types of data.

(1) Records from closed herds. These herds have been mildly inbred or linebred to a particular sire. The animals have descended from one or several related or unrelated foundation bulls. The average coefficient of inbreeding has been low and selection has been practiced.

(2) Herdbook data. The amount of inbreeding in pedigree matings has been calculated. The data generally have represented a wide sampling of bulls in the population. However, since both sires and progeny have been subject to selection, the data have represented intensely selected animals.

(3) Inbreeding experiments. Due to limitations in experimentation

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with large animals, this type of data is relatively rare. The experiments have generally been started with one or few foundation bulls. Different sire-lines have been developed by systematic mating. Inbreeding has been more intense than that found in the previous two types of data. Selection has usually been within or between lines. In some cases, contemporary control outbred animals from the same sire have been available, though the numbers of both outbred and inbred animals have been relatively small.

A brief review of inbreeding experiments with dairy cattle follows.

An experiment to study the effects of intense linebreeding with 16 cows of mixed breeding and a Guernsey bull was started in 1912 at Beltsville by the USDA, (Woodward and Graves, 1933). In the next year 11 Jersey cows and a registered Holstein bull were added. The female offspring were mated to their own sire for successive generations. The Guernsey group was discontinued after a few years due to severe incidence of brucellosis. In the major part of the experiment a Holstein bull for as long as he lived, was used on the grade cows and their offspring. When he died, he was replaced by an inbred son, and the inbred son was replaced by his inbred son, etc. The plan was to select for service those bulls most highly inbred. The progress of inbreeding was rapid at the beginning, reaching 50 per cent in the second generation of bulls, but few animals were produced with higher inbreeding coefficients than 60 per cent due to sterility and lack of vigor in the more inbred bulls.

At the California Agricultural Experiment Station in 1928 (Rollins et al., 1949) the primary objective of inbreeding in one Jersey and one Holstein herd was to study the inheritance of milk and fat yields within

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inbred lines and in crosses between the inbred lines. Five Jersey sires and one Holstein sire were selected for high production in their pedigrees. The foundation cows came from two station herds. Sire-daughter matings were employed whenever possible, but there were many irregularities in the matings. The original plan called for the development of three inbred lines in the Holstein herd through sire-daughter matings, with each sire to be followed by progency tested inbred sons descended from a succession of high producing females. Sires were selected for their ability to transmit high milk yield. During the 1930's one line was discontinued because of variable milk yield, and the two remaining lines were merged. Within sire groups there was no disposing of female progency unless a heifer failed to breed after repeated matings. Few animals were inbred more than 40 per cent. In the Jersey herd, four lines were started, but two were merged to form a single closed line. In 1946, three bulls related to each other but unrelated to the herd were introduced. Their outcross progency were used to start a second line. The inbreeding coefficients averaged 19 per cent.

An experiment was initiated at the New Jersey Station in 1931 to establish genetic factors for high milk production and high fat test in the Holstein-Friesian breed (Bartlett et al., 1939). The foundation animals included 45 Holstein cows selected for normal size, good type, mature equivalent fat production of at least 480 lb, and with milk testing at least 3.6 per cent butterfat. Four bulls were selected as foundation sires on pedigrees which contained high producing ancestors. Progency of the foundation animals were mated by one of the following schemes: (1) sire-daughter matings; (2) brother-sister matings; (3) matings with less than 50 per cent of the same blood; and (4) outbreeding. The last

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system of mating was used as a control for the inbreeding experiment. The rate of inbreeding was not high. The relationship of living animals to the foundation sire was slightly closer than a sire to daughter. The average inbreeding was very low. Three lines of the four were discarded, but genetic analysis of the defects which occurred was not made. In one line, the bulldog condition appeared, as well as various malformations of the reproductive organs. Another line was discarded because the sire was heterozygous for red, and the animals were of undesirable type. The third line was discarded because of low production.

In 1930 a project with Holstein cattle was inaugurated by the Iowa Agriculture Experiment Station to determine the consequence of mild inbreeding accompanied by selection for high production (von Krosigk and Lush, 1958). All bulls used since 1934 have been bred in the herd, and no females outside the herd have entered since 1937. In the closed herd the effect of inbreeding which automatically occurred in a small finite population could be measured in the herd under selection. Usually about 35 to 50 females of breeding age were in the herd. The breeding system was to use sons of the best producing cows and to keep them in service until sufficient cows (30 or more) were bred to each one so as to give a high probability of at least eight tested daughters per sire. This resulted in most of the bulls being used for slightly over one year each. This breeding system would be expected to increase the inbreeding about 2 to 3 per cent per generation or a little under 1 per cent per year. The inbreeding coefficients ranged up to 34 per cent with the majority in the lower part of the range.

An experiment was initiated with Guernseys at Iowa State as a

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replicate of the Holstein closed herd (Hillers and Freeman, 1964). The Guernsey herd was considerably smaller but was maintained in the same barn and under the same general management as the Holstein herd. The females came from within the Guernsey herd after 1943 except 12 females which left 10 daughters and 2 sons in the herd were purchased from four herds to broaden the genetic base in 1952. No bulls were brought into the herd from outside after 1946. Inbreeding in the herd ranged from 0 to 31 per cent with an average of 6.4 per cent. The average inbreeding of the cows calving in 1961 was 9.1 per cent. The herd was linebred to one superior cow born in 1942.

An inbreeding project with Holstein cattle was initiated by the University of Wisconsin in cooperation with two institutional herds in 1938 (Tyler et al., 1949). One of the first two herds had been a closed breeding herd since 1937. Most of the foundation cows were daughters of two sires. The herd maintained a high relationship to these two foundation sires through their sons and grandsons. Five unrelated sire lines were available for inbreeding in the second herd. In 1941 a third herd was added to the project. A sire and his 17 daughters formed the basis of one line and after 1941 two other lines were developed in the same herd. The plan of breeding in each herd was to mate the herd sires to their daughters or close collateral relatives and during the same period to mate them to unrelated cows to produce outbred offspring as control animals by the same sire. The inbreeding coefficients ranged up to 38 per cent. The average inbreeding of the offspring by each sire ranged from 3 to 17 per cent.

A cooperative study between the Wisconsin Agricultural Experiment Station and the USDA designed to study the effect of various mating

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systems of dairy cattle was started in 1948 (Mi et al., 1965; Holtman and Tyler, 1966). In this herd, foundation animals consisted of six Holstein proven sires, one or two outbred sons of each, and twenty daughters by each sire. Matings were to produce inbred daughters within each sire line and outbred daughters for each sire line sired by bulls of two other lines. Close inbreeding within each sire line and line-crossing was followed after the first generation. The average inbreeding coefficient of all inbreds was 25.3 per cent.

Other published information on effects of inbreeding in dairy cattle were investigations of the University of Missouri herd (Laben and Herman, 1950), the Winterthur herd, (Davis et al., 1953), the Holstein herd at the North Platte Experiment Station (Plum and Rumery, 1956), the survey of herdbook data in Great Britain (Robertson, 1954), and the analysis of data on field progeny testing bulls in Sweden (Hansson et al., 1961).

Another experiment on inbreeding is in an early stage of development. At the South Dakota Experiment Station two inbred lines of Holsteins are to be used for reciprocal crossing when inbreeding of individual animals within the lines exceeds 30 per cent. Another group of animals randomly sired by A. I. bulls is maintained for control (Voelker et al., 1958).

<u>Effects of inbreeding on growth and body measurements</u>. In the Beltsville experiment, Woodward and Graves (1933) found that inbreeding decreased birth weight and retarded growth of the calves. Mature weight was reduced but not proportionately as much as birth weight. Some heterosis in birth weight and rate of growth of the calves was indicated by comparisons of offspring from inbred cows and unrelated bulls with

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their inbred dams. Later, Woodward and Graves (1946) reported that effects of inbreeding became marked when coefficients of inbreeding above 25 per cent were reached. Calves inbred more than 50 per cent had an average birth weight of only 65.9 lb as compared with 81.5 lb for outbred calves. The differences diminished with increasing age.

In a study of body size and internal anatomy of outbreds and cows of varying intensities of inbreeding from the Beltsville experiment, Swett et al. (1949) found that inbreeding resulted in a decline of approximately 15 per cent in body weight or mass but did not affect skeletal size as represented by measures of such as wither height, hip width, body length, and chest depth. Outbred compared to highly inbred cows showed a superiority of 10 per cent in live weight, taken about three months after first calving. Inbreeding did not decrease variability in body size or skeletal dimensions; there was some indication that as inbreeding became more intense, variability increased slightly for some of the dimensions such as hip width, body length, and chest depth.

In a preliminary report of the New Jersey experiment, Bartlett et al. (1939) studied the body measurements of 31-54 outbred and 60 inbred animals at birth, 5 and 10 months of age with inbreeding ranging from 5 to 15 per cent. Measurements included weight, height at withers, and heart girth. There were no significant differences in measurements associated with inbreeding at 5 and 10 months of age. However, inbred females were significantly less than outbreds in birth weight. They stated that daughters of different sires could be inbred successfully provided a rigid system of selection was followed. If inbreeding resulted in inferior animals, they considered this to be due to mating

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genetically inferior animals and not to the system of mating used. Additional data were presented by Bartlett et al. (1942) from the same experiment supporting the earlier observations. They failed to discern any significant difference between inbred and outbred heifers at every age. However, at this stage, three of the four lines had been more or less discontinued. A majority of inbred animals in the herd were descendants of one of the foundation sires.

In a later report, Bartlett and Margolin (1944) found that at two years of age, inbred animals were considerably less in body weight and heart girth than outbred animals. Inbred animals showed more variation. Only animals with a coefficient of inbreeding of 20 per cent or over showed detrimental effects in all measurements. These animals were lighter in weight and less in height and heart girth measurements than other groups. The inbred animals with lower coefficients of inbreeding were equal in size of frame to the outbred animals, although they tended to weigh less. Maturity of inbred groups tended to be late.

Margolin and Bartlett (1945) presented further evidence that inbreeding did not necessarily cause a decrease in body weight or size at any age from birth to maturity provided the coefficients of inbreeding did not exceed 20 per cent. Rigid selection for size, type, production, and vigor had been practiced for all outbred and inbred matings in their experiments. The incidence of culling for the inbred animals of the blood line Ormsby Sensation 45th had not differed in the selection process from that of outbreds of the same blood line at any stage of their development. Females with an inbreeding coefficient higher than 20 per cent developed normally to the age of their first calving but showed a marked decrease in development thereafter as compared to outbred controls.

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This suggested a relationship between gestation or parturition and the failure of these animals to follow a normal growth pattern to maturity.

From the California experiment, Baker et al. (1945) analyzed growth in height at withers, body weight, and heart girth of 88 daughters of one Holstein bull. Coefficients of inbreeding ranged up to about 42 per cent. Measurements were made monthly from six months to 45 months of age. Inbreeding caused a significant decrease in size throughout the period studied.

Body measurements of 322 Jersey females sired by 15 bulls were analyzed by Rollins et al. (1949). The number at a given age ranged from 274 at birth to 63 at 56 months of age. Regression analyses of height, weight, and heart girth on the per cent of inbreeding indicated that inbreeding caused a decrease in each of these characteristics. The magnitude of the effect varied with age and characteristic. Weight was most affected. The variation with age was the same for each characteristic with the maximum effect occurring at six months of age. At that age, an increase of 1 per cent in inbreeding caused a decrease of 0.47 per cent in weight, 0.15 per cent in heart girth, and 0.16 per cent in height. The corresponding figures at 4.5 years of age were a decrease of 0.10 per cent in weight, 0.01 per cent in heart girth, and 0.01 per cent in height. For birth weight the decrease was 0.28 per cent. Inbreeding appeared to affect the prenatal and postnatal rate of growth. The inbred animals were smaller at birth and grew more slowly up to about six months of age than the outcrossed animals, but at some time between six and twelve months of age the inbreds began to grow more rapidly than the outcrossed and continued to do so for the remainder of the period under study. Later, using records of 680 Jersey calves of

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13 bulls, Rollins et al. (1956) reported a regression of birth weight on inbreeding of calf within sire and herd of -0.061±0.028 with length of gestation period held constant.

Dickerson (1940) made a preliminary analysis of the effects of inbreeding among the progeny of different sires on birth weight and body measurements at six months of age in the Wisconsin breeding project. There were 171 and 131 calves available at the two ages. Calves with an average inbreeding coefficient of 16 per cent were nearly 10 per cent lighter at birth than non-inbred calves by the same sires after correction for differences in weight due to sex and to age of dam. This decline in birth weight occurred in both sexes and for six of the eight sires. He explained further that birth weight was determined to an important degree by the calf's own inheritance of size since the dams of the inbred calves were not inbred animals themselves. The difference in size in favor of the outbreds became proportionately smaller rather than larger up to six months of age.

In a later study, Tyler et al. (1947) studied birth weight of 654 calves of 21 bulls from three Holstein herds in the Wisconsin project. The birth weight of the calves decreased 0.28 lb for each 1 per cent increase in inbreeding within sire and adjusted for dam's mature heart girth measurement. Considerable variation was found between sires in the influence of inbreeding on the birth weight of their calves. The partial regression coefficients differed significantly between sires, ranging from -0.823 to 1.090 lb. This was assumed to be due to differences in the average birth weight transmitted by different sires. The inbred calves of sires transmitting heavy birth weights tended to be heavier than the outbred calves because of having more of their sires' genes,

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which cancel, at least in part, the reduction in birth weight from increased homozygosity. In a second report, Tyler et al. (1949), used the average intrasire partial regression analysis holding size of the dam constant to study effects of inbreeding on body dimensions at six and 18 months of age and at maturity. The number of animals varied from 111 to 193 in the different analyses. The depressing effects of inbreeding were slight except on heart girth at 18 months of age. The partial regression coefficient of heart girth on per cent inbreeding was -0.17 cm ($p < .01$). In the Wisconsin study started in 1948, Mi et al. (1965) found an increase in age of 0.03 yr. and a decrease in weight of -2.2 lb at first calving for each 1 per cent increase in inbreeding. They found no curvilinearity of inbreeding effects within sire lines.

From the Iowa experiment, Nelson and Lush (1950) reported intra-sire regressions of birth weight in pounds on inbreeding per cent of calf of -0.09 and -0.16 for 179 male and 191 female calves. The weighted average of these two regressions was a decrease of about one-eighth of a pound in birth weight for each increase of 1 per cent in inbreeding. On the basis of this regression a first generation of mating parent with offspring or full sibs would be expected to lower average birth weight of the calf by about 3 lb. There was a decrease of approximately one-eleventh of a pound in birth weight for each increase of 1 per cent in inbreeding of the dam. For the five body measurements and weight at six months of age and over, an increase of 1 per cent in inbreeding resulted in a decrease of no more than 0.5 per cent and usually only about 0.1 per cent of the average of the respective measurement. The results indicated that the growth curve was changed by intensity of inbreeding. Inbreeding slowed the rate of growth

at early ages as shown in smaller calves at birth and slower gains during the first two years of life. After that age, the inbred animals apparently gained faster than the non-inbreds and by five years of age approached or exceeded the non-inbreds in weight.

In a more recent study of the Iowa data, Sutherland and Lush (1962) analyzed additional data with 808 calves of 41 sires from the same experiment. They reported that birth weight decreased with inbreeding of both calf and dam by approximately 0.2 to 0.3 lb for each per cent of inbreeding. At later ages, body size was negatively correlated with inbreeding. The declines were maximum at approximately three years of age and tended to diminish at later ages. They indicated that inbred animals tended to grow more slowly than outbreds at each age from six months to three years. At later ages, they appeared to grow more rapidly than the outbreds and tended to reach similar body size.

Hillers and Freeman (1964) using the Guernsey data from the Iowa herd found that as inbreeding increased, weight was depressed at all ages. They reported inbreeding appeared to exert its maximum effect at four years of age.

From a preliminary analysis of growth of 103 calves at the South Dakota station, Voelker and Bartle (1958) reported that birth weight was not significantly affected by inbreeding. From birth to three months inbred calves ($F = 0.10$) gained 19 per cent more in body weight than did calves with higher inbreeding--a significant effect. Highly inbred calves grew less rapidly in other body measurements than did calves with less inbreeding. There appeared to be more variation in growth rates of the more inbred group.

Effects of inbreeding and outbreeding on production. In their

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preliminary report, Woodward and Graves (1933) pointed out that there was no definite evidence that the moderate amount of inbreeding was detrimental to the production of milk and fat. Two successive matings to the Guernsey sire in the experiment increased the amount and percentage of fat and decreased milk production, though only five of the cows were inbred. In the Holstein group, two generations of sire-daughter matings appeared to cause an increase in milk production and a decrease in fat percentage. Woodward and Graves (1946) reported further on the results of the Holstein experiment, including animals up to the sixth generation. In the groups with inbreeding coefficients higher than 30 per cent, the milk and fat production decreased and the fat percentage remained the same. The effect of outbreeding was also studied on a limited amount of data. By comparing daughters from the same inbred dams and sired by either inbred bulls or unrelated registered bulls, the outbred maternal half-sisters were better in average milk yield. However, the authors pointed out the possibility of differences in transmitting ability for level of production of the inbred and outbred sires. Another comparison of production of daughters of four sires which were out of inbred grade cows in the experiment and out of registered cows in the Beltsville herd, failed to show heterosis in production traits.

Swett et al. (1949) analyzed records of 45 cows with inbreeding coefficients ranging from 12.5 to 64.6 per cent from the Holstein experiment. Simple correlations between intensity of inbreeding and milk, fat, and fat per cent were -0.26 ± 0.09, -0.34 ± 0.09, and -0.31 ± 0.09. Variability in milk, fat production and in fat per cent did not decrease significantly with inbreeding.

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Bartlett and Margolin (1944) compared the production records of 39 inbred and 40 outbred animals from the New Jersey experiment. Total milk and fat production were significantly less for inbred animals. Fat tests of inbred animals, however, were slightly but not significantly higher in groups by the same sires.

Preliminary results from the California experiment showed that females with inbreeding coefficients of 38 per cent and above produced 199 lb less fat than first-generation daughters or 206 lb less than the foundation females (Ralston et al., 1948). Crossing two inbred lines produced offspring which yielded 203 lb more fat than their dams and 52 lb more than the foundation cows. These were considered to be indications of heterosis.

An analysis by Laben et al. (1955) of the production records (305-day, 2x, 2-year-olds) of 164 cows, daughters of 22 sires, in the California Holstein herd showed significant intra-sire regressions of lactation yield on the coefficient of inbreeding amounting to -209.8 lb of milk, -4.9 lb of fat and -131.0 lb of FCM. There was a significant increase in fat test of 0.008 per cent for increase in each degree in inbreeding, but the authors reported this was probably due to negative correlation between milk yield and fat content rather than to inbreeding *per se*. There was some evidence that inbreeding might have less effect on production for inbreeding levels below 20 per cent than for those above 25 per cent. Significant differences were found between sires in the response of their daughters to inbreeding. Twenty-two inbred daughters of one sire, averaging only 5366 lb of FCM (fat corrected milk), were outcrossed to a third unrelated sire, and 26 daughters from these matings averaged 10,910 lb of FCM. This yield was significantly greater than that

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than that of any group of the herd; this increased yield was, therefore, attributed, at least in part, to heterosis.

In the Wisconsin experiment, the effect of inbreeding on milk production was studied by Tyler et al. (1949) on 47 outbred and 42 inbred daughters of five sires. With the corresponding performance of dam held constant, the 305-2x-ME lactation yield decreased within sire 74 lb of milk and 2.3 lb of fat for each per cent increase in the coefficient of inbreeding. The fat percentage of the milk was not affected. Considerable variation between sires in the effect of inbreeding on production was also observed. Later results from the Wisconsin study indicated in general that line crosses were 15 per cent superior to inbreds for the production characteristics studied: yield of milk, solids-not-fat, and fat, and per cent solids-not-fat and fat (Holtmann and Tyler, 1966). The changes in actual yield of milk, actual fat, fat test, M. E. milk, and M. E. fat per 1 per cent inbreeding were -52 lb, -1.4 lb, + 0.005 per cent, -70 lb, and -1.9 lb (Mi et al., 1965).

The lifetime average fat production (305-2x-ME) of 156 cows sired by 26 bulls during the early part of the Iowa project was analyzed by Nelson and Lush (1950). The average production was 477 lb fat and average inbreeding coefficient was 4 per cent ranging from zero to 28 per cent. The intra-sire regression was -4.5 lb per 1 per cent increase in inbreeding ($P < 0.01$). They concluded that if a breeding plan was followed in which the increase in intensity of inbreeding was less than 2 per cent per generation, enough selection should be possible to counterbalance the decline in production expected from inbreeding.

In a later report von Krosigk and Lush (1958) reported analyses of production of 534 cows, daughters of 69 bulls in the Iowa herd. The

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305-2x-ME records were used. Inbreeding ranged from zero to 34 per cent averaging 7.4 per cent. For each increase of 1 per cent in the coefficient of inbreeding, there was a decrease of 54±17 lb, 1.74±0.57 lb, and 0.003±0.003 per cent for milk, fat, and fat test. There was no evidence of curvilinearity in the effect of inbreeding on production, and differences among the individual sires' regressions were not significant. The production of the dams did not have a significant effect on the effects of inbreeding. That inbreeding caused some decrease in production through its detrimental effects on general body size was indicated by the differences in the regressions of first lactation record on inbreeding with and without heart girth held constant. The negative regression of production on inbreeding was more pronounced for the first lactation than for following lactations. This was assumed to be due to the depressing effect of inbreeding on rate of growth. The effect of inbreeding on the ultimate size of the animals was less than that of attaining this size.

Using the Guernsey data in the Iowa herd, Hillers and Freeman (1964), found the intra-sire regressions of production on inbreeding obtained from the analysis of covariance and the weighted average regressions, respectively, were -36±18 and -51±14 lb of milk per 1 per cent inbreeding, -1.66±0.83 and -2.23±0.66 lb of fat per 1 per cent inbreeding, and .001±.005 and .002±.004 per cent of test per 1 per cent inbreeding. The small size of the Guernsey herd prevented the results from being conclusive.

Laben and Herman (1950) studied the effects of inbreeding on production in the Holstein herd at the Missouri station. The 305-2x-ME lifetime averages of herd test records of 299 cows representing the

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progeny of 34 sires were used. The amount of inbreeding was small and had been the result of a general linebreeding program to the Ormsby family. Only 20 cows had coefficients of inbreeding above 20 per cent. Three-fourths of the cows with lactation records were either outbreds or inbred less than 6 per cent. On an intra-sire basis, milk production decreased significantly about 66 lb and fat production 2 lb for each increase of 1 per cent in inbreeding. The percentage of butterfat was not affected. The effect of inbreeding on average production was not noticeable up to $F = 0.15$. While the general trend of inbreeding effects on production was downward, considerable variation between sires existed. When all averages of production were regressed to a contemporary herd average, the intra-sire regressions of the most probable producing ability for milk, fat and fat test on per cent inbreeding were -30.74 lb, ($P < 0.01$), -0.88 lb ($P < 0.05$), and 0.002 per cent.

Plum (1934) found a negative intra-sire correlation between the coefficient of inbreeding and fat production in one Jersey herd in which the inbreeding coefficients ranged up to 22 per cent.

Davis et al. (1953) analyzed production of the Ormsby family of the Winterthur Holstein herd. Twenty bulls were involved and their 630 daughters averaged 8 per cent of inbreeding. The regression within sire on inbreeding was -30.8 lb of milk, -0.66 lb of fat, and 0.026 per cent fat. None of these regressions was statistically significant. The authors concluded that inbreeding did not depress production in this herd. However, there was great variation in effects of inbreeding among individual sires ranging from -404 to 635 lb milk, -15.2 to 27.7 lb fat, and -0.09 to 0.02 per cent fat for each 1 per cent increase in inbreeding.

Plum and Rumery (1956) analyzed production at one of the Nebraska

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stations where inbreeding had been incidental to selection in a closed line. A total of 118 offspring of 12 sires was used. Inbreeding was not intense and about one-tenth of the animals had F greater than .13. Production of fat in first lactation within sire decreased by .5 lb for each per cent increase in inbreeding.

Gaalaas et al. (1962) estimated the regression of milk and fat on inbreeding in different lactations of the same cows in an institutional herd. Data consisted of 305 day-2x-ME records of 111 grade Holstein cows with four successive lactations each. The yearly effects were removed by maximum likelihood methods. The average inbreeding of the cows was 5 per cent and of their dams, 3 per cent. The latter did not have significant effect on production, while the former was significant ($P < .05$) for milk and fat in first lactation only. Intra-sire regressions of pounds milk per 1 per cent inbreeding of cows were -105.3, -41.9, -18.0, -26.2, and -47.9 for first, second, third, fourth, and average records, respectively. Corresponding regressions of pounds fat were -3.62, -1.06, -1.32, -0.86, and -1.69. The linear regressions accounted for about 7 per cent of the total variation in the first lactation but less than 1 per cent in the other three lactations. The variation in regression coefficients for the individual sires within lactations was not statistically significant.

In Great Britain, Robertson (1954) compared the yield during the first lactation of 82 cows from sire-daughter matings with the yield from the same number of non-inbred daughters in the same herds and years. The milk yield of the inbred daughters was 74 gal less than that of the outbreds, corresponding to a yield of 0.32 per cent for each per cent increase in inbreeding.

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Hansson et al. (1961) analyzed first lactation records of field data collected in connection with the progeny testing of bulls of the Swedish Red and White breed and the Swedish Friesian breed. There were 12,897 daughters of 165 sires and 10,926 daughters of 111 sires for the two respective breeds. The degree of inbreeding of the daughters caused by the relationship of the sire to the maternal grandsire was calculated. About 2 per cent of the daughters of SRB and 5 per cent of the daughters of SLB had coefficients of inbreeding in the range of 11 to 29 per cent. The yield was converted to FCM and corrected for differences in age at first calving. Inbreeding had a significant depressing effect on the yield of fat-corrected milk in both breeds, the regression of the first lactation yield on inbreeding between sire within maternal grandsire being -11.5 kg ($P < .01$) and -10.7 kg ($P < .05$) for the two breeds. With herd average and the general breeding value of the sire adjusted, the partial regressions of yield on inbreeding were -14.3 and -10.1, kg.

Summary. Intensity of inbreeding was relatively low and artificial selection was usually practiced for high production or other desirable performance traits. Several lines of evidence concerning the effects of inbreeding and outbreeding in dairy cattle appear to agree with findings in other species of animals.

(1) Inbreeding increases the proportion of homozygous loci as shown by increased incidence of recessive lethals in inbred groups.

(2) There is a general decline in level of performance as inbreeding progresses.

(3) The closer the character is related to fitness, the more it is subject to inbreeding depression as shown by high mortality in inbred animals, particularly at early ages, (Johansson, 1961).

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(4) There are genetic differences in response to inbreeding as shown by variation among sires or lines in inbreeding effects.

(5) The change of performance with inbreeding tends to be directly proportional to the coefficient of inbreeding as shown by lack of non-linearity of inbreeding effects of various quantitative traits.

(6) Inbreeding appears to delay the development of physiological processes in animals as shown by a decrease in difference between inbred and outbred animals with advance of age.

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SOURCE AND DESCRIPTION OF DATA

Foundation animals. Foundation animals to establish an inbred Jersey herd were purchased from three dairymen who had been using a series of Jersey bulls from the long-time breeding experiments with dairy cattle at the University of California. These animals were brought to Michigan State University in August, 1951. Because the cattle were housed in undesirable quarters prior to October, 1952, the records of milk and fat production during the first year were not usable.

The method for computing the coefficient of inbreeding, F, as defined by Wright (1922) was used in this study. The registered Jersey cattle in the United States about 1915 - 1920 was considered the base population.

Four cows of mature age were from one California herd in which environmental conditions were poor. These four cows had eight records which averaged 6838 lb milk and 408 lb fat (305-2X-ME), and their average coefficient of inbreeding was .14. Seventeen females were obtained from another California herd, five of which had eleven completed lactation records that averaged 9218 lb milk and 538 lb of fat (305-2X-ME). This latter group included one mature cow, two four-year-olds, three three-year-olds, three two-year-olds, two senior yearlings, six females under one year of age, and three bulls which had inbreeding coefficients of .27, .28, and .03. Two bulls purchased from a third cooperating dairyman had inbreeding coefficients of .22 and .23. Sires produced from the foundation animals were used thereafter, the rate of increase in inbreeding and the degree of inbreeding being determined by the smallness of the

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The purpose of the project was to investigate characteristics such as vigor and longevity, reproduction, growth, development, yield and composition of milk, and physiology and/or biochemistry of certain phases of the previously mentioned characteristics.

Project modifications. In 1954 the herd was divided into two mating groups according to the closeness of each animal's relationship to each of two sets of full brothers available for service. These sets of full brothers were sons and grandsons of full sisters and were sired by the same sire. They were also paternal brothers of most of the females in the herd excluding the foundation cows purchased in California in 1951. Each of the females was mated with the bull most closely related to her.

In 1955 the breeding plans were altered slightly to increase the information coming from the project while still retaining the original inbred structure of the experiment. Members of the groups were shifted to place animals with closest genetic covariances with one of the dams of the sires into one group and those most closely related to her full sister, the dam of the other set of brothers, into the other group. One group was chosen by chance to be selected for production of milk and the other group was designated as the control herd. The two groups were kept together as one herd under like conditions with the size of each herd being maintained at about 15 cows in milk.

A third group of Jerseys unrelated to the original project herds and housed until August 1961 in a different location was incorporated into the plans in 1955. This third group was selected for type.

Selection procedures. (McGilliard, 1956)

I. Removal of cows from herds.

  A. Control herd.

    1. Retain all females until one record complete.

    2. Maintain herd size at about 15 cows in milk.

    3. When it is necessary to eliminate cows to maintain herd size, excess cows shall be removed at random from among cows which have completed at least one lactation.

  B. Selected herd.

    1. Maintain herd size at 15 cows in milk.

    2. When it is necessary to eliminate animals to maintain herd size, the animals ranking lowest in index value based on the milk production of the individual and of her relatives shall be removed from the herd.

  C. Both control and selected herds.

    1. Any heifer which has not conceived after 8 services or by 24 months of age shall be removed from the herd.

    2. Any cow which has not conceived within 10 months from the previous calving date shall be removed from the herd.

    3. Females which cannot be milked by machine because of udder structure, injury, etc., shall be removed from the herd.

    4. Animals shall be removed from the herds for any disease or injury for which removal is the recommended veterinary control.

II. Choice and removal of bulls.

  A. Control herd.

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1. After the birth of each bull, determine by chance whether he shall be retained or discarded.
2. When the number of bulls 6 months to 12 months of age exceeds three or the number over 12 months of age, exclusive of the herd sire, exceeds two, discard excess bulls from each age group at random.
3. Choose herd sire by chance from bulls of breeding age which have not previously served as herd sire.

B. Selected herd.

1. Designate periodically the best cows from which to save bulls on the basis of milk production of them and their close relatives.
2. When it is necessary to discard young bulls to maintain proper numbers for replacement, discard the bulls scoring lowest in index value based on milk production of close relatives.
3. Use the bull with the highest index value as herd sire.

C. Both control and selected herds.

1. When a bull is chosen to be herd sire, use him as soon as he is able to serve. Retain the previous herd sire or a substitute until the fertility of the new herd sire is ascertained.
2. Discard infertile bulls as well as those unable or unwilling to serve.

Management procedures. Every effort was made to conform to approved standardized procedures which were in keeping with good herd management and for which facilities were available. These procedures were:

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Feeding. In the main, efforts have been made to keep environmental conditions as constant as possible. However, the feeding regime has been altered slightly from time to time to utilize the animals and facilities in nutritional and managerial experiments. Calves were allowed to remain with their dams until 48 hours following freshening counting the day of birth as the first day. They were fed whole milk at the rate of 10 per cent of body weight until four months of age or longer if individual calves were small or unthrifty. Hay was fed *ad libitum* and calves were given sufficient grain to maintain good condition. The basic grain mixture contained approximately 14 per cent crude protein.

Heifers from 3 to 10 months of age were fed silage, grain, and hay at a rate designed to provide near maximum growth and development. Heifers were provided with pasture, when possible, from ten months to calving and were given silage, hay, and grain in sufficient amounts to bring them up to calving in good flesh but not carrying excessive fat.

For lactating cows, summer pasture, when available and practical, was given and supplemented with grass silage. In winter, feeding corn silage and a good quality legume hay was the standard procedure. Grain was fed in amounts according to milk production and in quantities to insure a sufficient nutrient intake to meet growth requirements of the young cows.

Reproduction. Detailed observations have been made routinely on the herd regarding various aspects of physiology of reproduction. Records of heat were kept beginning at 12 months of age, and prebreeding examinations of heifers not previously observed in heat were made at 14 months. Heifers were bred at first regular heat after they reached approximately

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550 lb of body weight or 15 months of age whichever came earlier. A heifer not pregnant by two years of age was discarded as a non-breeder. Cows were rebred at heat nearest 60 days after calving. Cows not in calf by 10 months after calving were removed from the herd. Manual palpations of the genital organs were made before breeding, 60 to 90 days past breeding, at post-partum, and at any time irregularities were reported.

Production. All cows were milked twice daily and the daily milk weights were recorded. However, annual milk yield and fat production were determined monthly from the DHIA testing program. All records were calculated to 305-2X-ME basis using the extension factors developed by Lamb and McGilliard (1960) and the age conversion factors developed by the American Jersey Cattle Club. Until March 1956 the policy was to begin the dry period at least 60 days prior to the due date. After that date, the policy was altered slightly in order to give cows with calving intervals of less than a year a milking period of at least 305 days and reduce the dry period. That is, the primary emphasis was put on the length of the lactation period and secondary emphasis was placed on the length of the dry period. For cows with calving intervals longer than one year the dry period was started after 305 days of lactation and 60 days before calving. However, cows with daily milk production below 6 lb were turned dry regardless of days in milk.

General practices. The herds were tested regularly for Brucellosis, TB; preventive care was exercised in the control of mastitis, and veterinary treatment followed when needed. All abnormal conditions possibly having a bearing upon the experiment were recorded in the herd health book.

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Most of the milking cows were classified at least once by an official classifier. An unofficial evaluation of body conformation was done at the time of each measurement.

Alterations in the procedures listed were made in accordance with suggestions and recommendations by the North Central Regional Dairy Cattle Breeding Technical Committee to insure greater standardization among all research projects.

Weights and Measurements. The data were records on the Michigan State University Jersey herd from 1951 to 1966. Seven characteristics, weight, chest circumference, wither height, chest depth, length from withers to hips, length from withers to pins, and length from hips to pins, were measured at ages three months, six months, twelve months, eighteen months, and three months after each calving. Birth weights were recorded for all births and recorded to the nearest pound. Chest circumferences were recorded to the nearest one-quarter inch, and all measurements of length and depth were recorded to the nearest one-quarter centimeter. The chest circumference measurements were taken with a steel tape in a plane perpendicular to the body axis immediately back of the elbows at the smallest part of the chest. Wither height, chest depth, and the three body length measurements were taken with calipers. Wither height was the vertical distance from the highest point over the withers to the ground. Chest depth was the vertical distance from the back to the floor of the chest at its shallowest part. The three body lengths were the horizontal distances from a point just in front of the withers to the middle of the hip bone, from the withers to the end of the pin bones, and from the middle of the hip bone to the end of the pin bones. Care was taken at each measurement to have the animal on a flat surface in a n

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METHODS AND RESULTS

Regression of weight and body measurements on inbreeding. An inbreeding experiment concerned with dairy cattle is necessarily a long-term project. This is especially so when there is no special effort to increase the inbreeding rapidly. The main reason is that the generation interval for dairy cattle is of the order of five years. One cannot hope to hold environmental conditions entirely constant during the time needed for inbreeding to accumulate. Even if it were possible economically to control feeding and management conditions, other extraneous factors such as temperature, quality of pasture, and incidence of disease are impossible to control wholly and some important effects of these even may be unknown. Furthermore, the mean genetic composition of the herd can scarcely remain constant during the experiment. Besides any general effects of inbreeding, natural selection may have changed the composition in unknown ways, and the very nature of inbreeding permits gene frequency to drift randomly. These sources of change are in addition to any general effects of inbreeding having lowered the average amount of heterozygosity. That more of the less inbred cows are alive in the earlier part of the experiment while the more highly inbred cows are more frequent in the later years confounds trends in average inbreeding with time trends in other factors. A dependable analysis must consider the possibilities which can arise from the confounding of these sources of variation.

Making the analysis within sire would bypass most of the effects of both genetic and environmental time trends by removing the variance

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they caused and leaving it unanalyzed. The comparisons are then only between daughters of the same sire. Since the sires in this experiment were nearly always used for few years, their daughters are likely to have lived nearly contemporarily. The pooled intra-sire regression of weight and body measurements on inbreeding is a average of the individual regressions for the daughters of the several sires weighted by the inverse of the variance of the measurement.

The assumption usual in regression that the independent variables are measured without error need not be fulfilled for complete validity of the analysis. The independent variables in the calculations are inbreeding coefficients calculated according to Wright (1922). These are merely expectations of the probable loss in heterozygosis and, therefore, differ from the actual loss for any one animal because of the random chance in Mendelian segregation and recombination. Provided that the only reason for there being any regression at all of weight and body measurements on inbreeding is the inbreeding itself, the dependent variable is correlated with these errors in the independent variable. This introduces a term in the numerator of $\Sigma xy/\Sigma x^2$ (x=independent variable, y=dependent variable) which cancels the effects of the denominator being too large. Berkson (1950) has advanced a more comprehensive explanation of the reason the regression is unbiased in such cases.

Some error in the independent variable could arise if different mortality caused the more heterozygous animals to be more likely to live than the less heterozygous ones which had the same inbreeding coefficients. This would tend to make the regression coefficient a bit nearer zero than it should be.

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since the type herd was unrelated to the original project herds, the analysis was done for each herd separately and also with the herds combined as one herd.

Birth weights and weights and body measurements at 3, 6, 12, and 18 months and 3 months after calving at first, second, third, and fourth and greater parities were analyzed. The number of females decreased from 265 at birth to 79 at third lactation.

Table 1 shows the partitioning of the corrected sum of squares and products for weight at birth for the inbred herd, type herd, and the combined herds. Tables 2, 3, and 4 give the intra-sire regression coefficients and standard errors of the regression coefficients for the weights and measurements of the inbred, type, and combined herds, respectively.

Regression of production on inbreeding. For the analysis 607 mature-equivalent records were used. The data were inbreeding to the nearest per cent, fat production to the nearest pound, milk yield to the nearest hundred pounds, and fat per cent to the nearest one-tenth of one per cent.

Tables 5, 6, and 7 show the partitioning of the corrected sums of squares and products.

The standard deviations within sire of hundred pounds milk yield, fat production, and fat per cent were 17.6, 95, and .47, respectively. That there was a difference among sires in inbreeding and also in milk and fat yield and fat per cent of their daughters is shown by F test. For milk yield F = 7.9, for fat production F = 8.5, fat test F = 3.2, and for inbreeding F = 31.2; all of these F values have probabilities less than one per cent. Where F is the ratio of mean squares.

The intra-sire regression of milk yield on inbreeding was -.12±.07 hundreds of pounds of milk per one per cent of inbreeding. Decoded, this regression becomes -12±7 lb of milk. The intra-sire regression of fat production on inbreeding was -.51±.42 lb of fat for each increase of one per cent in inbreeding. The intra-sire regression of fat test on inbreeding was .003±.002 per cent of test per one per cent of inbreeding. None of these regressions was statistically significant from zero, but the regressions for milk and fat production approach significance.

The correlations with per cent inbreeding were -.07 for milk, -.05 for fat, and .05 for fat test. These indicate that inbreeding actually accounted for only a small part of the total variance of the production traits.

Table 1

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Table 1 Sum of squares and products of weight at birth and inbreeding.

Source of variation	df	Weight	Products	Inbreeding
(Inbred herd)				
Total	199	9873	-663	21470
Among sires	19	1345	-981	9380
Within sires	180	8528	318	12090
		b = .026±.06 lb		
(Type herd)				
Total	64	3149	-1230	5132
Among sires	6	576	-397	1254
Within sires	58	2573	-833	3877
		b = -.215±.11 lb		
(Combined herd)				
Total	264	13830	1005	37024
Among sires	26	2727	1520	21056
Within sires	238	11102	-515	15968
		b = -.032±.05 lb		

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Table 2 Intra-sire regression coefficients and standard errors of weight and body measurements at different ages on inbreeding (Inbred herd)

	3 Mo.	6 Mo.	12 Mo.	18 Mo.
n	138	134	124	126
Weight (lb)	.03±.18	-.24±.33	-1.16±.56	-1.62±.69
Wither height (cm)	-.01±.04	-.04±.03	-.04±.04	-.10±.04
Chest cir. (in)	.00	-.01±.02	-.01±.02	-.04±.03
Chest depth (cm)	.00	-.01±.02	-.02±.02	-.02±.03
Withers to hips (cm)	.00	.02±.04	.01±.04	-.09±.04
Withers to pins (cm)	-.01±.07	-.10±.07	-.01±.05	-.13±.05
Hips to pins (cm)	-.01±.05	.04±.07	-.04±.02	-.04±.02
	1st cal.*	2nd cal.*	3rd cal.*	4th cal.*
n	106	73	49	30
Weight (lb)	-.54±88	-1.57±1.35	-1.25±1.57	-1.46±1.76
Wither height (cm)	-.03±.03	-.06±.04	-.04±.05	-.02±.06
Chest cir. (in)	.03±.03	-.03±.04	-.02±.04	-.01±.04
Chest depth (cm)	-.01±.02	-.02±.03	.01±.03	.01±.04
Withers to hips (cm)	-.01±.05	.01±.06	.04±.07	.15±.08
Withers to pins (cm)	-.06±.06	-.02±.06	-.01±.07	.09±.08
Hips to pins (cm)	-.05±.02	-.04±.02	-.02±.03	-.03±.03

* Weight and measurements taken three months after calving

Table 3 Intra-sire regression coefficients and standard errors of weight and body measurements at different ages on inbreeding (Type herd)

	3 Mo.	6 Mo.	12 Mo.	18 Mo.
n	40	39	41	43
Weight (lb)	-.25±.35	-.06±.56	-.47±.66	.12±.68
Wither height (cm)	.02±.05	.08±.06	.02±.05	-.09±.07
Chest cir. (in)	-.02±.03	.03±.03	-.03±.03	.02±.02
Chest depth (cm)	.01±.03	.02±.03	.00	.02±.03
Withers to hips(cm)	.03±.05	-.01±.05	-.12±.06	-.07±.04
Withers to pins(cm)	.03±.07	-.02±.07	-.12±.06	-.08±.05
Hips to pins (cm)	-.02±.02	.06±.04	-.02±.03	-.03±.02
	1st cal.*	2nd cal.*	3rd cal.*	4th cal.*
n	44	27	13	11
Weight (lb)	-2.86±1.65	-3.61±2.38	-1.30±2.10	.83±1.41
Wither height (cm)	.01±.06	-.08±.07	.05±.07	.03±.08
Chest cir. (in)	-.03±.05	.00	.12±.07	.06±.09
Chest depth (cm)	.03±.05	.03±.06	.09±.06	.09±.06
Withers to hips(cm)	-.05±.07	-.01±.08	-.16±.12	-.08±.10
Withers to pins(cm)	-.09±.08	-.04±.10	-.21±.13	-.18±.11
Hips to pins (cm)	-.05±.03	-.06±.05	-.01±.05	-.07±.05

* Weight and measurements taken three months after calving

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Table 4 Intra-sire regression coefficients and standard errors of weight and body measurements at different ages on inbreeding (Combined herds)

	3 Mo.	6 Mo.	12 Mo.	18 Mo.
n	178	173	165	169
Weight (lb)	-.05±.16	-.19±.29	-.94±.44	-1.10±.54
Wither height (cm)	.00±.03	-.00±.03	-.02±.03	-.09±.04
Chest cir. (in)	-.00±.02	.00±.02	-.01±.02	-.02±.02
Chest depth (cm)	.00	-.00±.02	-.01±.02	-.01±.02
Withers to hips(cm)	.01±.03	.01±.03	-.03±.03	-.09±.03
Withers to pins(cm)	.00	-.08±.05	-.04±.05	-.12±.04
Hips to pins (cm)	-.01±.04	.05±.05	-.04±.02	-.04±.02
	1st cal.*	2nd Cal.*	3rd cal.*	4th cal.*
n	150	100	62	41
Weight (lb)	-.37±.81	-2.05±1.19	-1.35±1.32	-1.02±1.50
Wither height (cm)	-.01±.03	-.06±.04	-.02±.04	.01±.04
Chest cir. (in)	.02±.03	-.02±.03	-.01±.03	.01±.03
Chest depth (cm)	.01±.02	.01±.05	-.01±.06	.03±.03
Withers to hips(cm)	-.03±.04	.01±.05	-.01±.06	.10±.07
Withers to pins(cm)	-.07±.05	-.03±.05	-.06±.06	.03±.06
Hips to pins (cm)	-.04±.02	-.04±.02	-.02±.02	-.04±.03

* Weight and measurements taken three months after calving

Table 5 Sum of squares and products of milk yield and inbreeding (Combined herds)

Source of variation	df	Milk	Products	Inbreeding
Total	606	244709	18739	121123
Among sires	27	66244	24760	71731
Within sires	579	178465	-6021	49391

b=-.12±.07 lb (10^2) per 1 per cent inbreeding

Table 6 Sum of squares and products of fat production and inbreeding (Combined herds)

Source of variation	df	Fat	Products	Inbreeding
Total	606	7258980	134196	121123
Among sires	27	2055520	159203	71731
Within sires	579	5203460	-25007	49391

b=-.51±.42 lb per 1 per cent inbreeding

Table 7 Sum of squares and products of fat per cent and inbreeding (Combined herds)

Source of variation	df	Fat test	Products	Inbreeding
Total	606	152.9	502.1	121123
Among sires	27	19.7	357.5	71731
Within sires	579	133.3	144.5	49391

b=.003±.002 per cent of test per 1 per cent inbreeding of squa

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Tables 8, 9, and 10 show the partitioning of the corrected sums of squares and products for the inbred herd and Tables 11, 12 and 13 give the same information for the type herd. In both herds the regressions for production on inbreeding per cent were negative but not statistically significant. The regression of fat per cent on per cent of inbreeding was negative for the inbred herd, and for the type herd the regression of fat per cent on inbreeding per cent was .012±.006, significant at the one per cent level of probability.

An F test for each herd indicated that there were differences among sires in inbreeding, milk yield, fat production, and fat per cent.

The correlations between per cent inbreeding and production were -.06 for milk, -.08 for fat, and -.04 for fat per cent in the inbred herd and -.13, -.09, and -17, respectively, for milk yield, fat production, and fat per cent in the type herd.

Inbreeding decreased production of both milk and fat; however, the decrease per one per cent increase in inbreeding was less than most of the other reports. From the Iowa data (Von Krosigk and Lush, 1958, and Freeman and Hillers, 1964), the decrease in production from inbreeding was about four times greater in the Holstein herd and about three times greater in the Guernsey herd than in this herd. In the Iowa study the average life time production was used rather than single records. Regressions calculated from an average could differ.

Table 11 Sum of squares and products of milk yield and inbreeding (Type herd)

Source of variation	df	Milk	Products	Inbreeding
Total	180	75294	4629	11306
Among sires	9	11468	-1742	3818
Within sires	171	63826	-2887	7488

$b = -.39 \pm .22$ lb (10^2) per 1 per cent inbreeding

Table 12 Sum of squares and cross products of fat production and inbreeding (Type herd)

Source of variation	df	Fat	Products	Inbreeding
Total	180	2351807	11248	11306
Among sires	9	370611	-669	3818
Within sires	171	1981196	-10579	7488

$b = -1.41 \pm 1.24$ lb per 1 per cent inbreeding

Table 13 Sum of squares and cross products of fat per cent and inbreeding (Type herd)

Source of variation	df	Fat test	Products	Inbreeding
Total	180	52.1	231.8	11306
Among sires	9	10.2	139.5	3818
Within sires	171	41.8	92.2	7488

$b = .012 \pm .006$ per cent of test per 1 per cent inbreeding from those estimated from single records since random errors tend to cancel out of an average. That the regressions calculated from an average were different can be seen from Table 14 which shows the regressions for the inbred herd, the type herd, and also the combined herds. This table also gives the regression coefficients for each lactation for the combined herds.

Table 14 Intra-sire regression coefficients and standard errors of milk, fat, and fat test on inbreeding (Combined herds)

Parity	Number of observations	Milk (10^2)	Fat	% Fat	Average inbreeding %
1st	212	-.20±.15	-.56±.83	.006±.004	18
2nd	138	-.21±.17	-1.04±.96	.001±.004	19
3rd	93	-.22±.17	-1.01±.92	.003±.005	19
4th	60	-.10±.26	-.48±1.0	.003±.006	18
Average Production	211	-.21±.13	-.75±.74	.005±.004	18
Average production (inbred)	132	-.26±.14	-1.14±.78	.002±.004	26
Average production (type)	79	-.24±.35	-.58±1.9	.011±.008	4

<u>Effects of inbreeding by multiple regression.</u> The methods of statistical analyses used in this phase were also based on the principle of least-squares. The method of analysis of data with unequal subclass numbers involving direct matrix arithmetic was illustrated by Harvey (1960).

A mathematical model was:

$$Y_{ij} = B_o + S_i + B_1\ FO_k + B_2FD_j + B_3YD_j + B_4\ (FO)_k^2 + E_{ij}$$

where Y_{ij} was the observation on the j<u>th</u> daughter of the i<u>th</u> sire; B_o, the constant term; S_i was the effect of the i<u>th</u> sire; and B_1, B_2, B_3 and B_4 were partial regression coefficients of Y_{ij} on the independent variables, FO_j, FD_j, YD_j, and $(FO)_j^2$. The independent variables were:

FO_k = the inbreeding coefficient of the ij<u>th</u> individual

FD = the inbreeding coefficient of the ij<u>th</u> individual's dam

YD = the measurement of the dam [If Y_{ij} = was birth weight, YD was birth weight of the individual's dam.]

$(FO)_k^2$ = square of the individual's inbreeding coefficient.

To be estimated were partial regression coefficients on the independent variable in question adjusted for variation in all other variables. The relative importance of each variable can be determined by the magnitude of the standard partial regression coefficient.

The other models were:

$$Y_{ij} = B_o + S_i + B_1\ FO_k + B_2FD_j + B_4\ (FO)_k^2 + E_{ij}$$

$$Y_{ij} = B_o + S_i + B_1FO_k + B_3YD + B_4\ (FO)_k^2 + E_{ij}$$

$$Y_{ij} = B_o + Si + B_1FO_k + B_2FD_j + B_3\ YD_j + E_{ij}$$

$$Y_{ij} = B_o + Si + B_1FO_k + B_4(FO)_k^2 + E_{ij}$$

$$Y_{ij} = B_o + Si + B_1FO_k + B_2FD_j + E_{ij}$$

$$Y_{ij} = B_o + Si + B_1FO_k + B_3YD_j + E_{ij}$$

$$Y_{ij} = B_o + Si + B_1FO_k + E_{ij}$$

The terms in the models have been defined above. The models with the independent variable $(FO)^2$ were to indicate non-linear effect of inbreeding on the dependent variable.

For this phase of the analysis data for type and inbred herds were combined, and only those individuals where the measurement on the dam was available were used. Hence, the number of observations varied from 166 at birth to 32 at the third lactation.

The partial and standard partial regression coefficients are in Tables 15 through 28 for each trait at the different ages of measurement.

Table 15 Within sires partial regression coefficients of weights (lb) from birth to 18 months of age

Age	Birth	3 Months	6	12	18
NS	17	18	18	20	20
ND	166	120	120	112	126
Y	52	133	247	440	619
F	31	31	31	31	30

	B	B'	B	B'	B	B'	B	B'	B	B'
FO	-.10	-.11	-.52	-.23	3.01	.66	-.23	-.04	-1.28	-.16
YD	.07	.06	.04	.03	.12	.13	.11	.12	.27	.31
FD	.06	.09	.21	.14	.04	.01	-.42	-.10	-.51	-.10
F2	.00	.07	.01	.03	-.04	-.57	-.01	-.12	-.03	-.21
FO	-.12	-.14	-.61	-.27	3.13	.69	-.18	-.03	-2.52	-.33
FD	.06	.09	.21	.13	.06	.02	-.43	-.10	-.09	-.02
F2	.00	.09	.01	.22	-.04	-.60	-.01	-.09	.02	.18
FO	-.12	-.14	-.02	-.01	3.13	.69	-1.19	-.19	.71	.09
YD	.07	.06	.03	.03	.12	.13	.11	.11	.25	.28
F2	.01	.12	.01	.03	-.04	.59	-.00	-.00	-.02	-.16
FO	-.05	-.05	-.08	-.03	.11	.02	-1.00	-.16	-.44	-.06
YD	.07	.06	.04	.04	.12	.14	.11	.12	.26	.30
FD	.06	.09	.20	.13	.15	.05	-.39	-.09	-.49	-.09
FO	-.14	-.16	-.06	-.03	3.31	.73	-1.14	-.19	-2.58	-.33
F2	.01	.14	.01	.08	-.05	-.63	.00	.03	.05	.18
FO	-.05	-.05	-.05	-.02	.12	.03	-.71	-.12	-1.03	-.13
FD	.06	.08	.19	.12	.17	.05	-.41	-.09	-.10	-.02
FO	-.02	-.02	-.12	-.06	.18	.04	-1.20	-.19	-.65	-.08
YD	.06	.06	.03	.03	.12	.13	.11	.11	.25	.28
FO	-.02	-.03	-.14	-.06	.21	.05	-.91	-.15	-1.07	-.14

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average weight of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=weight (birth, 3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table

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F2

FO
YD
F2

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YD
FD

FO
F2

FO
FD

FO
YD

FO

Table 16 Within sire partial regression coefficients of weight (lb) 3 months after calvings

Lact.	1st	2nd	3rd	4th
NS	15	13	10	11
ND	106	66	32	64
Y	800	941	1032	1071
F	26	26	19	19

	B	B'	B	B'	B	B'	B	B'
FO	-10.6	-.95	-11.63	-1.15	-15.72	-1.29	-6.55	-.96
YD	.26	.25	.27	.28	-.10	-.10	-.19	-.18
FD	1.20	.16	1.49	.20	1.03	.09	1.94	.29
F2	.17	.91	.18	.91	.26	1.09	.16	.96
FO	-8.51	-.85	-9.62	-.95	-15.43	-1.28	-4.39	-.65
FD	.98	.13	1.35	.18	.66	.06	1.95	.29
F2	.15	.73	.15	.75	.34	1.07	.11	.69
FO	-9.18	-.91	-10.57	-1.04	-14.69	-1.22	-7.79	-1.15
YD	.26	.27	.25	.27	-.04	-.07	-.19	-.19
F2	.16	.81	.15	.79	.33	1.00	.18	1.21
FO	-2.23	-.22	-2.83	-.28	-2.46	-.20	-.10	-.01
YD	.27	.27	.22	.22	-.07	-.05	-.13	-.12
FD	.91	.12	1.01	.14	.31	.03	2.36	.36
FO	-7.63	-.78	-8.74	-.86	-14.73	-1.22	-5.63	-.83
F2	.14	.71	.13	.64	.23	1.00	.15	.94
FO	-2.46	-.25	-2.49	-.25	-2.47	-.21	.19	.02
FD	.92	.12	.98	.13	.12	.01	2.28	.34
FO	-3.01	-.30	-2.95	-.29	-2.50	-.21	.47	.07
YD	.28	.30	.22	.22	.06	.03	-.11	-.11
FO	-1.92	-.19	-2.62	-.26	-2.49	-.21	.70	.10

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average weight of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=weight (1st, wnd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

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F2

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FD

F0
FD

F0

Table 17 Within sire partial regressions coefficients of wither height (cm) from 3 to 18 months of age

Age	3 Months		6		12		18	
NS	18		18		20		20	
ND	120		120		112		126	
Y	79		91		105		115	
F	31		31		31		30	
	B	B'	B	B'	B	B'	B	B'
FO	-.08	-.19	.01	.02	-.30	-.57	.06	.12
YD	-.08	-.06	.18	.16	.17	.14	.28	.27
FD	.02	.08	.03	.09	.07	.20	.01	.04
F2	.00	.25	-.00	-.02	.00	.52	-.00	-.27
FO	-.04	-.10	-.02	-.04	-.28	-.53	-.07	-.14
FD	-.03	-.09	.03	.07	.06	.18	.03	.08
F2	.00	.16	.00	.06	.00	.53	-.00	-.07
FO	.03	.08	.11	.21	-.13	-.26	.07	.14
YD	-.07	-.05	.17	.15	.14	.12	.29	.28
F2	.00	.18	.00	.04	.00	.09	-.00	-.27
FO	.03	.08	.01	.01	-.01	-.01	-.08	-.17
YD	-.06	-.05	.17	.16	.17	.14	.28	.26
FD	.03	.07	.03	.09	.06	.17	.01	.04
FO	.03	.08	.06	.12	-.14	-.27	-.05	-.11
F2	.00	.06	.00	.07	.00	.30	-.00	-.08
FO	.03	.07	.01	.02	.02	.03	-.11	-.21
FD	.03	.09	.03	.07	.05	.15	.03	.08
FO	.05	.13	.02	.04	.03	.06	-.08	-.15
YD	-.08	-.06	.17	.15	.15	.12	.28	.27
FO	.05	.13	.03	.05	.04	.08	-.10	-.19

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average wither height (cm) of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=wither height (cm) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table I

Lact.

NS
ND
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F

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ND
FD
F2

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F0
ND
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F0
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FD

F0
F2

F0
FD

F0
ND

F0

Table 18 Within sire partial regression coefficients of wither height (cm) 3 months after calving

Lact.	1st	2nd	3rd	4th
NS	18	13	10	11
ND	120	66	32	64
Y	123	125	127	127
F	26	26	26	19

	B	B'	B	B'	B	B'	B	B'
FO	-.01	-.05	-.02	-.05	-.01	-.02	-.05	-.26
YD	.27	.29	.28	.29	.44	.38	.47	.47
FD	.01	.01	-.01	-.05	.05	.22	.08	.41
F2	.00	.29	-.00	-.31	.00	.04	.00	.00
FO	-.02	-.09	-.02	-.08	.10	.33	.13	.72
FD	.02	.02	.02	.09	.05	.19	.07	.37
F2	.00	.38	-.00	-.42	-.00	-.34	.00	.57
FO	-.03	-.13	.02	.08	.06	.20	-.08	-.41
YD	.28	.29	.28	.29	.42	.36	.42	.42
F2	.00	.31	-.00	-.28	-.00	-.19	.00	.29
FO	-.05	-.31	-.01	-.03	.01	.02	-.05	-.25
YD	.29	.31	.29	.30	.44	.38	.47	.47
FD	.01	.02	-.01	-.03	.05	.22	.07	.41
FO	-.01	-.06	.01	.03	.15	.50	.09	.49
F2	.00	.27	-.00	-.36	-.00	-.53	-.00	-.26
FO	-.01	-.05	-.10	-.32	.01	.00	.03	.17
FD	.02	.02	.02	.07	.05	.21	.06	.33
FO	-.09	-.43	-.10	-.34	.00	.00	-.02	-.10
YD	.25	.28	.29	.30	.43	.37	.39	.39
FO	-.11	-.32	-.10	-.32	-.01	-.03	.05	.24

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average wither height of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=wither height (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 19 Within sire partial regression coefficients of chest circumference (in) at 3 to 18 months of age

Age	3 Months		6		12		18	
NS	18		18		20		20	
ND	120		120		112		126	
Y	34		42		53		60	
F	31		31		31		30	
	B	B'	B	B'	B	B'	B	B'
FO	-.06	-.22	.21	.63	-.03	-.10	.07	.21
YD	.00	.00	.18	.18	.15	.15	.29	.31
FD	.02	.08	-.01	-.03	.00	.00	-.00	-.02
F2	.00	.10	-.00	-.40	.00	.01	-.00	-.27
FO	-.06	-.21	.24	.72	-.02	-.05	-.05	-.17
FD	.02	.08	-.01	-.02	.00	.00	.01	.06
F2	.00	.10	-.01	-.61	.00	.02	.00	.07
FO	-.02	-.06	.19	.58	-.03	-.10	.06	.20
YD	.00	.00	.19	.18	.15	.15	.29	.30
F2	.00	.01	-.00	-.31	.00	.01	-.00	-.27
FO	-.03	-.11	.03	.07	-.03	-.09	-.02	-.07
YD	.00	.00	.19	.19	.15	.15	.28	.29
FD	.02	.09	.00	.00	.00	.00	-.00	-.01
FO	-.02	-.06	.23	.67	-.01	-.03	-.05	-.15
F2	.00	.01	-.01	-.45	.00	.01	-.00	-.06
FO	-.03	-.11	.03	.08	-.01	-.02	-.03	-.10
FD	.02	.09	.01	.02	.00	.00	.01	.06
FO	-.01	-.05	.03	.08	-.03	-.08	-.02	-.07
YD	.00	.00	.19	.19	.15	.15	.28	.29
FO	-.01	-.05	.03	.09	-.01	-.02	-.03	-.09

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average chest circumference of offspring (in)
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=chest circumference (in) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 2

Lact.

NS
ND
Y
P

.	.	.–	.–	.	.	.–	.–	FO
.	.	.	.	.	.	.	.	YD
.–	.–	.	.	.–	.–	.	.	FD
.–	.–	.	.	.–	.–	.	.	F2
.–	.–	.–	.–	.	.	.–	.–	FO
.	.	.	.	.–	.–	.	.	FD
.	.	.	.	.–	.	.	.	F2
.	.	.–	.–	.	.	.–	.–	FO
.	.	.	.	.	.	.	.	YD
.–	.–	.	.	.–	.–	.	.	F2
.–	.–	.–	.–	.	.	.–	.–	FO
.	.	.	.	.	.	.	.	YD
.	.–	.	.	.	.	.	.	FD
.–	.–	.–	.–	.	.	.–	.–	FO
.–	.–	.	.	.–	.–	.	.	F2
.–	.–	.–	.	.	.	.–	.–	FO
.	.	.	.	.	.	.	.	FD
.–	.–	.–	.–	.	.	.–	.–	FO
.	.	.	.	.	.	.	.	YD
.–	.–	.–	.–	.	.	.–	.–	FO

Table 20 Within sire partial regression coefficients of chest circumference (in) 3 months after calving

Lact.	1st		2nd		3rd		4th	
NS	15		13		10		11	
ND	106		66		32		64	
Y	65		69		71		72	
F	26		26		26		19	
	B	B'	B	B'	B	B'	B	B'
FO	-.16	-.58	-.26	-.82	-.32	-1.05	.11	.51
YD	.23	.25	.25	.22	.15	.12	-.07	-.06
FD	.01	.08	.03	.13	.08	.32	.06	.30
F2	.00	.49	.00	.68	.01	1.02	-.00	-.23
FO	-.17	-.64	-.21	-.65	-.28	-.93	.08	.41
FD	.02	.15	.03	.11	.09	.36	.06	.29
F2	.00	.48	.00	.55	.01	.93	-.00	-.16
FO	-.15	-.50	-.24	-.76	-.27	-.91	.06	.31
YD	.23	.26	.24	.21	.31	.25	-.05	-.04
F2	.00	.38	.00	.59	.01	.83	.00	.04
FO	-.09	-.25	-.06	-.17	-.01	-.10	.06	.28
YD	.24	.27	.21	.18	.08	.07	-.05	-.04
FD	.01	.07	.02	.08	.07	.29	.05	.28
FO	-.17	-.61	-.19	-.60	-.19	-.60	.05	.23
F2	.01	.60	.00	.48	.00	.56	.00	.09
FO	-.08	-.25	-.04	-.14	-.01	-.20	.05	.25
FD	.02	.14	.02	.07	.08	.32	.05	.29
FO	-.08	-.26	-.06	-.18	-.02	-.17	.07	.35
YD	.24	.27	.21	.18	.25	.20	-.05	.05
FO	-.07	-.24	-.05	-.14	-.01	-.04	.06	.32

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average chest cir. (in) of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=chest circumference (inches) (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Tabl

Age

NS
ND
Y
F

FO
YD
FD
F2

FO
FD
F2

FO
YD
F2

FO
YD
FD

FO
F2

FO
FD

FO
YD

FO

Table 21 Within sire partial regression coefficients of chest depth (cm) from 3 to 18 months of age

Age	3 Months	6	12	18
NS	18	18	20	20
ND	120	120	112	126
Y	35	43	53	60
F	31	31	31	30

	B	B'	B	B'	B	B'	B	B'
FO	.03	.12	.18	.64	.05	.15	.06	.21
YD	.07	.06	.17	.18	.22	.22	.37	.39
FD	.01	.03	.00	.00	.00	.00	-.01	-.06
F2	-.00	-.11	-.00	-.51	-.00	-.16	-.00	-.19
FO	.02	.06	.17	.61	.05	.18	-.11	-.37
FD	.01	.03	-.01	-.04	.00	.00	.01	.05
F2	-.00	-.04	-.00	-.51	-.00	-.12	.00	.29
FO	.05	.18	.17	.59	.04	.16	.05	.16
YD	.08	.06	.17	.18	.22	.22	.35	.37
F2	-.00	-.15	-.00	-.38	-.00	-.16	-.00	-.16
FO	.00	.01	.03	.09	-.01	-.02	.01	.01
YD	.07	.06	.17	.18	.22	.22	.36	.38
FD	.01	.04	.00	.00	.00	.00	-.01	-.06
FO	.03	.11	.15	.52	.06	.25	-.10	-.34
F2	-.00	-.08	-.00	-.41	-.00	-.15	.00	.29
FO	.01	.01	.03	.12	.02	.05	-.02	-.05
FD	.01	.03	.00	.00	.01	.03	.01	.05
FO	.01	.02	.03	.09	-.01	-.02	-.01	-.01
YD	.07	.06	.17	.18	.22	.22	.34	.37
FO	.01	.03	.03	.12	.02	.06	-.01	-.04

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average chest depth (cm) of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=chest depth (cm) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Tabl

Lact

NS
ND
Y
P

F0
YD
FD
F2

F0
FD
F2

F0
YD
F2

F0
YD
FD

F0
F2

F0
FD

F0
YD

F0

Table 22 Within sire partial regression coefficients of chest depth (cm) 3 months after calving

Lact.	1st		2nd		3rd		4th	
NS	15		13		10		11	
ND	106		66		32		64	
Y	66		69		71		72	
F	26		26		26		19	
	B	B'	B	B'	B	B'	B	B'
FO	-.07	-.29	-.14	-.54	-.17	-.76	.16	.91
YD	.29	.36	.44	.38	.20	.19	-.16	-.18
FD	.01	.05	-.01	-.06	.03	.19	.05	.29
F2	.00	.18	.00	.37	.00	.92	-.00	-.36
FO	-.12	-.47	-.11	-.42	-.14	-.65	.12	.68
FD	.01	.06	-.01	-.07	.05	.28	.04	.22
F2	.00	.23	.00	.30	.00	.84	-.00	-.27
FO	-.07	-.29	-.15	-.57	-.15	-.70	.08	.46
YD	.29	.36	.44	.37	.32	.31	.08	.09
F2	.00	.15	.00	.41	.00	.83	-.00	-.07
FO	-.01	-.04	.05	.19	-.03	-.16	.09	.52
YD	.31	.37	.43	.37	.17	.16	-.11	-.13
FD	.00	.00	-.02	-.09	.02	.16	.04	.25
FO	-.12	-.47	-.11	-.44	-.09	-.40	.10	.55
F2	.00	.21	.00	.35	.00	.55	.00	.08
FO	-.01	-.05	-.03	-.13	.04	.17	.07	.43
FD	.01	.04	-.02	-.09	.04	.24	.03	.21
FO	-.03	-.14	-.05	-.18	.03	.13	.07	.89
YD	.28	.29	.44	.37	.27	.26	.08	.09
FO	-.01	-.05	-.03	-.12	.03	.15	.08	.47

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average chest depth cm of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=chest depth cm (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 23 Within sire partial regression coefficients of withers to hips (cm) from 3 to 18 months of age

Age	3 Months		6		12		18	
NS	18		18		20		20	
ND	120		120		112		126	
Y	49		60		74		81	
F	31		31		31		30	
	B	B'	B	B'	B	B'	B	B'
FO	-.32	-.79	-.11	-.23	.17	.32	-.37	-.87
YD	-.12	-.11	.15	.14	.05	.04	.14	.15
FD	.03	.09	.03	.07	-.01	-.03	-.03	-.10
F2	.01	.75	.00	.21	-.00	-.32	.01	.75
FO	-.33	-.80	-.10	-.20	.16	.31	-.42	-.95
FD	.03	.11	.03	.09	.01	.02	-.02	-.08
F2	.01	.73	.00	.16	-.00	-.30	.01	.83
FO	-.26	-.62	-.03	-.06	.14	.27	-.40	-.91
YD	-.13	-.12	.15	.15	.04	.04	.13	.14
F2	.00	.66	.00	.08	-.00	-.28	.01	.77
FO	.02	.05	.00	.00	-.02	-.03	-.03	-.07
YD	-.12	-.11	.15	.14	.04	.04	.16	.17
FD	.02	.06	.02	.06	.00	.00	-.03	-.10
FO	-.25	-.61	.01	.01	.14	.28	-.43	-.98
F2	.01	.61	.00	.01	.00	.00	.01	.84
FO	.01	.01	-.01	-.02	-.01	-.03	-.04	-.08
FD	.02	.09	.03	.08	.00	.00	-.02	-.08
FO	.04	.09	.01	.03	-.02	-.03	-.04	-.09
YD	-.12	-.11	.15	.15	.04	.04	.15	.15
FO	.03	.07	.01	.02	-.01	-.03	-.05	-.10

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average withers to hips (cm) of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=withers to hips (cm) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 24 Within sire partial regression coefficients of withers to hips (cm) 3 months after calving

Lact.	1st	2nd	3rd	4th
NS	15	13	10	11
ND	106	66	32	64
Y	89	94	96	97
F	26	26	26	19

	B	B'	B	B'	B	B'	B	B'
FO	-.11	-.22	-.14	-.31	-.59	-1.24	-.34	-1.10
YD	.24	.24	.19	.18	.15	.18	.03	.05
FD	-.03	-.10	-.02	-.07	-.07	-.18	-.04	-.15
F2	.00	.18	.00	.22	.01	1.18	.01	1.18
FO	-.07	-.15	-.06	-.13	-.45	-.95	-.32	-1.04
FD	-.05	-.16	-.01	-.05	-.06	-.14	-.05	-.15
F2	.00	.12	.00	.04	.01	.89	.01	1.10
FO	-.08	-.15	-.15	-.34	-.63	-1.32	-.31	-1.01
YD	.26	.25	.19	.18	.12	.14	.03	.05
F2	.00	.10	.00	.26	.01	1.28	.01	1.06
FO	-.04	-.09	-.05	-.10	-.03	-.06	.00	.00
YD	.24	.23	.18	.17	.08	.08	-.04	-.07
FD	-.03	-.10	-.02	-.08	-.08	-.21	-.02	-.09
FO	-.11	-.22	-.07	-.16	-.51	-1.08	-.28	-.94
F2	.00	.18	.00	.07	.01	1.04	.01	.97
FO	-.02	-.04	-.04	-.09	-.02	-.05	.00	.00
FD	-.02	.06	-.01	-.06	-.07	-.18	-.02	-.07
FO	-.04	-.08	-.04	-.09	-.01	-.03	.00	.00
YD	.26	.25	.17	.16	.02	.08	-.03	-.06
FO	-.05	-.11	-.04	-.09	-.01	-.03	.00	.00

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average withers to hips of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=withers to hips (cm) (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 25 Within sire partial regression coefficients of withers to pins (cm) from 3 to 18 months of age

Age	3 Months	6	12	18
NS	18	18	20	20
ND	120	120	112	126
Y	71	87	108	119
F	31	31	31	30

	B	B'	B	B'	B	B'	B	B'
FO	-.86	-1.15	-.10	-.11	.11	.16	-.47	-.84
YD	-.05	-.05	-.11	-.10	.08	.07	.24	.22
FD	.00	.00	.07	.10	-.02	-.04	-.03	-.07
F2	.01	.97	-.00	-.11	-.00	-.18	.01	.68
FO	-.79	-1.07	-.09	-.09	-.09	.15	-.54	-.96
FD	-.01	-.01	.08	.11	-.01	-.01	-.02	-.03
F2	.01	.91	-.00	-.13	-.00	-.16	.01	.77
FO	-.86	-1.16	.12	.13	.07	.11	-.50	-.86
YD	.05	-.07	-.11	-.11	.08	.07	.24	.21
F2	.01	.97	-.00	-.29	-.00	-.14	.01	.69
FO	-.05	-.07	-.21	-.22	-.02	-.03	-.07	-.11
YD	-.04	-.06	-.11	-.10	.08	.07	.25	.24
FD	-.02	-.04	.01	.11	-.01	-.02	-.03	-.07
FO	-.81	-1.09	.15	.15	.08	.12	-.55	-.90
F2	-.01	-.92	-.00	-.32	-.00	-.13	.01	.78
FO	-.05	-.06	-.22	-.23	-.02	-.02	-.09	-.15
FD	-.02	-.04	.08	.13	-.01	-.01	-.01	-.04
FO	-.07	-.06	-.17	-.18	-.03	-.04	-.08	-.14
YD	-.05	-.07	-.12	-.11	.08	.07	.25	.23
FO	-.05	-.07	-.17	-.18	.02	-.03	-.10	-.16

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average withers to pins (cm) of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=withers to pins (cm) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 26 Within sire partial regression coefficients of withers to pins (cm) 3 months after calving

Lact.	1st	2nd	3rd	4th
NS	15	13	10	11
ND	106	66	32	64
Y	130	137	140	142
F	26	26	26	19

	1st		2nd		3rd		4th	
	B	B'	B	B'	B	B'	B	B'
FO	-.19	-.38	-.24	-.48	-.73	-1.56	-.35	-1.11
YD	.24	.24	.23	.22	.13	.14	-.02	-.04
FD	.01	.02	.01	.01	-.06	-.17	-.07	-.23
F2	.00	.21	.00	.30	.01	1.42	.01	1.21
FO	-.12	-.24	-.16	-.33	-.64	-1.37	-.36	-1.15
FD	.08	.09	.01	.02	-.07	-.17	-.06	-.22
F2	.00	.18	.00	.12	.01	1.22	.01	1.25
FO	-.11	-.22	-.23	-.47	-.79	-1.71	-.32	-1.02
YD	.25	.25	.23	.22	.12	.14	.00	.01
F2	.00	.17	.00	.29	.01	1.59	.01	1.07
FO	-.08	-.17	-.09	-.19	-.07	-.14	.01	.04
YD	.25	.24	.21	.21	.04	.09	-.07	-.13
FD	.00	.00	.00	.00	-.09	-.23	-.05	-.18
FO	-.08	-.16	-.16	-.32	-.70	-1.52	-.32	-1.01
F2	.00	.09	.00	.11	.01	1.39	.01	1.07
FO	-.08	-.14	-.11	-.22	-.07	-.15	.02	.06
FD	.00	.00	.01	.01	-.09	-.23	-.04	-.13
FO	-.07	-.14	-.10	-.20	-.05	-.12	.01	.02
YD	.25	.25	.21	.21	.02	.02	-.04	-.09
FO	-.04	-.07	-.11	-.22	-.06	-.12	.01	.04

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average withers to pins of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=withers to pins (cm) (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 27 Within sire partial regression coefficients of hips to pins (cm) from 3 to 18 months of age

Age	3 Months	6	12	18
NS	18	18	20	20
ND	120	120	112	126
Y	23	28	34	38
F	31	31	31	30

	B	B'	B	B'	B	B'	B	B'
FO	.32	.64	.15	.18	-.08	-.36	.02	.09
YD	.00	.00	.07	.07	.25	.23	.27	.25
FD	.02	.06	-.07	-.11	.02	.11	-.00	-.01
F2	-.00	-.54	.00	.05	.00	.12	-.00	-.23
FO	.32	.63	.13	.16	-.05	-.25	-.01	-.04
FD	.02	.06	-.06	-.10	.02	.09	.01	.04
F2	-.01	-.54	.00	.06	.00	.04	-.00	-.19
FO	.38	.75	-.06	-.07	-.04	-.19	.02	.09
YD	.00	.00	.06	.05	.25	.22	.27	.25
F2	-.00	-.61	.00	.24	-.00	-.01	-.00	-.23
FO	.03	.03	.20	.24	-.05	-.24	-.03	-.14
YD	.00	.00	.07	.07	.25	.23	.27	.25
FD	.03	.08	-.07	-.11	.02	.10	-.00	-.01
FO	.37	.75	-.06	-.07	-.02	-.11	-.01	-.02
F2	-.01	-.61	.00	.23	-.00	-.06	-.00	-.19
FO	.04	.08	.18	.22	-.04	-.20	-.05	-.24
FD	.00	.00	-.06	-.11	.01	.08	.01	.04
FO	.04	.08	.16	.19	-.04	-.20	-.03	-.14
YD	.00	.00	.06	.06	.24	.22	.27	.25
FO	.04	.08	.15	.18	-.04	-.17	-.05	-.23

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average hips to pins (cm) of offspring
F=average inbreeding of offspring
FO=inbreeding of offspring
YD=hips to pins (cm) (3, 6, 12, and 18 months) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Table 28 Within sire partial regression coefficients of hips to pins (cm) 3 months after calving

Lact.	1st		2nd		3rd		4th	
NS	15		13		10		11	
ND	106		66		32		64	
Y	42		44		44		45	
F	26		26		26		19	
	B	B'	B	B'	B	B'	B	B'
FO	-.14	-.67	-.10	-.49	.02	.07	-.01	-.10
YD	.20	.22	.11	.13	-.12	-.13	.15	.14
FD	.03	.22	-.02	-.19	.00	.00	.01	.01
F2	.00	.19	.00	.11	-.00	-.06	.00	.02
FO	-.15	-.72	-.11	-.57	.07	.05	-.02	-.12
FD	.03	.19	-.03	-.22	.01	.07	-.01	-.07
F2	.00	.21	.00	.16	-.00	.03	.00	.05
FO	-.12	-.61	-.11	-.56	.00	.00	-.02	-.11
YD	.17	.19	.14	.17	-.12	-.13	.15	.13
F2	.00	.16	.00	.21	-.00	-.07	.00	.03
FO	-.08	-.37	-.08	-.39	-.01	-.05	-.01	-.08
YD	.21	.22	.11	.14	-.12	-.14	.15	.14
FD	.03	.21	-.01	-.20	.00	.00	.00	.02
FO	-.14	-.69	-.13	-.67	.02	.12	-.01	-.07
F2	.00	.18	.00	.30	-.00	-.11	.00	.01
FO	-.09	-.42	-.08	-.41	.01	.01	-.01	-.07
FD	.03	.19	-.03	-.23	.01	.08	.01	.07
FO	-.06	-.31	-.07	-.36	-.01	-.05	-.01	-.07
YD	.18	.20	.15	.18	-.12	-.13	.14	.13
FO	-.08	-.37	-.08	-.39	.00	.01	-.01	-.09

NS=number of sire groups
ND=number of daughter-dam pairs
Y=average hips to pins of offspring
F=average inbreeding of offspring
FO=offspring inbreeding
YD=hips to pins (cm) (1st, 2nd, 3rd, and 4th lactation) of dam
FD=inbreeding of dam
F2=square of inbreeding of offspring
B=partial regression coefficient
B'=standard partial regression coefficient

Losses of females between birth and first parturition. During the last several years mortality and reproductive failures almost completely destroyed the effectiveness of selection because female replacements were too few to maintain the size of the herds.

Most of the calf losses were due to death shortly after birth or during the first month of life. If the females survived, failure to breed was the major reason for heifers not going into the producing herd.

On the average, the inbreeding of the inbred calves which died at birth or during the first three months of life was three per cent higher than their contemporaries. However, the average inbreeding of heifers lossed between 12 months of age and first calving was five per cent higher.

Tables 29 and 30 give yearly for female births, the average inbreeding coefficient, and the number of calves lost between birth and three months, and the females lost from the herd between twelve months of age and first parity. This latter group was primarily females failing to breed.

Effects of inbreeding on type rating. An unofficial type classification was made each time the animals were measured, beginning at 6 months of age. Each of five classes "poor", "fair", "good", "good plus", "very good", and "excellent" were divided into three sub-classes, low, middle, high. The numerical values assigned ranged from zero for low poor through 17 for high excellent.

The results reported in Table 31 are for the inbred herd, the type herd, and the combined herds for three different ages and four parities. The regression coefficients are for dairy character, mammary system, and overall rating and are coded by 10^{-1}.

Table 29 Inbreeding of female losses between birth and first parturition (Inbred herd)

			Deaths or removals			
			3 Months		12 Mo. to 1st calving	
Year	Number of births	Average inbreeding	Number	Average *F*	Number	Average *F*
1951	1	3				
52	4	6	2	0	1	24
53	12	19				
54	5	20			1	18
55	12	24	1	24		
56	21	21	5	18	2	33
57	19	28			3	33
58	14	32	2	25	3	35
59	14	32	2	37	1	33
1960	14	32	2	34	7	31
61	12	32	2	35	4	38
62	20	34	6	37	1	39
63	11	36	7	35	7	39
64	15	36	7	34	2	36
65	14	36	2	39		
66	5	38	2	38		
	193	29	37	31	32	34

Table 30 Inbreeding of females losses between birth and first parturition (Type herd)

			Deaths or removals			
			3 Months		12 Mo. to 1st calving	
Year	Number of births	Average inbreeding	Number	Average F	Number	Average F
1957	3	8				
58	9	9			4	9
59	8	12			1	16
1960	10	14	5	16		
61	7	14	5	13		
62	6	15	3	16	2	17
63	2	28				
64	11	18	5	19	1	18
65	3	20	1	22		
66	6	21	5	21		
	65	15	24	17	8	13

Table 31 Intra-sire regression coefficients (10^{-1}) of type rating on inbreeding

(Months) Age Inbred herd	Number Observed	Average inbreeding	Dairy character	Mammary system	Over-all rating
6	124	31	-.05±.05	.00	-.26±.15
12	121	31	.00	-.07±.07	.08±.08
18	123	30	-.15±.05	-.10±.05	-.17±.11
1st Parity	68	28	-.28±.10	-.09±.10	-.36±.23
2nd	45	26	.04±.02	-.14±.14	-.35±.32
3rd	71	22	.16±.13	-.14±.09	-.21±.31
4th	72	20	.15±.12	-.10±.08	-.18±.17
Type herd					
6	42	11	-.04±.06	-.07±.07	.16±.16
12	47	11	.10±.09	.00	.13±.13
18	47	10	.02±.01	.06±.06	.00
1st Parity	47	6	-.07±.08	.26±.11	.33±.26
2nd	29	6	.01±.01	.27±.13	.37±.35
3rd	17	9	-.01±.01	.26±.17	.60±.43
4th	33	4	-.19±.11	.11±.10	.21±.25
Combined herds					
6	166	26	-.05±.04	.02±.04	-.11±.11
12	168	25	.05±.05	-.04±.04	.10±.10
18	170	25	.01±.01	-.09±.04	-.10±.11
1st Parity	115	22	-.24±.06	.09±.07	-.02±.03
2nd	92	22	-.18±.08	.03±.04	-.13±.13
3rd	88	22	.03±.03	.00	-.03±.03
4th	105	16	.08±.09	-.02±.03	.05±.02

Maximum likelihood method for estimating the effects of inbreeding. There is always some question of whether regressions within sires actually are free of environmental and genetic trends. This question may not be completely answerable, but Henderson (1959) proposed to estimate these time trends by maximum likelihood. A term can be added to the model to estimate the effect of inbreeding on production independently of changes in general yearly environment and producing ability of the herd. Of course, like all statistical methods, the validity of this method rests on assumptions which may or may not be fulfilled.

If records of production are correctly adjusted for varying ages of the cows at calving, the average differences between the records of the same cows made in different years should be the differences due to environmental things which changed between those years. Then, if the average production of the herd is corrected for these yearly environmental changes, the rest of the change in the mean must be changes in the producing ability of the herd. But not all cows have an equal numbers of records, and the question arises as to how to weight them properly. Of course, this is an over-simplified situation because the effects of sampling errors and selection have been left out for brevity.

Nelson (1943) presented a least squares solution to the problem and used the method to estimate the genetic change in the Iowa State herd. The method of least squares would probably be effective if the cows were not selected for production. However, when a herd has been under selection, each year cows with best records are saved and those with the poorest are culled. When those cows saved make records the following year, they generally produce less than they did the year they were selected because of the incomplete repeatability of records. This makes the environment appear to be getting worse in successive years. Consequently, the producing ability of the herd appears wrongly to increase more or decrease less than it actually does.

The main difference between methods of least squares and maximum likelihood is that the latter takes into account the incomplete repeatability of records. As with least squares, either an overall regression of production on inbreeding or a constant for each inbreeding level can be fitted with the maximum likelihood method. Fitting a constant for levels of inbreeding was chosen for these data to indicate whether the effect of inbreeding tended to be curvilinear.

Maximum likelihood estimates the parameters of the specified population which make the likelihood of the observed frequency in this supposedly random sample as large as possible. The model for this problem was:

$$Y_{ijkl} = \mu + a_i + f_j + g_k + c_{kl} + e_{ijkl}$$

where Y_{ijkl} designates a 305 day-2X-M.E. production record made in the i^{th} year by the l^{th} cow with inbreeding in the j^{th} class and belonging to the k^{th} time group, μ is the population mean, a_i is the amount the environment of the i^{th} year raised or lowered production from the average of all years, f_j is the deviation associated with the j^{th} inbreeding class, g_k is the deviation of the average producing ability of the cows in the k^{th} group and e_{ijkl} is a random error of measurement. In this analysis the groups were made on the basis of the year in which the cows were born. c_{kl} is the deviation of the l^{th} cow's producing ability from the mean producing ability of her group, the k^{th} group.

To estimate by maximum likelihood some assumptions of distribution are needed. Those assumed were that the c_{kl}'s are normally and independently distributed about a particular g_k with a variance σ_c^2, that the e_{ijkl}'s are normally and independently distributed with mean zero and variance, σ_e^2, and that temporary environment, inbreeding, and real producing ability are independent and additive.

From the above assumptions, the joint frequency function $f(c_{kl}, e_{ijkl})$ can be written. When it is multiplied by the number of observations in the sample, we have L, the likelihood function. This is merely the joint frequency distribution of two independent normal distributions with the parameters given.

$$L = \Big[\prod_{kl} (2\pi\sigma_c^2)^{-\frac{1}{2}} \exp - c_{kl}^2 (2\sigma_c^2)^{-1}\Big]\Big[\prod_{ijkl} (2\pi\sigma_e^2)^{-\frac{1}{2}} \cdot$$

$$\exp - (2\sigma_e^2)^{-1} (Y_{ijkl} - (\mu + a_i + f_j + g_k + c_{kl}))^2\Big]$$

$$= (2\pi\sigma_c^2)^{-\frac{n_{kl}}{2}} \exp - (2\sigma_c^2)^{-1} \sum_{kl} c_{kl}^2 \, (2\pi\sigma_e^2)^{-\frac{n_{ijkl}}{2}} \cdot$$

$$\exp - (2\sigma_e^2)^{-1} \sum_{ijkl} \Big[Y_{ijkl} - (\mu + a_i + f_j + g_k + c_{kl})\Big]^2.$$

The estimators which maximize the likelihood for the sample at hand are obtained by partially differentiating log (L) with respect to each parameter, setting the partial derivatives equal to zero, and solving the resulting equations simultaneously.

$$\log (L) = -\frac{n_{kl}}{2} \log 2\pi - \frac{n_{kl}}{2} \log \sigma_c^2 - \frac{1}{2\sigma_c^2}\, {}_{kl}\, c_{kl}^2 -$$

$$\frac{n_{ijkl}}{2} \log 2\pi - \frac{n_{ijkl}}{2} \log \sigma_e^2 - \frac{1}{2\sigma_e^2} \sum_{ijkl}$$

$$\Big[Y_{ijkl} - (\mu + a_i + f_j + g_k + c_{kl})\Big]^2$$

Let summation over a particular subscript be denoted by a dot.

The general equations to be solved are:

$$\frac{\partial \log(L)}{\partial \mu} = \frac{1}{\hat{\sigma}_e^2}\Big[Y_{....} - n_{....}\hat{\mu} - \sum_i n_{i...}\hat{a}_i - \sum_j n_{.j..}\hat{f}_j -$$

$$\sum_k n_{..k.}\hat{g}_k \quad {}_{kl} n_{..}\sum_{kl}\hat{c}_{kl}\Big] = 0$$

$$\text{or} \quad n_{....}\hat{\mu} + \sum_i n_{i...}\hat{a}_i + \sum_j n_{.j..}\hat{f}_j + \sum_k n_{..k.}\hat{g}_k +$$

$$\sum_{k\,l} n_{..kl}\hat{c}_{kl} = Y_{....}$$

$$\frac{\partial \log(L)}{\partial a_i} = \frac{1}{\hat{\sigma}_e^2}\Big[Y_{i...} - n_{i...}\hat{\mu} - n_{i...}\hat{a}_i - \sum_j n_{ij..}\hat{f}_j -$$

$$\sum_k n_{i.k.}\hat{g}_k - \sum_{k\,l} n_{i.kl}\hat{c}_{kl}\Big] = 0$$

$$\text{or} \quad n_{i...}\hat{\mu} + n_{i...}\hat{a}_i + \sum_j n_{ij..}\hat{f}_j + \sum_k n_{i.k.}\hat{g}_k +$$

$$\sum_{kl} n_{i.kl}\hat{c}_{kl} = Y_{i...}$$

$$\frac{\partial \log(L)}{\partial f_j} = \frac{1}{\hat{\sigma}_e^2}\Big[Y_{.j..} - n_{.j..}\hat{\mu} - \sum_i n_{ij..}\hat{a}_i - n_{.j..}\hat{f}_j -$$

$$\sum_k n_{.jk.}\hat{g}_k - \sum_{kl} n_{.jkl}\hat{c}_{kl}\Big] = 0$$

$$\text{or} \quad n_{.j..}\hat{\mu} + \sum_i n_{ij..}\hat{f}_j + \sum_k n_{.jk.}\hat{g}_k +$$

$$\sum_{kl} n_{.jkl}\hat{c}_{kl} = Y_{.j..}$$

$$\frac{\partial \log(L)}{\partial g_k} = \frac{1}{\hat{\sigma}_e^2}\Big[Y_{..k.} - n_{..k.}\hat{\mu} - \sum_i n_{i}.\hat{a}_i - \sum_j n_{.jk.}\hat{f}_j -$$

$$n_{..k.}\hat{g}_k - \sum_l n_{..kl}\hat{c}_{kl}\Big] = 0$$

$$\text{or } n_{..k}\hat{\mu} + \sum_i n_{i.k.}\hat{a}_i + \sum_j n_{.jk.}\hat{f}_j + n_{..k.}\hat{g}_k +$$

$$\sum_l n_{..kl}\hat{c}_{kl} = Y_{..k.}$$

$$\frac{\partial \log(L)}{\partial c_{kl}} = -\frac{1}{\hat{\sigma}_e^2}\Big[c_{jk}\Big]\ \frac{1}{\hat{\sigma}_e^2}\Big[Y_{..kl} - n_{..kl}\hat{\mu} - \sum_i n_{i.kl}\hat{a}_i -$$

$$\sum_j n_{.jkl}\hat{f}_j - n_{..kl}\hat{g}_k - n_{..kl}\hat{c}_{kl}\Big] = 0$$

$$\text{or } n_{..kl}\hat{\mu} + \sum_i n_{i.kl}\hat{a}_i + \sum_j n_{.jkl}\hat{f}_j + n_{..kl}\hat{g}_k +$$

$$n_{..kl} + \frac{\hat{\sigma}_e^2}{\hat{\sigma}_c^2}\ \hat{c}_{kl} = Y_{..kl}$$

$$\frac{\partial \log(L)}{\partial \sigma_c^2} = -\Big[\frac{n_{kl}}{2}\Big]\Big[\frac{1}{2\hat{\sigma}_c^2} + \frac{\sum_{kl}\hat{c}_{kl}}{2\hat{\sigma}_c^4} = 0$$

$$\text{or}\quad \hat{\sigma}_c^2 = \frac{\sum_{kl}\hat{c}_{kl}^2}{n_{kl}}$$

$$\frac{\partial \log(L)}{\partial \sigma_e^2} = -\Big[\frac{n_{ijkl}}{2}\Big]\Big[\frac{1}{2\hat{\sigma}_e^2}\Big] + \frac{1}{2\hat{\sigma}_e^4}\Big[\sum_{ijkl}(Y_{ijkl} - (\hat{\mu} +$$

$$\hat{a}_i + \hat{f}_j + \hat{g}_k + \hat{c}_{kl})\Big] = 0$$

$$\text{or}\quad \hat{\sigma}_e^2 = \frac{\sum_{ijkl}\Big[Yijkl - (\hat{\mu} + \hat{a}_i + \hat{f}_j + \hat{g}_k + \hat{c}_{kl})\Big]^2}{nkjkl}$$

The coefficient $\frac{\sigma_e^2}{\sigma_c^2}$ of c_{kl} in the c_{kl} equation is closely related to repeatability as defined by $r = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$.

Then $\frac{\sigma_e^2}{\sigma_c^2} = \frac{\sigma_e^2}{\sigma_e^2+\sigma_c^2} \Big/ \frac{\sigma_c^2}{\sigma_e^2+\sigma_c^2} = (1-r)/r$. For 0.4 the general value of r for fat production, $\frac{1-r}{r} = 1.5$.

The work of writing and solving the equations is simplified somewhat if μ and g_k are combined into a single parameter, $(\mu + g_k)$.

The general equations then become:

$$\mu + g_k:\ n_{..k.}\,(\widehat{\mu + g_k}) + \sum_i n_{i.k.}\,\hat{a}_i + \sum_j n_{.jk.}\,\hat{f}_j +$$

$$\sum_l n_{..kl}\,\hat{c}_{kl} = Y_{..k}$$

$$a_i:\ \sum_k n_{i.k.}\,(\widehat{\mu + g_k}) + n_{i...}\,\hat{a}_i + \sum_j n_{ij..}\,\hat{f}_j +$$

$$\sum_{kl} n_{i.kl}\,\hat{c}_{kl} = Y_{i...}$$

$$f_j:\ \sum_k n_{.jk.}\,(\widehat{\mu + g_k}) + \sum_i n_{ij..}\,\hat{a}_i + n_{.j..}\,\hat{f}_j +$$

$$\sum_{kl} n_{.jkl}\,\hat{c}_{kl} = Y_{.j..}$$

$$c_{kl}:\ n_{..kl}\,(\widehat{\mu + g_k}) + \sum_i n_{i.kl}\,\hat{a}_i + \sum_j n_{.jkl}\,\hat{f}_j +$$

$$n_{..kl} + \frac{\hat{\sigma}_e^2}{\sigma_c^2}\ \hat{c}_{kl} = Y_{..kl}$$

The mechanics of the maximum likelihood method are illustrated by a sample of 15 cows. The mature equivalent records and other necessary information are in Table 32 from which the c_{kl} equations can be written. For instance, the c_{11} equation is

$3(\mu + g_1) + a_1 + a_2 + a_3 + 3_{f4} + 4.5\ c_{11} = 1425$, where $(\mu + g_1)$ stands for the group of cows born in 1949, a_1 for the year of freshening 1951, c_{11} for the first cow of group 1 by year of birth. The coefficient, 3, of $(\mu + g_1)$ because c_{11} had three records and belonged to the group g_1. The coefficient, 1, of a_1, a_2, and a_3 comes from c_{11} having one

Table 32 Sample of records to illustrate method of maximum likelihood

Year of birth	Cow number	Inbreeding per cent	Lb of fat in freshening			Sum of records of c_{kl}
			1951 a_1	1952 a_2	1953 a_3	
1949	c_{11}	4	496	516	413	1425
	c_{12}	4	353	382		735
	c_{13}	0	440	405	340	1185
	c_{14}	0	327	437		764
	c_{15}	8	376			376
1950	c_{21}	8		449	371	820
	c_{22}	8		303	204	507
	c_{23}	0		381		381
	c_{24}	0		586	566	1152
	c_{25}	4		436	400	836
1951	c_{31}	4			459	459
	c_{32}	8			485	485
	c_{33}	4			320	320
	c_{34}	8			464	464
	c_{35}	0			439	439
Sum of records of a_i			1992	3895	4461	10348

record in each of those years. She had three records, and her inbreeding coefficient was 4 per cent; therefore, the coefficient of f_4 is 3. The coefficient of all other c_{kl}'s is zero. The coefficient, 4.5, of c_{11} is $(n_{..kl} + \frac{\sigma_e^2}{\sigma_c^2})$, or the total number of records for the first cow plus 1.5. The right hand side is 1425, the sum of the three records of c_{11}. Table 33 shows the 15 c_{kl} equations.

The rest of the necessary equations can be formed by summing the appropriate terms in Table 33. The $(\mu + g_1)$ equation then is $11(\mu + g_1) + 5a_1 + 4a_2 + 2a_3 + 5f_0 + 5f_4 + 1f_8 + 3c_{11} + 2c_{12} + 3c_{13} + 2c_{14} + 1c_{15} + 0c_{21} + \ldots\ldots + 0c_{35} = 4485$. The coefficient of $(\mu + g_1)$ is 11 because the cows belonging to this group made a total of 11 records; of the 11 records five were made in the year a_1, five by cows with an inbreeding coefficient of 4 per cent, and three of them by c_{11}, etc. The right hand side is the sum of the 11 records. The $(\mu + g_k)$, a_i, and f_j equations are given in Table 34. Since the necessary terms for the c_{kl}'s in these equations can be read by going down the corresponding columns in Table 3, they will not be written down again.

It is not necessary to solve all 24 of the equations because the c_{kl} and $(\mu + g_k)$ equations can be absorbed into the a_i and f_j equations. The absorption of the c_{kl} equations can be facilitated if two new tables are prepared. Table 35 is formed by taking each number, n, except the c_{kl}'s, in Table 33 and replacing it by

$$\frac{(n)\, n_{..kl}}{n_{..kl} + \frac{\sigma_e^2}{\sigma_c^2}}$$

Table 33 Cow equations for illustrative sample

Cow	$\mu + g_1$	$\mu + g_2$	$\mu + g_3$	a_1	a_2	a_3	f_0	f_4	f_8	c_{k1}	R.H.S
c_{11}	3	0	0	1	1	1	0	3	0	4.5	1425
c_{12}	2	0	0	1	1	0	0	2	0	3.5	735
c_{13}	3	0	0	1	1	1	3	0	0	4.5	1185
c_{14}	2	0	0	1	1	0	2	0	0	3.5	764
c_{15}	1	0	0	1	0	0	0	0	1	2.5	376
c_{21}	0	2	0	0	1	1	0	0	2	3.5	820
c_{22}	0	2	0	0	1	1	0	0	2	3.5	507
c_{23}	0	1	0	0	1	0	1	0	0	2.5	381
c_{24}	0	2	0	0	1	1	2	0	0	3.5	1152
c_{25}	0	2	0	0	1	1	0	2	0	3.5	836
c_{31}	0	0	1	0	0	1	0	1	0	2.5	459
c_{32}	0	0	1	0	0	1	0	0	1	2.5	485
c_{33}	0	0	1	0	0	1	0	1	0	2.5	320
c_{34}	0	0	1	0	0	1	0	0	1	2.5	464
c_{35}	0	0	1	0	0	1	1	0	0	2.5	439

Table 34 Group, year, and inbreeding equations for illustrative sample

	$\mu + g_1$	$\mu + g_2$	$\mu + g_3$	a_1	a_2	a_3	f_0	f_4	f_8	R.H.S
g_1	11	0	0	5	4	2	5	5	1	4485
g_2	0	9	0	0	5	4	3	2	4	3696
g_3	0	0	5	0	0	5	1	2	2	2167
a_1	5	0	0	5	0	0	2	2	1	1992
a_2	4	5	0	0	9	0	4	3	2	3895
a_3	2	4	5	0	0	11	3	4	4	4461
f_0	5	3	1	2	4	3	9	0	0	3921
f_4	5	2	2	2	3	4	0	9	0	3775
f_8	1	4	2	1	2	4	0	0	7	2652

Table 35 Factors for absorption of the c_{kl} equations into the $(\mu + g_k)$ and f_j equations

Cow	$\mu + g_1$	$\mu + g_2$	$\mu + g_3$	a_1	a_2	a_3	f_0	f_4	f_8	R.H.S.
c_{11}	2.0000			0.6667	0.6667	0.6667		2.0000		950.05
c_{12}	1.1429			0.5714	0.5714			1.1429		419.98
c_{13}	2.0000			0.6667	0.6667	0.6667	2.0000			790.04
c_{14}	1.1429			0.5714	0.5714		1.1429			436.55
c_{15}	0.4000			0.4000					0.4000	150.40
c_{21}		1.1429			0.5714	0.5714			1.1429	468.55
c_{22}		1.1429			0.5714	0.5714			1.1429	289.70
c_{23}		0.4000			0.4000		0.4000			152.40
c_{24}		1.1429			0.5714	0.5714	1.1429			658.25
c_{25}		1.1429			0.5714	0.5714		1.1429		477.69
c_{31}			0.4000			0.4000		0.4000		183.60
c_{32}			0.4000			0.4000			0.4000	194.00
c_{33}			0.4000			0.4000		0.4000		128.00
c_{34}			0.4000			0.4000			0.4000	185.60
c_{35}			0.4000			0.4000	0.4000			175.60

The quantity of $n_{..kl}$ is the total number of records made by each cow in the corresponding c_{kl} column. Table 35 is used for absorption of the c_{kl} equations into the $(\mu + g_k)$ and the f_j equations. Table 36 is used to absorb the c_{kl} equations into the a_i equations and is formed by replacing each number, n, except the c_{kl}'s, in Table 33 by

$$\frac{n}{n_{..kl} + \frac{\sigma_e^2}{\sigma_c^2}}$$

The reduced equation for $(\mu + g_1)$ with the c_{kl} equations absorbed is $4.3142\ (\mu + g_1) + 2.1238\ a_1 + 1.5238\ a_2 + 0.6666\ a_3 + 1.8571\ f_0 + 1.8571\ f_4 + 0.6000\ f_8 = 1737.98$. The coefficient of $(\mu + g_1)$, 4.3142, is 11 (the element of $(\mu + g_1)$ in Table 34) minus the sum of the elements of Table 35 for the cows in the $(\mu + g_1)$ column. The coefficient of a_2, 1.5238, is calculated by taking the element, 4, of a_2 in the $(\mu + g_1)$ equation of Table 34 and subtracting the sum of the terms in column a_2 for the cows which had records in the year a_2 and also belonged to the $(\mu + g_1)$ group.

The right hand side, 1737.98, is calculated by summing the right hand sides in Table 35 for those cows belonging to the $(\mu + g_1)$ group and subtracting this sum from the right hand side of the $(\mu + g_1)$ equation in Table 34. The f_j equations in Table 37 are formed similarly. The a_i equations in Table 37 are calculated the same way, except that Table 36 is used instead of Table 35.

The equations in Table 37 do not have a unique solution. However, differences among the years and among the classes of inbreeding can be estimated. In this case a_3 and f_0 were the bases of comparison. Then, the constants obtained are the differences between a_3 and each of the

Table 36 Factors for absorption of the c_{kl} equations into the a_i equations

Cow	$\mu + g_1$	$\mu + g_2$	$\mu + g_3$	a_1	a_2	a_3	f_0	f_4	f_8	R.H.S.
c_{11}	0.6667			0.2222	0.2222	0.2222		0.6667		316.64
c_{12}	0.5714			0.2857	0.2857			0.5714		209.99
c_{13}	0.6667			0.2222	0.2222	0.2222	0.6667			263.31
c_{14}	0.5714			0.2857	0.2857		0.5714			218.27
c_{15}	0.4000			0.4000					0.4000	150.40
c_{21}		0.5714			0.2857	0.2857			0.5714	234.27
c_{22}		0.5714			0.2857	0.2857			0.5714	144.85
c_{23}		0.4000			0.4000		0.4000			152.40
c_{24}		0.5714			0.2857	0.2857	0.5714			329.13
c_{25}		0.5714			0.2857	0.2857		0.5714		238.85
c_{31}			0.4000			0.4000		0.4000		183.60
c_{32}			0.4000			0.4000			0.4000	194.00
c_{33}			0.4000			0.4000		0.4000		128.00
c_{34}			0.4000			0.4000			0.4000	185.60
c_{35}			0.5000			0.5000	0.4000			175.60

Table 37 Reduced equations, with c_{kl}'s absorbed

	$\mu + g_1$	$\mu + g_2$	$\mu + g_3$	a_1	a_2	a_3	f_0	f_4	f_8	R.H.S.
g_1:	4.3142	0	0	2.1238	1.5238	0.6666	1.8571	1.8571	0.6000	1737.98
g_2:	0	4.0288	0	0	2.3144	1.7144	1.4572	0.8572	1.7144	1649.41
g_3:	0	0	3.0000	0	0	3.0000	0.6000	1.2000	1.2000	1300.20
a_1:	2.1238	0	0	3.5842	-1.0158	-0.4444	0.7619	0.7619	0.6000	833.39
a_2:	1.5238	2.3144	0	-1.0158	6.4414	-1.5872	1.7905	1.1905	0.8572	1787.29
a_3:	0.6666	1.7144	3.0000	-0.4444	-1.5872	7.4128	1.3619	1.9619	2.0572	2067.15
f_0:	1.8571	1.4572	0.6000	0.7619	1.7905	1.3619	3.9142	0	0	1708.16
f_4:	1.8571	0.8572	1.2000	0.7619	1.1905	1.9619	0	3.9142	0	1615.68
f_8:	0.6000	1.7144	1.2000	0.6000	0.8572	2.0572	0	0	3.5142	1363.75

other levels of a_i, and similarly for f_0 and the inbreeding constants. Fixing these bases requires deletion of the a_3 and f_0 equations and elements in other equations, both rows and columns.

The solution to the equations in Table 37 then is: $(\mu + g_1) = 413.2$, $(\mu + g_2) = 435.2$, $(\mu + g_3) = 497.0$, $a_1 = 38.2$, $a_2 = 60.4$, $a_3 = 0$, $f_0 = 0$, $f_4 = -23.9$ and $f_8 = -52.8$. These are all in pounds of fat. Logically the inbreeding constants should be measured from the zero class, but perhaps the estimates for years should be in terms of deviations from the mean of all years. This is done by subtracting the mean of the years, 32.9, from each year. Then the year constants become: $a_1 = 5.3$, $a_2 = 27.5$, and $a_3 = -32.9$. The constants for the $(\mu + g_k)$'s are estimates of the average producing abilities of the cows belonging to each group under the average environment of the three years and also if they were inbred the average of the population.

This maximum likelihood method was used to estimate the effects of inbreeding on milk and fat yield with 586 records of 211 cows producing in the Michigan State University inbred Jersey herd from 1948 to 1964. Records prior to 1951 were made in California. Constants were fitted for 17 years.

The cows were classed in intervals of 3 per cent of inbreeding except that those with no inbreeding were left at zero and all those over 42 per cent were placed in one class. This made a total of 16 classes of inbreeding.

The 17 groups of cows were made according to when the cows were born. Group one was those cows born in 1945 and groups were numbered consecutively for each year up to 1962.

Estimates of repeatability. Intracow correlations from the data were near .4 and .5, repeatabilities used in the maximum likelihood

equations. Henderson et al. (1959) indicated the repeatability used depends on the choice of grouping; hence, the data were divided into groups by year of birth, and the results are shown in Table 38. Standard errors of the intraclass correlations were approximated by the method of Osborne and Patterson (1952).

Maximum likelihood estimates. Tables 39 to 41 show the solution of the maximum likelihood equations. Table 39 gives the estimates of the producing ability of the herd where the cows were inbred as much as they actually were and produced under an environment which was characteristic of an average for all years.

In Table 40 estimates of the average yearly environmental effects are recorded, and Table 41 gives the coefficients for the effect of inbreeding for each of the 16 classes. These inbreeding constants are measured from the zero class, and the environmental constants are measured from the mean deviation of all years.

Table 38 Analysis of variance for repeatability

Source of variation	d.f.	Mean squares ME milk	 ME fat	 Per cent fat	E.M.S.
Between groups	17	6339118	17617	.885118	E + 5.081C+33.023 G
Between cows/ groups	192	7825307	23087	.480307	E + 2.688C
Residual	397	2103753	6365	.115005	E
C = component of variance between cows		2128554	6221	.135901	
r = repeatability = $\frac{C}{C+E}$		.50±.03	.49±.03	.54±.03	

$$\sigma_r^2 = \frac{2\,(1+(n-1)r)^2\,(1-r)^2}{n\,(n-1)\,b}$$

n = average number of records = 2.688 per cow/group

b = d.f for between cows/groups

Table 39 Maximum likelihood estimates of group constants using repeatabilities of .50 and .40

Group (year of birth)	Number of cows	Number of records	Milk 0.50	Milk 0.40	Fat 0.50	Fat 0.40
1945	2	16	7729	7887	377	383
46	1	9	8354	8510	367	373
47	1	8	5574	5737	273	282
48	3	18	6580	6702	355	359
49	6	36	7198	7334	342	347
1950	11	60	7428	7637	381	388
51	5	8	7125	7331	403	412
52	9	23	6337	6924	341	352
53	21	53	7320	7431	386	391
54	14	41	7276	7387	373	378
55	17	38	6794	6880	363	366
56	26	83	7764	7843	415	417
57	25	46	6813	6880	358	360
58	22	52	6491	6538	356	355
59	14	39	6755	6812	372	373
1960	14	32	6422	6459	356	356
61	20	24	6099	6132	359	360

Table 40 Yearly environmental deviations from maximum likelihood with repeatabilities of .5 and .4

Year of calving	Number of records	Milk lb		Fat lb	
		0.50	0.40	0.50	0.40
1948	3	1314	1278	110	108
49	3	79	43	62	59
50	6	-715	-747	-9	-10
51	12	-717	-748	-31	-32
52	18	598	553	30	28
53	28	346	300	20	19
54	31	8	13	-5	-7
55	44	-810	-842	-44	-46
56	47	-64	-80	-15	-15
57	48	-9	-22	-11	-11
58	54	-60	-56	-9	-9
59	53	-222	-187	-24	-22
1960	57	239	288	5	7
61	44	-4	-20	-15	-13
62	51	-328	-280	-41	-41
63	36	188	247	-14	-11
64	46	157	231	-9	-6

Table 41 Maximum likelihood estimates of inbreeding constants using repeatability values of .50 and .40

Inbreeding class (%)	Number of records	Milk lb		Fat lb	
		0.50	0.40	0.50	0.40
0	131	0	0	0	0
1-3	36	113	111	2.6	2.5
4-6	31	-82	-79	-2.1	-2.0
7-9	14	-36	-34	-1.7	-1.5
10-12	43	-13	-16	-1.7	-1.6
13-15	21	-12	-11	-6.8	-7.3
16-18	13	38	38	3.0	3.8
19-21	23	54	53	2.9	2.9
22-24	36	58	57	3.2	3.0
25-27	53	33	30	2.4	2.5
28-30	65	-22	-20	-11.0	-10.1
31-33	35	-19	-18	-1.9	-1.9
34-36	38	-23	-20	-2.7	-2.7
37-39	24	-14	-15	-.5	-.5
40-42	17	-65	-65	-1.8	-1.8
43	6	-132	-130	-6.3	-7.0

DISCUSSION

Mean and variation. As the mean increases the variance tends to increase; therefore, a fraction often relates the standard deviation to the mean of the sample as a fraction of the sample mean, the resulting statistic being the relative standard deviation or coefficient of variation. Results from the several characteristics can be compared more meaningful by the relative variation since many of the measurements did increase with the age of the animal and since they so diverse in mean and variance.

Table 42 lists the means, standard deviations, and coefficients of variation in per cent for each character from three months through fourth parity. Since the coefficient of variation is a ratio of two averages having the same unit of measurement, it is itself independent of the unit employed. Thus, it is in standard measure whether inches, feet, or centimeters are used for the original measurement.

Figures 1 through 7 show graphs of the means, standard deviations, and coefficients of variation listed in Table 42. The coefficient is informative and useful in the presence of the mean and standard deviation because an increase in the coefficient can be due to a rising standard deviation or a falling mean. Likewise a saw-tooth appearance of the coefficient curve may result from irregularities in either the mean or standard deviation or both. The mean weight and wither height are compared to the Ragsdale standards for Jersey cattle, (Petersen 1950).

The animals used in this study were slightly lighter at birth, at twelve months of age, and at first and second parity than the average Jerseys reported by Ragsdale. However, the average weight at three, six,

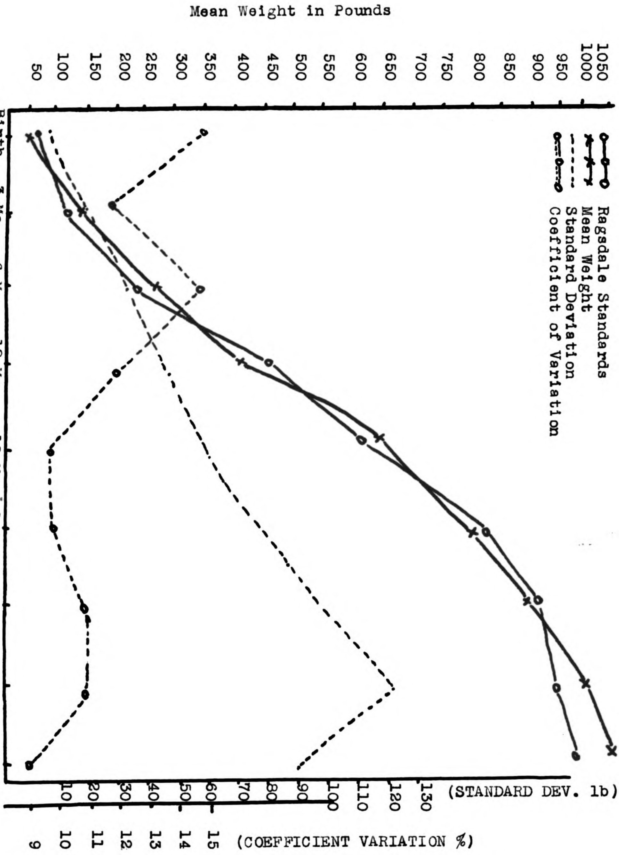
Table 42 Means, standard deviations, and coefficients of variation for each characteristic at each age

Characteristic		Age (Months)				Parity			
		3	6	12	18	1st*	2nd*	3rd*	4th*
Weight (lb)	$\bar{X}$	132	247	441	619	800	941	1032	1071
	S.D.	16.8	35.8	49.5	62.8	77.4	102.3	124.4	90.4
	C.V.	12.7	14.5	11.2	10.1	9.7	10.9	12.1	8.5
Wither ht (cm)	$\bar{X}$	79	91	106	115	122	125	127	128
	S.D.	3.0	4.0	4.2	4.1	3.3	3.1	3.2	2.5
	C.V.	3.9	4.4	3.9	3.6	2.7	2.5	2.5	1.8
Chest cir. (in)	$\bar{X}$	35	42	53	60	65	69	71	72
	S.D.	2.0	2.6	2.5	2.5	2.7	2.6	3.1	2.7
	C.V.	5.8	6.3	4.7	4.1	4.1	3.7	4.4	3.7
Chest depth (cm)	$\bar{X}$	35	43	54	60	66	69	71	72
	S.D.	2.0	2.2	2.2	2.4	2.4	2.6	2.2	2.3
	C.V.	5.6	5.1	4.1	4.0	3.6	3.7	3.1	3.2
Withers to hips (cm)	$\bar{X}$	49	60	74	81	89	94	96	98
	S.D.	3.1	3.8	4.1	3.5	4.3	4.6	4.9	4.1
	C.V.	6.3	6.4	5.6	4.4	4.8	4.9	5.1	4.2
Withers to pins (cm)	$\bar{X}$	71	87	108	119	130	137	140	143
	S.D.	5.6	7.3	5.3	4.6	5.1	5.0	4.8	4.1
	C.V.	7.8	8.2	5.0	3.8	4.0	3.6	3.4	2.9
Hips to pins (cm)	$\bar{X}$	23	28	34	38	41	44	45	45
	S.D.	3.8	1.5	1.7	1.8	2.0	2.0	1.4	1.7
	C.V.	16.4	5.4	5.1	4.8	4.8	4.6	3.0	3.9

* Weights and measurements taken 3 months after each calving.

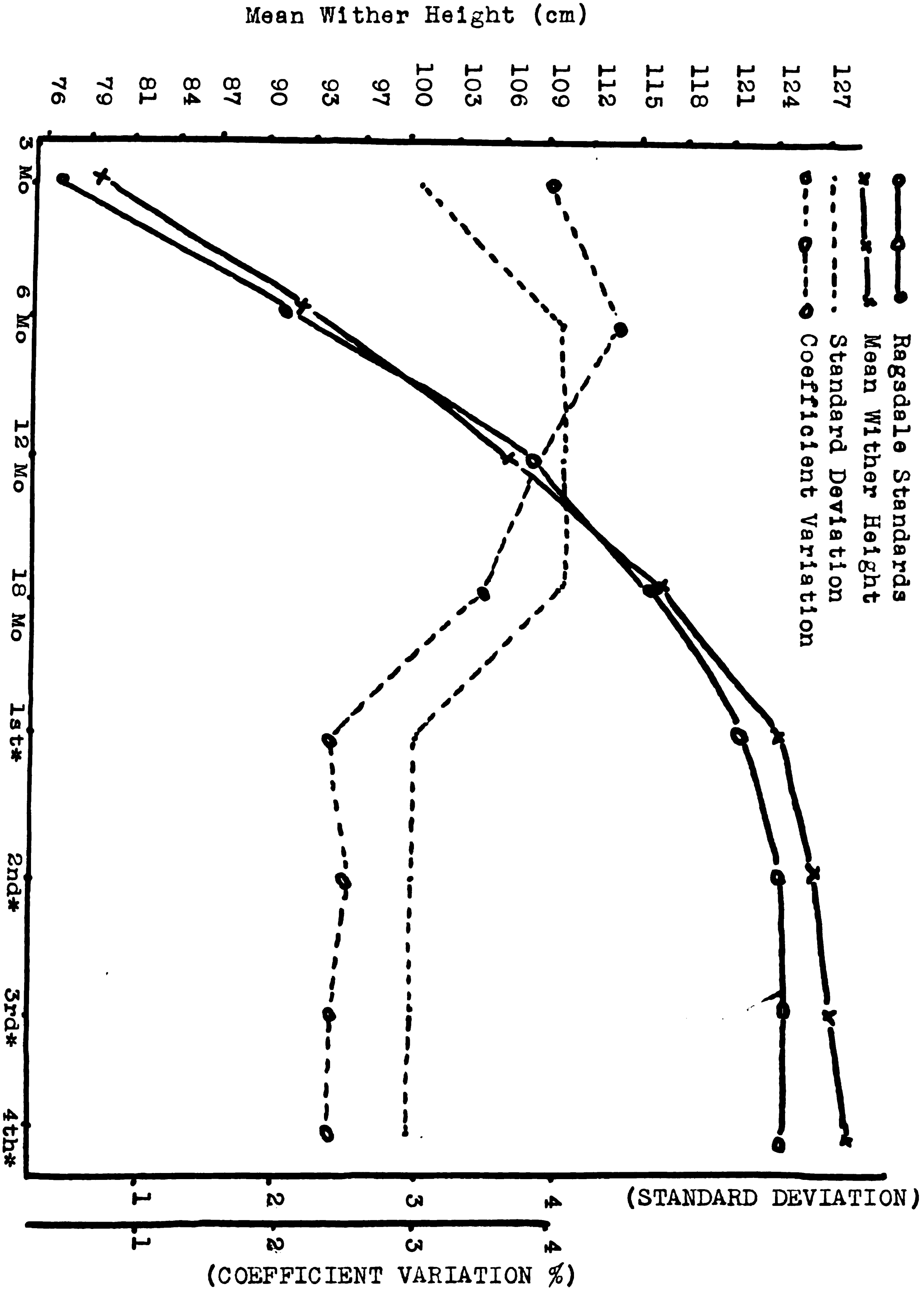
Parity	Av. age at measurement
1	30 months
2	44 months
3	56 months
4	72 months

Figure 1. Graph of average weight, standard deviation and coefficient of variation from birth to fourth lactation



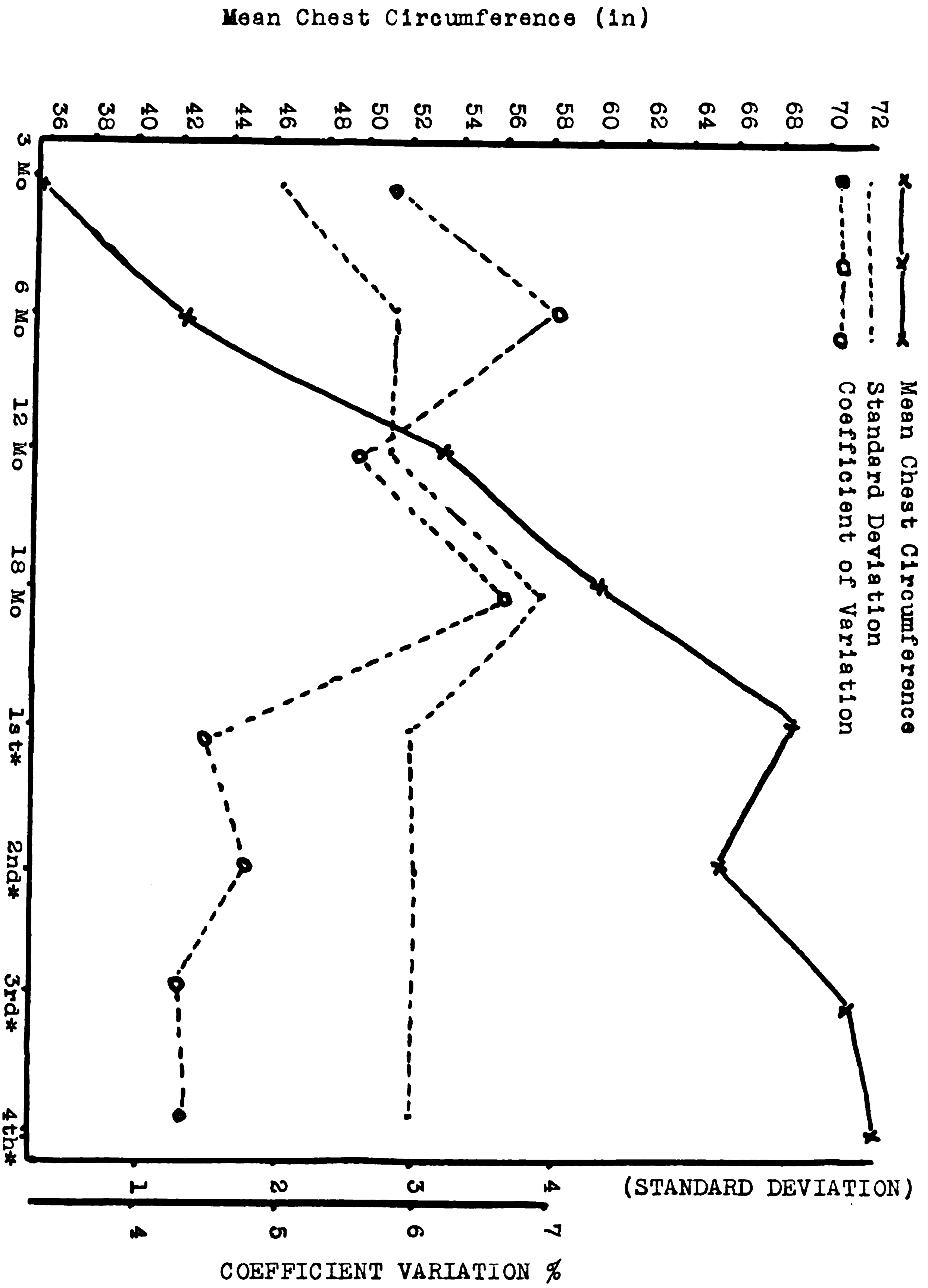
*Measurements taken 3 months after calving

Figure 2. Graph of average wither height, standard deviation, and coefficient of variation from three months to fourth lactation



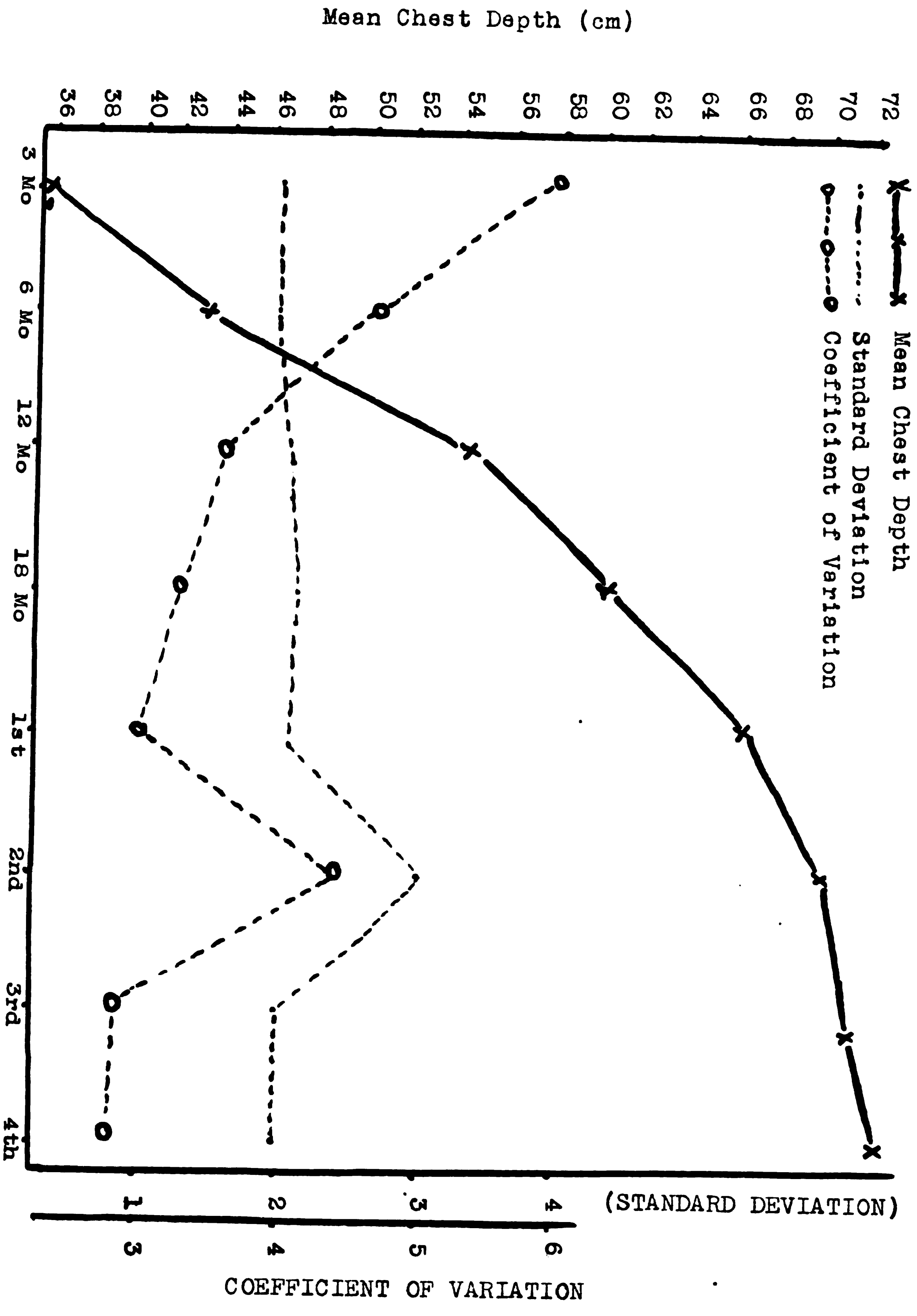
*Measurements taken 3 months after calving

Figure 3. Graph of average chest circumference, standard deviation, and coefficient of variation from three months to fourth lactation



*Measurements taken 3 months after calving

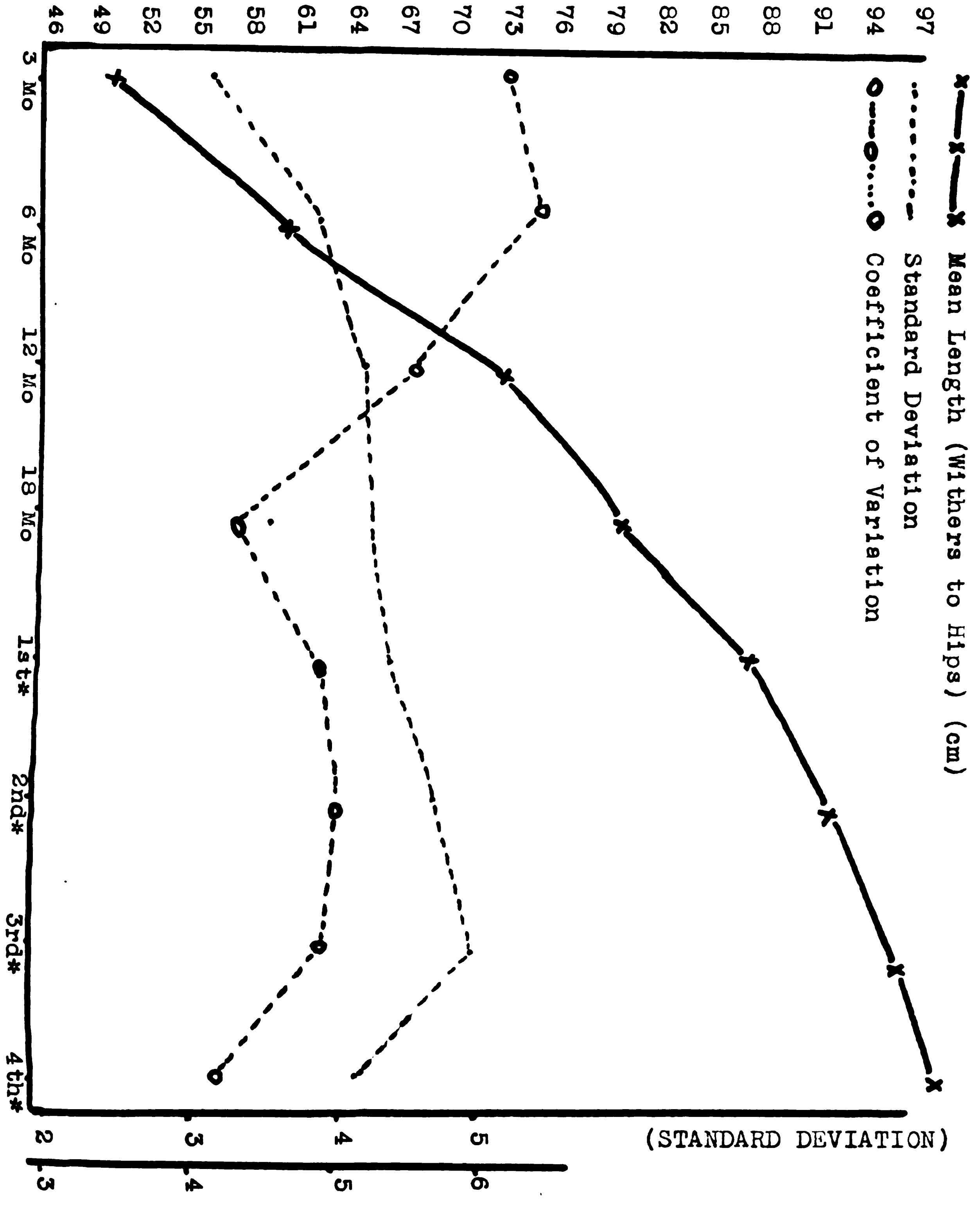
Figure 4. Graph of average chest depth, standard deviation, and coefficient of variation from three months to fourth lactation



*Measurements taken 3 months after calving

Figure 5. Graph of average length (withers to hips), standard deviation, and coefficient of variation from three months to fourth lactation

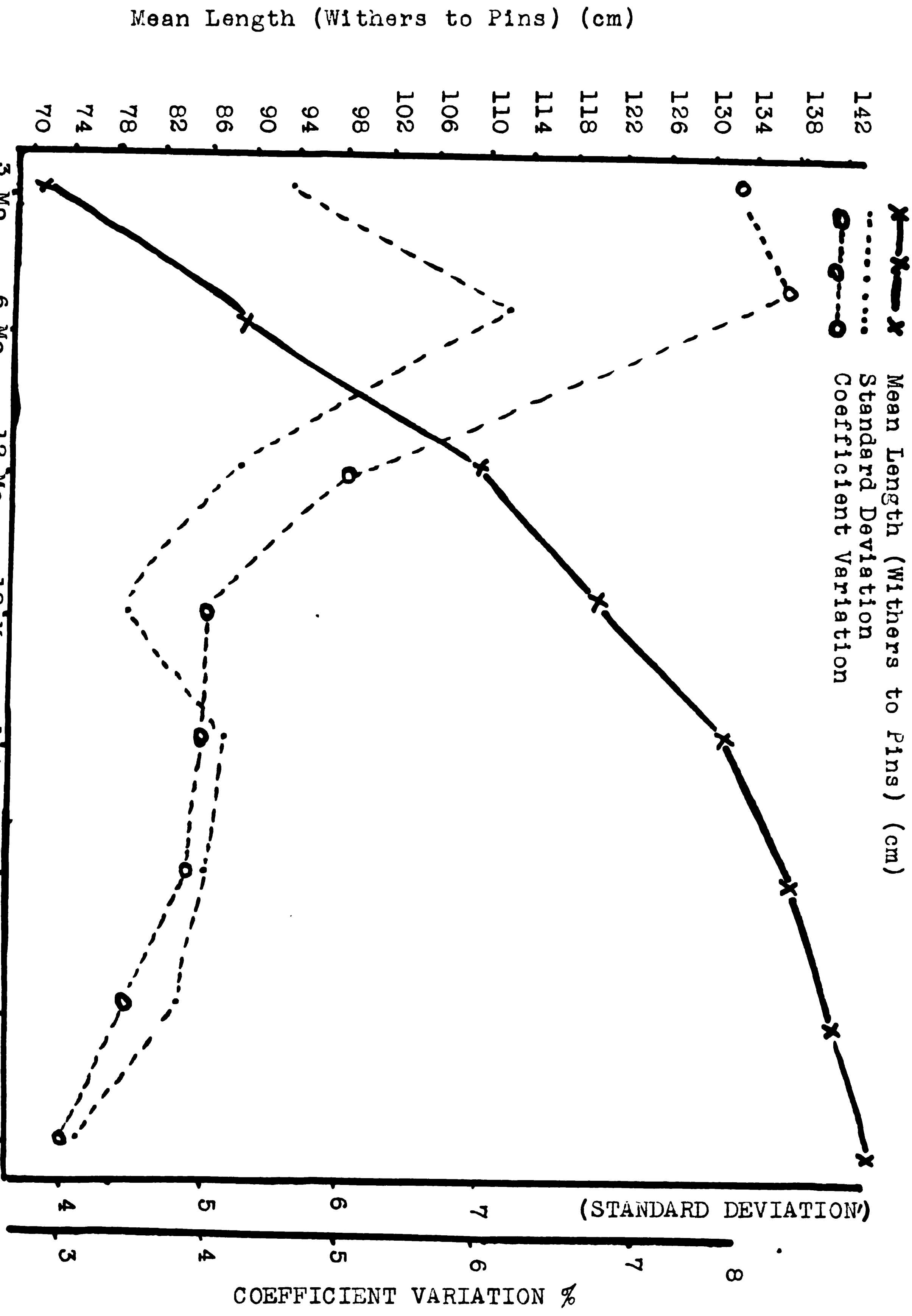
Mean Length (Withers to Hips) (cm)



COEFFICIENT VARIATION %

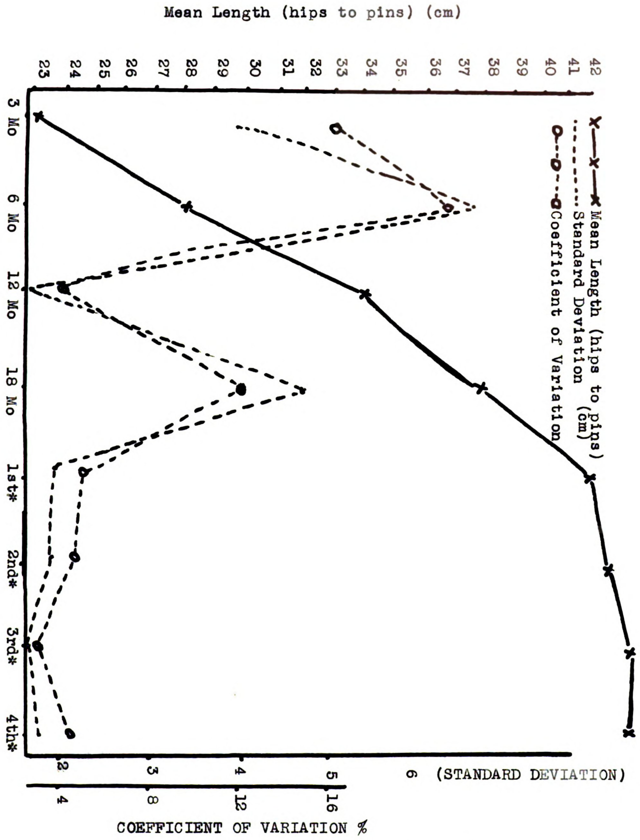
*Measurements taken 3 months after calving

Figure 6. Graph of average length (withers to pins), standard deviation, and coefficient of variation from three months to fourth lactation



*Measurements taken 3 months after calving

Figure 7. Graph of average length (hips to pins), standard deviation, and coefficient of variation from three months to fourth lactation



*Measurements taken 3 months after calving

and eighteen months was somewhat more than the standards. This increase seemed even more pronounced at third and fourth parity. The animals used in this study were slightly heavier than the average Jersey.

The measurement taken at the withers is a skeletal measurement and is not influenced by condition of the animals. The comparison of the average wither height for this herd with those reported by Ragsdale support the hypothesis that these cows were on the average larger than the average Jersey.

Mean weight and mean chest circumference tended to increase from birth to fourth parity; however, the rate of increase after first parity was somewhat less than from birth to 18 months of age. These two measurements are affected directly by the condition of the animal, whereas the skeletal measurements such as wither height and length from withers to pins are relatively free of condition.

The skeletal measurements tended to increase at a faster rate from 3 months to 18 months of age than did weight and chest circumference. However, after 18 months the rate of increase in skeletal measurements was somewhat less than the increase in weight and chest circumference during the same age period. This same trend was true in most of the skeletal measurements.

The coefficients of variation for each of the body measurements were generally largest at three to six months of age and decreased to values of 2.5 to 4.5 per cent at parity for each of the measurements except body weight. For body weight the trend was the same, but the coefficient was about four times greater than for the other measurements.

In most cases the decrease in the coefficient of variation was due to the increase in the mean, the standard deviation changing less as age increased from birth to fourth parity. The coefficients of variation for birth weight found from these data were about one to two per cent higher than those reported by Nelson (1942) from the Iowa Holstein herd. Although he reported data from two, three, four, and five year old animals rather than by parity, the ages should be close enough for meaningful comparisons. The same trend was found for the coefficients of variation for wither height, body length, chest depth, and heart girth. In every case the average measurement for the Iowa data was larger and the coefficient of variation smaller.

Body weight. Since 1951, 265 heifer calves on which birth weight has been recorded have been born in the herd. Of these, 200 were from the original inbred herd and 65 were born in the type herd which was incorporated into the plans in 1955. The average birth weight of these calves was 52 lb with a standard deviation of 8.2 lb. The inbreeding coefficient ranged from zero to 50 per cent with an average of 31 per cent.

The intra-sire regression of birth weight on the inbreeding of the calf was -.03±.05 which indicates a decrease of approximately .03 of a pound in birth weight with each increase of one per cent inbreeding. However, when the data were analyzed separately for the inbred herd, the coefficient was +.026±.06 indicating large birth weight with increasing inbreeding, although the regression coefficient was positive it was not statistically different from zero. The type herd analyses indicated a coefficient of -.215±.11 which approached significance.

The effect of inbreeding on weight at three months and over is shown in Table 4. The intra-sire regressions show that on the average the more intense the inbreeding the less the weight at the various ages.

This is true for all ages except three months for the inbred herd and fourth parity in the type herd. However, when the data were combined, the coefficients were all negative. The only coefficients that are statistically significant are those at 12 and 18 months. However, the fact that all of them are negative, for the combined data, makes it possible to attach some significance to them, since if they were all the result of chance we would have expected some of them to be positive.

In Tables 2 and 3 are the intra-sire regression coefficients for the inbred and type herd respectively. The most obvious conclusions from these separate tables are:

(a) the inbred herd had positive coefficients at birth and three months and from 6 months to 4th parity negative coefficients, whereas the type data yielded negative regression estimates at each age.

(b) the regression values tended to be larger for the type herd after 18 months of age than for the inbred herd while at 6, 12, and 18 months of age the coefficients calculated from the inbred data were larger.

The regression coefficients in Table 4 increase from birth up to 18 months of age and then were somewhat irregular from 1st to 4th parity, however the average weight from birth to 4th parity increased steadily from 52 lb to 1071 lb (Table 42). The increase of the regression coefficients from birth to 3 months to 6 months etc. as compared to the increase in weight for these same periods, show trends more clearly than do the regression coefficients themselves. For example the regression coefficients increase by a factor of two from birth to 3 months, by a factor of four from three months to six months, and by a factor five from 6 months to 12 months. Whereas, the average weight for these same periods increases by factors of 3, 2, and 2. A study of these values indicates that not only does increased inbreeding decrease birth weight but also the growth rate decreases from birth to 18 months. The weight after 18 months still decreases for increased inbreeding, but the rate of growth is faster for the higher inbreds than for those animals with lower coefficients of inbreeding. These results indicate that inbreeding decreases weight and the rate of growth up to 18 months but the inbreds will tend to reach the same weight as non-inbreds.

Wither height. The intra-sire regression coefficients indicate that inbreeding had very little effect on wither height at the various ages. As shown in Tables 2, 3, and 4 only the coefficients at 18 months for the inbred herd and the combined data were different from zero, most other values were negative but smaller than their standard errors. The same trend regarding growth rate can be seen, namely the rate of growth is slower up to 18 months of age and then tends to increase with age up to 4th parity.

Other measurements. The effect of inbreeding on the other measurements, (Tables 2, 3, and 4) are really not much different from the effects on wither height. In the main the coefficients were negative for most ages but smaller than their standard errors. The general trend in growth rate indicates slower rate up to 18 months and then a faster rate of growth up to 4th parity. At 18 months the regression coefficients for weight, wither height, withers to hips, withers to pins, and hips to pins were large enough to be different from zero, whereas at the other ages none of the coefficients were statistically significant.

Loss of females. The average inbreeding of the 37 calves which

died during the first three months of birth--most deaths occurred shortly after birth--was 32 per cent as compared to the average of 29 per cent for all calves born in the inbred herd, (Table 29). The difference of 3 per cent has a standard error of about 4 per cent indicating no difference between the inbreeding of these two groups. However, the trend from 1959 through 1966 might suggest a real difference between average inbreeding of the early deaths and those animals that did not die during the first three months.

The inbreeding coefficient of animals leaving the herd between 12 months of age and first calving was about 5 per cent higher on the average than the inbreeding coefficient of female calves born. No definite conclusions can be drawn from these data except that the losses are higher than would be expected from a herd of this size. Whether these losses are a result of inbreeding or management or both may not be answerable.

The results from the type data, (Table 30), are similar to the inbred data. The average inbreeding of the calf losses during the first three months was about 2 per cent higher than the average inbreeding of calves born and female losses between 12 months and first calving about 2 per cent lower.

Type rating. The type classification at Michigan State University was not official, but each type class was intended to mean, as nearly as the classifiers could make it, the same thing as the corresponding official class. Each type class was subdivided into low, medium and high. Thus, one unit of type as used in the analysis is one-third of a class. The regression coefficients were nonsignificant at all ages, but the fact that most were negative indicates a trend similar to that for the body measurements and should not be ignored. The regressions were small, averaging around -.01 (.003 of a class) per 1 per cent of inbreeding. If effects were linear, this would mean that animals 22 per cent inbred (the average F for 2nd parity of the combined data) would average about 0.07 of a class lower than if outbred. The effects of inbreeding did not appear to change with age.

The data for the type herd yielded positive regression coefficients for each age group and for the inbred herd negative coefficients. For each of these separate analyses, the regression coefficients were about three times as large as for the combined data. The results are not surprising since the type herds were selected for body conformation; however, some bias on the part of the classifier may have inflated these coefficients.

Production. Intra-sire regressions of -21.4 lb of milk, -.75 lb of fat and +.005 per cent fat, for each increase of 1 per cent inbreeding are a little lower than those reported from other workers. Most of the investigations, including this one, have found a slightly positive regression of fat per cent on inbreeding. That environmental conditions which affect milk and fat production adversely tend to raise fat percentage. Perhaps this is enough to explain the apparent but very slight effect of inbreeding on fat percentage.

Although none of the regression coefficients was significantly different from zero, the coefficients increased from first through the third parity and were the smallest for the fourth lactation. For the four lactations the average coefficient of inbreeding ranged from 17.6 to 19.4 and the average for all records was 17.8.

The results of the inbred and type herds when compared separately showed the regression coefficients to be -26.4, -1.14, and +.002 for milk, fat, and fat per cent, respectively, for the inbred herd and -24.1, -.58, and +.011 for the type herd. The average inbreeding coefficient was higher for the inbred herd than for the type herd, (25.9 vs. 3.5); however, the average production was also greater for the inbred herd. The inbred herd's average ME 305-day production was 8548 lb milk and 479 lb fat and for the type herd the production was 6919 lb milk and 377 lb fat.

SUMMARY

Data collected over a 15-year period from the Michigan State University Jersey herd were used to study the effect of inbreeding on weight, wither height, heart girth, chest depth, body length, type, and production. The inbreeding ranged from zero to 50 per cent and averaged about 30 per cent. The number of animals used in each analysis varied but at the most, 265 birth weights were available.

Since the type herd was brought into the study in 1955 and was unrelated and less inbred than the original herd, most of analyses was done for each herd separately as well as for the combined data.

The regression coefficients were generally negative although only a few were statistically significant indicating that inbreeding had a depressing effect on the body measurements observed in this herd. The rate of growth was slower for inbreds than non-inbreds from birth to 18 months and then tended to increase after 18 months.

The results show a tendency for inbreeding to cause poorer type although none of the coefficients were significant. However, when the two herds were analyzed separately, the regression coefficients were positive for the type herd and negative for the inbred herd.

Intra-sire regressions of the average of each cow's records were -21±13 lb of milk, -.75±.74 lb of fat, and .005±.004 per cent milk fat for each increase of 1 per cent in inbreeding.

Maximum likelihood method was used to estimate simultaneously the effect of years, changes in average real producing ability of the herd, and the effect of inbreeding. The real producing ability of the herd appeared to have remained unchanged over the years studied. The maximum likelihood estimates of inbreeding effects indicated a decline in production up to inbreeding coefficients of 12 and then an increase in production for animals inbred from 16 to 30 per cent and large negative estimates for animals inbred greater than 30 per cent.

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APPENDIX

Maximum likelihood program for absorption of cow equations and ML estimates

```
JOB,291809,MAXLI,4.DAYTON,ARTHUR D.
FTN,L,X,X,A,R
      PROGRAM MAXLI
      Ⓒ
      DIMENSION NCOW(69),Y(74),Z(69.5),SUM(74),SUMC(74),IBUF(10)
      DOUBLE PRECISION X,Y,Z,A,B,SUM,SUMC,ACK,BCK
      I=ID=IBUF=0
      Ⓐ
    5 READ 10,ID,IBUF
   10 FORMAT(R2,R6,9A8)
      IF(ID.EQ.8H000000EN)60,15
   15 IF(ID.EQ.8H000000  )40,20
   20 I=I+1
      DECODE(80,25,IBUF)(X(I,J),J=1,33)
   25 FORMAT(3X40D2.0)
      READ 25,(X(I,J),J=34,69)
      READ 30,(X(I,J),J=70,74)
   30 FORMAT(3X,D6.0,D5.0,D4.1,D6.0,D5.0,D1.0,D2.0)
      DO 35 J=1,74
   35 SUM(J)=SUM(J)+X(I,J)
      GO TO 5
   40 NCOW(I)=NCOW(I)+1
      DECODE(80,45,IBUF)(Y(J),J=1.69)
   45 FORMAT(3X69D1.0)
   50 READ 30,(Y(J),J=1,69
      ACK=ACK+A
      BCK=BCK+B
      A=A/B
      DO 55 J=1,74
      S(I,J)=X(I,J)-Y(J)*A
   55 SUMC(J)=SUMC(J)+Y(J)
      GO TO 5
   60 PRINT 61,I,ACK,BCK,NCOW
   61 FORMAT(*1NUM EQ=*I3*  SUM OF MULTIPLIERS=*F10.0,10X*SUM
                             OF DIVISOR
     1S=*F10.0/*0NUMBER OF COW EQ FOR EACH EQ*/(45I3/))
      PRINT 62,SUM
   62 FORMAT(*0SUM OF EQS BEFORE MODIF*/1H027F5.0/1H027F5.0/
     1 1H015F5.0/1H05F15.1)
      PRINT 63,SUMC
   63 FORMAT(*0SUM OF COW EQS*/1X27F5.0/1H027F5.0/1H027F5.0/
     1 1H015F5.0/1H05F15.1)
      PRINT 70
   70 FORMAT(*-REDUCED EQNS*)
      CALL PRSL1B(69)
```

```
      PRINT 75,((X(I,J),J=70,74),I=1,69)
   75 FORMAT(*-RHS*/(F27.8))
      PRINT 80,((X(I,J),J=70,74),I=1,69)
   80 FORMAT(*-RHS IN DBL PREC FORMAT*/(5D27.15))
      CALL DIN(X,Y,69,69,0,8HBIG           )
      PRINT 85
   85 FORMAT(*-INVERSE*)
      CALL PRSUB(69)
      PRINT 90
   90 FORMAT(*-INVERSE IN DBL PREC FORMAT*)
      CALL PRSUBD(69)
      CALL DMMUL(X,69,69,X(1,70),5,Z)
      PRINT 95,((Z(I,J),J=1,69)
   95 FORMAT(*-COEFFICIENTS*/(5F27.8))
      PRINT 100,((Z(I,J),J=1,69)
  100 FORMAT(*-COEFFICIENTS IN DBL PREC FORMAT*/(5D27.15))
      STOP
      END
 79RUN,3,5000,7
 END OF DATA
 7      SCOPE
 9LOAD
      ACK=BCK=0
      DO 3 J=1,74
A   3 SUM(J)=SUMC(J)=0
      DO 4 J21,69
      NUM(J)=J
    4 NCOW(J)=0
      PRINT 72
B  72 FORMAT (*-REDUCED EQNS IN DBL PREC FORMAT*)
      CALL PRSUBD(69)
C     COMMON/1/X(69,74),NUM(69)
```

```
      SUBROUTINE PRSUB(N)
      COMMON/1/X(69,74),NUM(69)
      DOUBLE PRECISION X
      DO 20 K=1,N,10
      L=K+9
      IF(L-N)10,10,5
    5 L=N
   10 PRINT 15,(NUM(J),J=K,L)
   15 FORMAT (I10,9I13)
      DO 20 I=1,N
   20 PRINT 25, (X(I,J),J=K,L)
   25 FORMAT(10F13.8)
      RETURN
      ENTRY PRSUBD
      DO 120 K=1,N,5
      L=K+4
      IF(L-N)110,110,105
  105 L=N
  110 PRINT 115,(NUM(J),J=K,L)
  115 FORMAT(I12,4I27)
      DO 120 I=1,N
  120 PRINT 115,(X(I,J),J=K,L)
  115 FORMAT(5D27.15)
      END
```