INHERITANCE OF MATERNAL EFFECTS
IN BEEF CATTLE

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

The estimate of all cattle in Oklahoma as of January 1, 1961 is approximately three and a half million head. Of this total number it is estimated that the number of beef cows and heifers (two years old and older) is approximately 1,490,000 head.

In the past decade there has been a trend in the beef cattle business toward the marketing, slaughter, and consumption of fat cattle at considerable younger ages. As a result many steer operators have converted to a cow and calf operation. It is quite probable that there will be additional conversions to cow and calf operations in Oklahoma if the present market for younger fat cattle continues to exist.

In view of the number of beef cows in Oklahoma today, plus the probability of their numbers being increased rapidly in the future, the knowledge of and the selection for maternal effects in beef cows may be the most important economic trait that the cow and calf operator will need to consider.

Economists have estimated that about a thousand dollars are managed in each brood cow. This high capital invested in the beef cow could justify the spending of considerable time and effort by the cow and calf operator in selecting maternal effects. This is especially true if "the relative economic value of a trait" is to be considered as the first step in setting up a breeding program.

Data secured over a five-year period from five different herds in the northeastern section of Oklahoma are used in this study to estimate the heritability of maternal effects.

REVIEW OF LITERATURE

Approximately one hundred years ago Gregor Mendel, an Austrian monk, discovered that definite hereditary differences between individuals of a species exist. In further experiments he found that selected characteristics were transmitted by the parents to future generations in a definite manner and that he could use this newly acquired knowledge of outcome to add precision to his selection methods. Today these basic principles are used by animal breeders to make permanent improvement in their herds for traits that are of economic importance.

The manner in which the characteristics develop, segregate, and are transmitted from generation to generation is commonly called "Mendelian Inheritance." To be most meaningful, an animal breeder should have a real understanding of its physical background, its interpretations, and its application.

Bogart (1959), Lush (1945, 1948), and Snyder (1946) have discussed the physical background of Mendelian Inheritance, which can be summarized as follows: (1) The characteristics of an individual are influenced by paired genes located at similar positions on homologous chromosomes. These paired genes are called allelic genes.

(2) One member of a gene pair may dominate a situation more or less completely in the developed individual so that the other member of the pair is not outwardly expressed. This feature of inheritance is called cominance. It is commonly observed but is not universal. (3) The genes are organized into groups, each group forming a chromosome, which is visible in the nucleus of the cell. (4) As a result of reduction division in germ cell formation one member of each homologous pair of chromosomes is found in each daughter cell. (5) The distribution of the homologous chromosomes to the daughter cell is at random. (6) Previous to reduction division equal interchanges of chromatin material may take place between homologous pairs of chromosomes. This is called a chromosome crossover. Genes that are located on the same chromosome are called linked genes. (7) The chromosomes are always organized in a definite manner; each gene has a definite fixed position on the chromosome, and the genes are arranged in a linear series. (8) The genes may change (perhaps a chemical change) in such a way as to produce a different effect on the individual from its previous effect. These gene changes are called mutations. They represent a change in the structure of the gene. Mutations are rare occurrences (the mutation rate for most genes is something in the order of 1 per 100,000 to 1 per 1,000,000). (9) Care should be taken not to oversimplify the matter of genes and their behavior in inheritance. The genes themselves are probably very complex in structure. They are closely associated with the

cytoplasm of the cells, and the full development of the individual is the result of the interaction between the genes themselves, between the genes and the cytoplasm of the cells, and between the cells and their environment. The interaction, the interrelationship, between all of these forces causes the development of a new individual rather than the individual actions of separate genes. (10) Inheritance is the interaction between genes, cytoplasm, and environment.

After this basic acceptance as to the theory of genetics some of the early workers turned their attention to how this inheritance could be identified in individuals. Wright (1921) developed a system of path coefficients. Fisher et al. (1932) made a statistical interpretation of quantitative inheritance. They found that the heritable variance observable among any group of organisms may be regarded as the sum of the variances due the individual factors. The portion of the variance which is heritable may be easily estimated from the co-variances or mean products, of the measurements of related individuals, so that without being able to recognize any single factor there is a direct means of estimating their total contribution to the heritable variance.

Lush (1935), summarizing different papers on inheritance of productivity in farm livestock, concluded that most of us would hold that all characteristics are developmental, depending for their full expression upon the interaction of the genes with each other and with the environment as well. From this standpoint, highly hereditary characteristics are those in which most of the variance that we ordinarily see is due to differences in the genes that different individuals have. Slightly hereditary characteristics are those in which most of the variance ordinarily occurring is due to differences in the environment to which different individuals have been exposed. To aid in selection we must know, first, what portion of the observed variance is genetic in the narrow sense (this includes only those gene combination effects that can be expressed by some additive scheme), second, what portion of the variance is due to gene combination effects that cannot be expressed additively, and, third, what portion of the initial variance is purely environmental in origin. Only the genetic variance that can be expressed additively is subject to simple mass selection. Thus a definite numerical value for heritability is a description of the population from which it was derived and may not, without other knowledge, be safely applied to populations where the variations in environment or in heredity may be quite different. Whatley (1942) in his study of Poland-China swine stated that the degree of heritability of a characteristic is a measure of the amount of observed variance that can be attributed to the additive effects of genes. All methods of estimating heritability depend in some manner on the degree to which related individuals resemble each other more than unrelated ones do. Dickerson and Hazel (1944) reported that annual improvement from selection in a closed herd or breed is a ratio of the average genetic superiority of parents (compared with the unselected group from which they were chosen) to the average age of parents to which the offspring are born.

These basic principles indicate that the animal breeder can make permanent improvement in his breeding herd. The rate of genetic improvement expected from applying a definite breeding plan to a particular population is mathematically predictable provided certain biological, economic, and genetic constants are known. The scientific application of animal breeding consists of obtaining estimates of these constants and integrating them into the ultimate plan possible for each class of livestock. From this one can compute the improvement likely to result from various combinations of methods of selection and of mating systems. Then general plans having maximum effectiveness per unit of cost or per unit of time can be formulated and recommended for practical breeders.

The important biological parameters, such as (1) reproductive rates and (2) generation intervals, can be estimated from vital statistics of farm animals (Lindley *et al.* 1958).

The economic parameters, such as relative economic values of several characteristics in which improvement may be desired, can be estimated from market summaries and cost accounting records of farm livestock enterprises.

The genetic parameters, such as (1) heritability and (2) genetic correlation between characters, can be estimated from observed correlations between related individuals. Still others, such as (3) dominance and epistatic variance and (4) interaction between genotype and environment, can be estimated accurately by resorting to inbreeding, crossing inbred lines, comparing identical and fraternal twins or from any type of experiment designed expressly for the purpose in hand (Hazel, 1949).

Heritability Estimates

All methods of estimating heritability rest on the degree to which animals with similar genotypes resemble each other more than less closely related animals (Lush, 1940).

Most heritability estimates are computed by the paternal half-sib correlation method and the intra-sire regression of offspring on dam method. Lush (1948) presented a thorough discussion on the estimate of heritability by the paternal half-sib correlation method. The sire component of variance is needed to estimate the additive genetic portion of the variance. Under conditions of random mating, genetic values of half-sibs have a correlation of .25. The probability of joint transmission of combinations of non-allelic genes leads to the expectation that an epistatic effect requiring n non-allelic genes will be correlated $(1/4)^n$ between half-sibs. If epistasis is negligible and environmental correlations among half-sibs have been adequately discounted, the expected value of the sire component of variance is $1/4\sigma_G^2$ under random mating. The expected value of the mean square within sires is $3/4\sigma_G^2 + \sigma_E^2$. An estimate of heritability is $\frac{4\sigma_S^2}{\sigma_S^2 + \sigma_E^2}$.

Heritability estimates computed from the intra-sire regression of daughter's performance on the dams' performance is made merely by doubling the intra-sire regression coefficient computed by the least squares method. The intra-sire regression of daughter on dam is essentially a parent-offspring resemblance, but computing it on an intra-sire basis tends to automatically discount certain environmental contributions and any peculiarities of the mating system (Lush, 1940).

With the use of the two techniques for estimating heritability that were previously described, workers have reported heritability estimates for many traits in most classes of livestock. Some of the early studies reported in swine have been by Lush (1936), Whatley (1942), Hazel et al. (1943), and Nordskog et al. (1944). Studies in sheep have been reported by Hazel and Terrill (1945) and in dairy cattle by Lush and Arnold (1937) and Lush and Norton (1941).

In beef cattle Knapp and Nordskog (1946) made a study of records from 177 steer calves from 23 sires at the U. S. Range Experiment Station, Miles City, Montana. They estimated the relative effect of heredity on weights, gains, and efficiency of gains. Two methods were used, namely, the intra-class correlation obtained by analysis of variance and the sire-progeny regression obtained by covariance analysis. Heritabilities obtained from intra-class correlation for the various weights and gains were: birth weight, 23 per cent; weaning weight, 12 per cent; final feed lot weight, 81 per cent; gain in the feed lot, 99 per cent; and efficiency of gain, 75 per cent. Heritabilities obtained from sire-progeny regressions were: birth weight, 42 per cent; weaning weight, 0 per cent; final weight, 69 per cent; daily gain, 46 per cent; and efficiency of gain, 54 per cent. Where adjustments were made for differences in feeding of the sires each year, the heritabilities were found to be 34 per cent for birth weight, 30 per cent for weaning weight, and 94 per cent for final weight, 97 per cent for daily gain, and 48 per cent for efficiency of gain. Knapp and Nordskog stated that the estimates of heritability obtained from their work seemed to be a little higher than would be reasonable and that the cause or causes of these high estimates were not known.

Knapp and Clark (1950) reported revised heritability estimates based on the progeny of 64 to 110 Hereford sires. These studies were conducted at the U. S. Range Livestock Experiment Station, Miles City, Montana, in cooperation with the Bureau of Animal Industry and the Montana Agricultural Experiment Station. The following estimates were obtained by the half-sib correlation method: birth weight, 53 per cent; weaning weight, 28 per cent; final feed lot weight at fifteen months, 86 per cent; gain on feed, 65 per cent; weaning score, 28 per cent; slaughter steer grade, 45 per cent; carcass grade, 33 per cent; and area of eye muscle, 68 per cent. The estimate based on sire-offspring regression for final feed lot weight at fifteen months was 92 per cent, and for rate of gain in the feed lot it was 77 per cent. They reported that these figures indicate the relatively high influence of heredity in determing growth after weaning. Growth measures were more highly influenced by heredity than were measures of quality and conformation.

Koch and Clark (1955a) reported heritability estimates of 35 per cent for birth weight, 24 per cent for weaning weight, 21 per cent for gain from birth to weaning, 18 per cent for weaning score, 47 per cent for yearly weight, 39 per cent for gain from weaning to yearly age, and 26 per cent for yearling score. They further concluded that maternal environment had an important effect on birth weight, gain from birth to weaning, and weaning score. Maternal environment appeared to be of little importance for yearly gain and score. These estimates were based on the half-sib correlation technique.

Koch and Clark (1955b) in a continuation of their study of genetic and environmental relationships among economic characters of beef cattle reported heritability estimates based on offspring-dam and offspring-sire correlations. These estimates were on records of 4,234 dam-offspring pairs and 85 sire-offspring groups which were used in estimating correlations among characters and correlations between parent and offspring for various economic traits. Heritability estimates calculated from the regression of offspring on dam and progeny average on sire were, respectively: 44 and 35 per cent for birth weights; 11 and 25 per cent for weaning weights; 7 and 17 per cent for gain from birth to weaning; 16 and 15 per cent for weaning score; 43 per cent (offspring on dam) for fall yearling weight; 18 per cent for gain from weaning to fall yearling age; and 14 per cent for fall yearling score.

Shelby et al. (1955) studied data collected during ten years (1942-1951) of record of performance testing at the U. S. Range Experiment Station, Miles City, Montana. The data consisted of records on 635 steers from grade cows mated to 88 sires from nine lines. From the paternal half-sib correlation they reported the following heritability estimates: birth weight, 72 per cent; weaning weight, 23 per cent; and gain in the feed lot, 60 per cent.

Rollins and Wagnon (1956) made a genetic analysis of weaning weights in two experimental range herds of similar breeding. The herds were managed alike except that in one herd the cows were given supplementary feed during the fall and winter when the range was nutritionally deficient but that the cows in the other herd were not given any supplementary feed.

They reported a heritability estimate of 30 per cent for weaning weight. The experimental evidence indicated that the difference in the nutritional level of the two herds did not significantly influence the inheritance of weaning weight.

Anderson and Chambers (1957) used a total of 2,613 grade and purebred Hereford cattle to study (1) the relationship between the amount of pigmentation in the skin of the eyelids and the occurrence of cancer eye lesion, (2) the inheritance of the amount of lid pigmentation, and (3) the inheritance of susceptibility to cancer eye.

The amount of lid pigmentation was found to be highly heritable, and selection for an increased amount of pigmentation would be expected to reduce the incidence of lid lesions. This heritability estimate was .44 by the regression of offspring on dam. They reported further that because of the high heritability of this trait a breeder could select directly for lid pigmentation and decrease the amount of cancer of the eye lid.

Lindley et al. (1958) studied the reproductive performance of a purebred herd for the period from 1935 through 1952. They reported heritability estimates of reproductive performance as determined by the paternal half-sib intra class correlation method, the correlation between daughters and dams records, and the regression of daughters' records on dams' records. They reported that most of these heritability estimates were essentially 0. Cows more than ten years old declined rapidly in performance. All correlations and regressions of performance on age of cow were positive and significant. A rapid decline at the older ages caused the regressions to be curvilinear.

Maternal Effects

It is generally accepted that a cow influences birth weight, gain from birth to weaning, and weaning score by the genes she transmits and the maternal environment that she provides. This influence of maternal effect appears in two periods of the calf's life, first, during the prenatal period (conception to birth) and, second, during the period from birth to weaning. These maternal effects may be described as follows: (1) the amount of nutrients provided for the developing fetus, (2) the quantity of milk provided the calf during the preweaning period, (3) the amount of protection and desirable environment provided from birth to weaning by the offspring's dam.

Lush and Arnold (1937) studied 676 daughter and dam production records of the Iowa Cow Testing Association to find what share of the difference between single records was really due to permanent differences between the individual cows and what share of these permanent differences was transmitted to their daughters. To measure the degree to which variation in single records are inherited, the authors divided the dams of the daughters mated to each sire into a high half and a low half according to the amount of fat each produced in the first lactations. Then the records of the daughters of the high cows and of the low cows were averaged separately. When the difference between the average records of the two groups of daughters was doubled and divided by the average difference between the first records of their dams, a heritability estimate of 28 per cent was obtained.

Gregory _et al._ (1950) studied some of the factors that influenced the birth and weaning weights of beef calves. They reported that the weight of the dam had a significant influence on the birth weight of her offspring. The correlation between the weaning weight of the calf and the weight of the cow at weaning was significant at the .05 level for data obtained at the North Platte station, but negative and not significant for data from the Valentine station. Also, cows making the smallest gains during the nursing period tended to produce calves making the largest gains from birth to weaning. This probably was a result of increased milk flow among these cows. They reported that calves heavier at birth tended to maintain this advantage and thus were heavier at weaning.

Cows tended to repeat their previous performance for gain of their calves from birth to weaning and the weaning weight of their calves to a higher degree than for birth weight. Gain from birth to weaning and weaning weight seem to be influenced to a great extent by such environmental factors as milk flow of the dam, and the repeatability of mothering ability. The influence of these environmental factors, probably is quite high in beef cows.

Dawson _et_ _al_. (1954) studied the six-month weaning weights of 446 calves produced in a Brahman-Angus population during the years 1945-1950. Rather than actual weights, the weaning weights in this study were expressed as deviations from the mean of calves of the same sex, born in the same year and out of dams of comparable ages. By regressing the six-month weight of offspring on the six-month weight of dam (within sire of the dam) a heritability estimate of 15 per cent was obtained. Paternal half-sib correlations among daughters of the sires used for this study and based on the weights of calves raised by the daughters yielded a heritability estimate of 19 per cent for maternal abilities. These workers concluded that because of the importance of maternal effects in a population the following selection procedures should be followed: (1) retain a high percentage of heifers for one or two calf crops and select those which demonstrate their ability to wean heavy calves for further use in the herd; (2) select sires from among the sons of cows that have repeatedly demonstrated their ability to wean heavy calves and that are grandsons of those whose daughters have on the average produced heavy calves at weaning; (3) where possible, use sires whose daughters have proved to have good maternal abilities.

Rollins and Guilbert (1954) made a study of the relation between the calf's rate of growth from birth to four months of age and its 240-day weaning weight. The data analyzed were from eight monthly weights of each of 159 purebred Hereford bulls and heifer calves out of 57 cows.

Correction factors were estimated for the effects of sex, age of dam, year, and season of birth for growth and weaning weight. A second degree regression curve described adequately the effect of age of dam on both growth rate and weaning weight. Dams in the age range from seven to ten years produced calves that grew fastest up to four months of age and were heaviest at weaning. From four to eight months, however, the calves from first-calf heifers and to a lesser extent from second-calf cows grew faster than those from cows in the optimum age range.

Differences between cows accounted for 34 per cent and 48 per cent of the variances of growth and weaning weight, respectively. The following correlations between growth and weaning weight were found: within dams .62; between dams .91; between dams based on the single record .73.

They concluded that the lactating ability of the cow makes a major contribution to the growth of the calf throughout the entire suckling period.

Koch and Clarke (1955c) compared the theoretical composition of paternal and maternal half-sib correlations, the correlations between offspring and dam, and offspring and sire with observed values to estimate the influence of maternal environment. These comparisons suggest that maternal environment from conception to birth and from birth to weaning had a large influence on birth weight, gain from birth to weaning, and weaning score, but a small influence on yearly gain and yearly score. The results further suggest that a negative correlation exists between maternal environment from birth to weaning and weaning score and gain. The consequences of selecting for various traits were examined particularly as to the effect on maternal environment. Selecting for weaning gain will increase genetic value for growth response and to a slight extent increase genetic value for maternal environment. All of the gain, however, could be nullified by the negative genetic correlation between maternal environment and growth response. Selecting cows that produce heavy calves would place greater emphasis on milking ability than on growth response so far as genetic value of the cow is concerned. After taking maternal environment into account, they estimated heritabilities of .42 for birth weight, .19 for weaning weight, .12 for weaning gain, .40 for yearly gain, and .27 for yearly score.

Dinkel and Musson (1956) analyzed data from eleven ranches that contained the weaning weights on 646 calves by 62 bulls. From this study they reported that in addition to selecting on the basis of the individual's weaning weight, selections can also be practiced on the mothering ability of the cow herd.

They concluded that some of the variation apparent in the data presented is no doubt due to differences in the milking ability of the cows. Selecting for milking ability in the cow herd should also result in heavier calves at weaning. Estimates of heritability of milk production in dairy breeds indicate that the amount of milk produced is inherited to about the same extent as weaning weight in calves.

Nelms and Bogart (1956) analyzed the data from 103 purebred Hereford and Angus calves. The data were analyzed, using the least squares method. They reported time of birth and birth weight both affected rate of gain during the suckling period. There was a difference of 0.115 pounds per day in rate of suckling gain associated with each difference of ten pounds in birth weight. There was little or no effect of age of dam even though large differences appeared to exist between two-year-old and older cows.

There was apparently no direct effect of sex on rate of suckling gain. This would indicate that, no removal of the birth weight effect, the females approach the males in suckling gain.

Guilbert and Hart (1957), summarizing their work in California, reported that one can greatly improve milking ability by selecting bulls on the same basis recommended for dairy cattle. Some bulls transmit, with reasonable uniformity, superior milking yields to their daughters. The best method is to seek a bull whose dam and sire have both produced good milking daughters. True transmitting ability of the parent is the best recommendation for the prospective sire. They concluded also that, if there is no opportunity to observe or to secure information on the daughters of the parent animals, then the milking ability of the mother and of the sire's mother is the next best criterion.

Chambers et al. (1958) regressed the production of daughters on their dams and estimated the heritability of mothering ability to be .28. They made this estimate by dividing the dams of the heifers by each sire into a high-producing group and a low-producing group and then by comparing the production of their unselected daughters with that of their selected dams. They concluded that selection of heifers based on two or more records of their dams should be more effective than on one record of dam or on one record of daughter (by same sire). Their study indicates the importance of the sire influence upon productivity of his daughters. Initial selection of sires can be made on average lifetime production of his dam and on his unselected sisters, but the real proof is on the production of his own daughters.

Stonaker (1958) in his work in Colorado concluded that cattlemen can make improvement by (1) selection of heifer replacements from better producing cows and (2) selection of bull calves from cows known to be heavy producers and by sires known to have sired heavy producing daughters.

Drewry et al. (1959) on very limited data studied the relationship among certain factors related to mothering ability in beef cattle. Their data indicated that older cows were more protective and were heavier milk producers. Heavier calves were from older cows and were born later in the calving season. Calves suckling heavy producing cows made larger total gains from birth to six months but required more milk per pound of live weight gained. Older calves suckling lighter producing dams spent more time suckling and suckled more frequently in early lactation (about one month). There was, however, a tendency for calves suckling heavier producing dams to spend more time suckling and to suckle more frequently in late lactation. Multiple correlations and standard partial regression coefficients would indicate that factors other than milk production may contribute to mothering ability, as measured by the total gain of the calf.

Lactation number, mothering score, average daily milk production of the dam, birth weight, age, and suckling time of the calf accounted for 75 per cent, 77 per cent, and 60 per cent of the variability associated with total gain of the calf up to 1, 3, and 6 months of age, respectively.

Kieffer (1959) estimated the inheritance of maternal effects for birth weight, weaning weight, and weaning score by regressing the performance of the daughters' calves on the performance of the dams' calves and from the intra-class correlations of the average performance of calves produced by paternal half sisters.

Of the different record combinations used to estimate heritabilities of maternal effects for birth weight, weaning weight, and weaning score, the estimates obtained from the regression of the average record of the daughter on the average record of the dam were considered to be the most reliable.

Estimate of heritability computed from the sums of squares and the sums of the cross products of average records pooled over all herds were .40, .42, and a -.09 for birth weight, weaning weight, and weaning score, respectively.

The records of calves produced by a total of 498 paternal half sisters were utilized for the heritability estimates of maternal effects obtained by the paternal half-sib correlation method. Heritability estimates obtained from the sums of squares pooled over all herds were .60, .39, and .04, for birth weight, weaning weight, and weaning score, respectively.

Repeatability of Production

The measure of repeatability is the coefficient of correlation between several records made by the same dam in the same herd. If a dam tends to produce almost exactly the same for a particular trait each year, the trait is considered highly repeatable, and the first record is a reliable measure of future production (Lush, 1945). Koger and Knox (1947) investigated the repeatability of weaning weights and grades of calves from range cows. The average correlation of the weight of all adjacent calves was .49. The correlation of the weight of the first calf with the second was .66. They concluded that considerable progress can be made in selecting range cows on the basis of the first calf crop record. Koch (1951) noted that differences between cows accounted for 52 per cent of the variance in the calves' corrected weaning weights. He therefore concluded that the extent to which weaning weight of calves is a permanent characteristic of range Hereford cows is 0.52. Botkin and Whatley (1953) estimated repeatability of weaning weight .43, birth weight .18, and gain from birth to weaning .38. They indicated that considerable progress could be made in selecting cows on the basis of their first records, particularly by using weaning weights. Koch and Clark (1955a) reported repeatability estimates for birth weight, 0.26; weaning weight, 0.34; gain from birth to weaning, 0.34; weaning score, 0.22; yearling weight, 0.20; and gain from weaning to yearling age, 0.09. Chambers et al. (1956) used two methods to estimate the repeatability of weights of calves by the same cow at approximately 0.30 for 112 and 210 day weights. Chambers et al. (1957) studied the repeatability of 2 measures of reproduction efficiency of range cows. The calving intervals were analyzed by an analysis of variance, and the intra class correlation was obtained. The repeatability of calving interval derived in this manner was -.09. This estimate indicates that, under conditions of a limited breeding season, calving interval is not likely to be of any use to breeders as a measure of reproductive performance for which they may effectively select brood cow replacements. The successful exposures were analyzed by an analysis of variance, and the intra class correlation was obtained from the pooled sums of squares of the four herds. The repeatability of successful exposure derived from intra class correlation uncorrected for temporary environmental variance was .14; when the data were corrected for temporary environmental variance, an estimate of .25 was obtained; when the data were corrected for temporary environmental variance, omitting the first record, an estimate of .38 was obtained.

MATERIALS AND METHODS

The data used in this study were the weaning weights and weaning scores of 680 calves produced by cows located in 5 different herds. Two of the herds were registered horned Hereford herds, two were registered Angus herds, and one was a registered Polled Hereford herd. These herds are located in northeastern Oklahoma, but because of herd differences in management the analysis was made on an intra-herd basis. The correction of data for known variables and the statisticial procedures were the same for all herds, but because of differences in location and management the data are described separately.

Description of the Data

MCSPADDEN RANCH

The McSpadden Ranch is located in the northern part of Rogers County and consists of approximately 2500 acres. The pasture forage is predominantly native grass, but bermuda, overseeded with Korean lespedeza, has been established in old fields. This ranch has about 225 to 250 Hereford cows, of which about 125 are registered. The data used in this study were secured from the registered herd over a 5-year period. Most of the calves were born during the winter months of November, December, January, and February. Calves were not creep-fed, and the cows were wintered on dead grass and cotton seed cake supplemented with alfalfa hay and prairie hay as needed.

DIEM ANGUS RANCH

The Diem Angus Ranch is located in the southern part of Rogers County and Mayes County. It consists of approximately 3000 acres, of which 300 acres are in farm land (part of which is irrigated), 1200 acres in native grass, and approximately 1500 acres in improved pasture consisting of bermuda, Korean lespedeza, yellow hop clover, and rye grass. The winter pasture consists of wheat, oats, rye, brome, and vetch.

The ranch maintains approximately 200 head of registered Angus brood cows and about the same number of commercial Angus cows. The data for this study were secured from the registered herd over a 4-year period. The cow herd calves mostly from October to February, and the calves are creep-fed during the winter months. The registered cow herd is wintered on the temporary and permanent pastures with supplementary feed of 32 per cent protein cubes, sargo silage, and prairie hay.

BLACK KETTLE FARMS

Black Kettle Farms is located in the eastern part of Mayes County. It consists of approximately 1100 acres of native and improved pastures. Approximately 100 head of registered Angus brood cows are maintained in this unit. The cows calve mostly during October to February. The herd is wintered on the permanent pastures, supplemented during this period with protein cake and prairie and oat hay. The calves are not creep-fed. The data obtained from this herd were secured over a 4-year period.

R K L RANCH

R K L Ranch is located in the southern part of Rogers County and consists of approximately 700 acres. Approximately 120 head of registered Polled Hereford cows are maintained on 213 acres of improved pastures. These improved pastures have a bermuda grass base, overseeded with rye grass, fescue, southland brome, Balbo rye, vetch, big and little hop, ladino, white Dutch clovers, and Korean lespedeza. The ranch has approximately 300 acres of cultivated land, of which 200 acres are irrigated. Fall-planted small grains provide winter pasture for the cow herd. A complete fertilizing program is used at this ranch for maximum production per acre. The cow herd is supplemented with protein, hay, or silage, depending on pasture and weather conditions. The cows calve mostly during October through February. The calves are creep-fed whole oats. The data used in this study were obtained over a 5-year period.

PHILSON FARMS

Philson Farms is located in the southern part of Washington County and extends into Nowata County and Rogers

County on the east. The ranch consists of approximately 4400 acres, of which all but 600 acres are in the native climax grasses. The 600 acres are old fields that have been planted to bermuda grass, overseeded with Korean lespedeza and clovers. Approximately 450 head of registered and commercial Hereford brood cows are maintained on the ranch. The data used in this study were secured from the 100 head of registered cows on the ranch over a 3-year period. The cows calve mostly during late fall and early winter. The feed for this cow herd is supplemented with 32 per cent protein cake during the winter period. The calves have access to a creep feed during the nursing period. The herd receives hay only when the grass is covered with snow or in early spring, when the dead grass has weathered and matured to the point where its feed value is not adequate to meet the cows' requirements. This of course varies from year to year.

Correction of the Data for known Variables

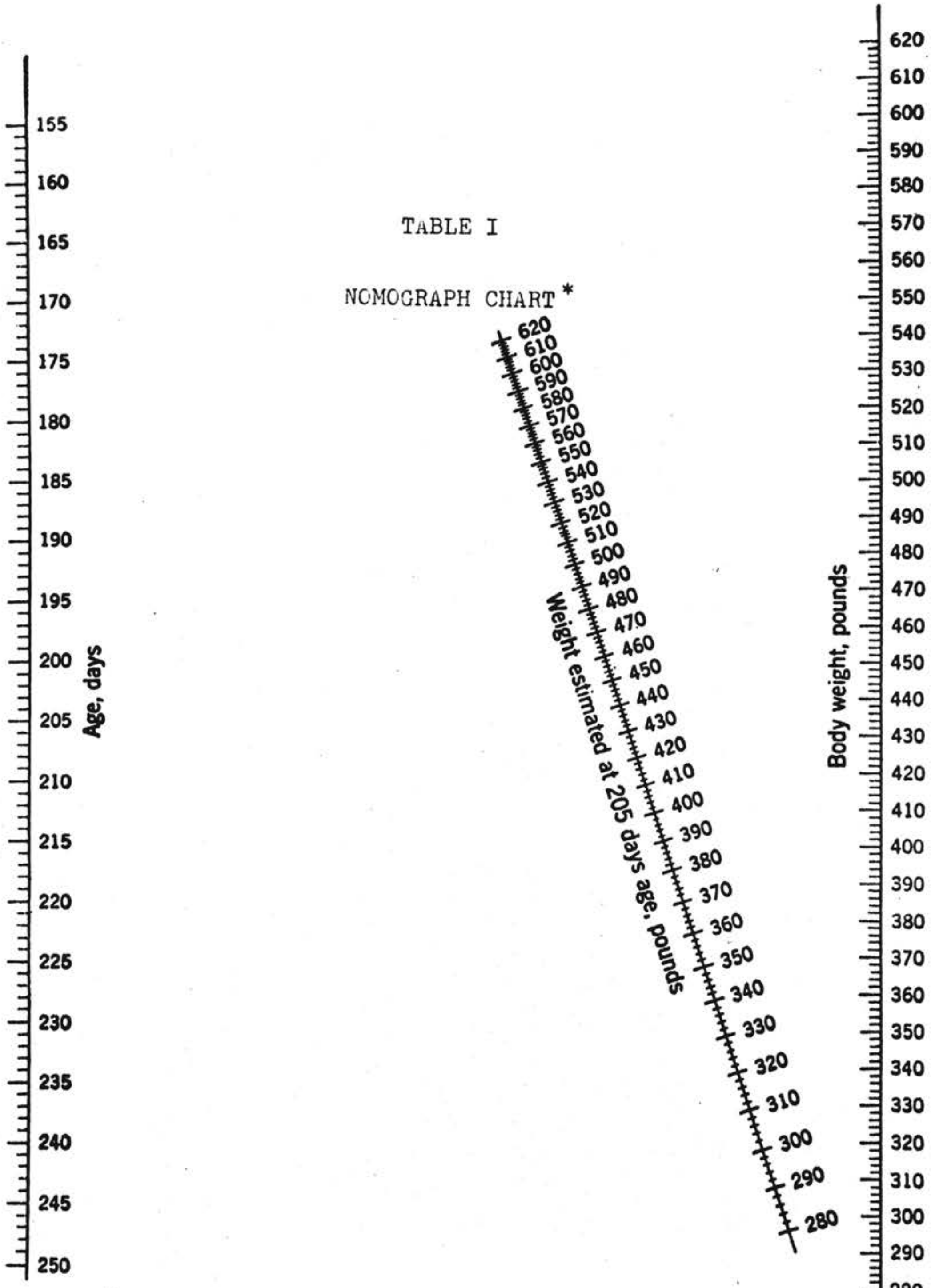
The data secured from all ranches within the respective years were weaning weights and weaning scores of calves. All data have been corrected for age of calf, age of dam, and sex of calf.

Age of calf

The method used to adjust the age of calf to 205 days was the nomograph chart (Table I) developed by Koger and Knox (1945b). Their regression of weight on age estimates

TABLE I

NOMOGRAPH CHART *



* A means of estimating the weights of calves at a constant 205 days of age. Use a straight edge to connect actual age in days at left with actual weaning weight at right and read off the estimated weight at 205 days on the center scale. (Journal of Animal Science, 1945, Vol. 4, p. 287.)

what the weight would have been if birth date had been 205 days previous to the date of weighing. Burgess *et al.* (1954) reported that there was a deviation of 1.67 pounds in weaning weight for each day of deviation in age. Marlowe *et al.* (1958) reported that age of calf appeared to have little influence on pre-weaning growth rate. The average daily gain of non-creep-fed nursing calves from birth to weaning was about the same regardless of when the weight was taken within the 90 to 240 days range of age.

Age of dam

Burgess *et al.* (1954), in a study of the variables affecting weaning weight, reported that the age of the dam had a significant effect on weaning weight. Koch and Clark (1955d) reported that the age of the dam had a marked influence on all traits studied except fall yearling weight and score. The cow's productivity with regard to birth weight, weaning weight, and weaning score of calves increased steadily from three to six years of age and then declined. Nelms and Bogart (1956), however, on limited data reported no effect of age of dam on suckling gain of beef calves. Lindley *et al.* (1958) reported that cows more than ten years old declined rapidly in reproductive performance. All correlations and regressions of performance on age of cow were positive and significant, but the rapid decline at the older ages caused the regression to be curvilinear. Marlowe *et al.* (1958) found that age of dam was the most important source of variation in their study of growth rate to weaning weight. After growth rate had been adjusted for sex, age, and season of birth of the calf, the average values were, 1.44, 1.57, 1.63, 1.66, 1.70, 1.74, 1.68, 1.73, and 1.67 pounds per day for two, three, four, five, six, seven, eight, nine, and ten year old and older cows, respectively. Stonaker (1958) reported that age of dam had an appreciable effect on percentage calf crop, on calving difficulty, and weight of calf at weaning. Drewry et al. (1959) found that older cows were more protective and were heavier milk producers than younger cows. They also found that heavier calves at birth were from older cows and were born later in the calving season.

The data used in this study were secured from dams of all ages. Since age of dam is a major source of variation in the calf's weight, an age adjustment factor was made for all dams to a mature equivalent of 6-7 years of age. Table II lists how the adjustment was made. The correction factors in this table have been modified and extended from data published by Knox and Koger (1945). The 2-year-old and 13-year-old and older dams received the largest adjustment.

Sex of calf

Koger and Knox (1945a) determined that the mean weights of the two sexes corrected for differences in weaning age were 443 pounds for 419 steers and 411 pounds for 444 heifers. The difference of 32 pounds in favor of steers was hightly significant. Gregory et al. (1950) noted

TABLE II

AGE OF DAM ADJUSTMENT*

Year	Month	Factor	Year	Month	Factor
2	0-1	1.16	7	11	1.00
	2-3	1.15	8	0-11	1.01
	4-5	1.14	9	0-5	1.02
	6-7	1.13		6-11	1.03
	8-9	1.12	10	0-3	1.04
	10-11	1.11		4-7	1.05
3	0-1	1.10		8-11	1.06
	2-3	1.09	11	0.2	1.07
	4-5	1.08		3.5	1.08
	6-7	1.07		6-8	1.09
	8-9	1.06		9-11	1.10
	10-11	1.05	12	0-1	1.11
4	0-1	1.04		2-3	1.12
	2-5	1.03		4-5	1.13
	6-11	1.02		6-7	1.14
5	0-11	1.01		8-0	1.15
6	0	1.00		10-11	1.16
			13 &	older	1.16

*The correction factors in this table have been modified and extended from data published by Knox and Koger (1945).

significant differences in birth weight in favor of male calves. Chambers et al. (1953) adjusted for sex difference by adding or substracting the average difference between sexes to adjust to steer or heifer equivalent. Burgess et al. (1954) observed significant sex differences in weaning weight in a Hereford herd. Rollins and Guilbert (1954) reported that heifer calves weighed 68 pounds less than bull calves at weaning. Koch and Clark (1955d) found that male calves were 5.6 pounds heavier at birth than heifers and 26.2 pounds heavier at weaning. Sex differences in weaning score were negligible. Marlowe et al. (1958) reported that sex of calf had a significant effect on growth rate. Bull calves grew 4 per cent faster than steer calves, and steer calves about 8 per cent faster than heifer calves. Koch et al. (1959) found that bull calves averaged 1.067 times heavier at birth than heifers and that from birth to weaning they gained 1.037 times faster than heifers. Stonaker (1958) reported sex correction factors for heifers, steers, and bulls. These correction factors are a modification of data reported by Burgess et al. (1954).

The differences due to sex were standardized by adding 50 pounds to all heifer calves' and 25 pounds to all steer calves' weaning weight. The sex adjustment used is an adjustment based on the very limited data available. A more dependable comparison of sex effects of steer calves vs. bull calves is needed. For the purposes of this study all calves were adjusted to a bull equivalent basis.

Weaning score

When the calves were weighed to secure weaning weights, they were also given a weaning score. Table III gives the numerical classification that was worked out for scoring calves for type, conformation, and breed characteristics. This classification is a modification of a system developed by Albaugh et al. (1956). The scoring is done independently of the individual weight, and separate analyses were made for weaning score.

Statistical Procedures

Paternal half-sib correlations were calculated for the daughters of the various sires, using the weaning weights and weaning scores of their calves as the criteria of maternal effects. In the hierarchical design, data were analyzed on an intra-year, intra-herd basis; this eliminated the differences between years and between ranches that occurred over the 5-year period during which these measurements were obtained. In the cross-classification design, year and ranch variances were partitioned in the analysis of variance. Sires of the individual calves were treated as random environmental effects. Eighteen analyses of variances were computed, using the method described by Snedecor (1956) for a hierarchical classification. The sums of squares for the analysis of variance for each ranch were pooled within years and then pooled over the 5 years. The intra class correlation was computed from the

TABLE III

SCORING SYSTEM*

Score	Description
	Breeding Cattle
96-100 91-95	The top of the grade represents outstanding animals. The middle and lower end of the grade represents excellent breeding animals from standpoint of type, conformation, quality, and breed characteristics.
86-90 81-85	Cows in this grade are good enough to retain for breeding test in purebred herds. This is a practical top for commercial herd sires. The top of this grade represents the lower end of herd bulls acceptable for use in a registered herd. Cattle in this grade are not of show caliber.
76-80	Cows usually should be culled from purebred herds; good commercial cattle; bulls rarely capable of making much improvement except on very plain cattle.

*This classification is a modification of a system developed by Albaugh *et al.* (1956).

pooled sums of squares. Since the data contained unequal numbers of observations from dams by the various sires, the average number of daughters per sire was calculated as suggested by Snedecor (1956).

The mathematical model that was considered adequate for the hierarachical design was as follows:

$Y_{ij} = M + D_i + E_{ij}$, where

Y_{ij} is the observed phenotypic value for the j^{th} daughter sired by the i^{th} sire.

M is the effect common to all daughters. It is the mean if all other effects are zero.

D_i is the effect common to all daughters sired by the i^{th} sire.

E_{ij} is the effect common to the j^{th} daughter and sired by the i^{th} sire.

The mathematical model assumed for the cross classification design is given below:

$Y_{ijkm} = M + A_i + B_j + C_{jk} + D_{jkm} + E_{ijkm}$ where

Y_{ijkm} is the observed phenoptypic value for the m^{th} dam, who was sired by the k^{th} sire on the j^{th} ranch, in the i^{th} year.

M is the effect common to all dams. It is the population mean if all other effects are zero.

A_i is the effect common to all dams whose calves were weaned in the i^{th} year.

B_j is the effect common to all dams who weaned calves on the j^{th} ranch.

C_{jk} is the effect common to the k^{th} sire on the j^{th} ranch.

D_{jkm} is the effect common to the m^{th} dam who was sired by the k^{th} sire on the j^{th} ranch.

E_{ijkm} is the composite interaction of years with ranch-sire-dam combinations.

Two statistical designs were set up to obtain heritability estimates of maternal effects by the paternal half-sib correlation method described by Lush (1948).

One design partitioned the variance into that between sires and the variance of dams within sires. The latter is the error term that is the remainder when variance between sires is substracted from total variance. These data were analyzed on an intra-year, intra-herd basis. The respective variance terms were then pooled for the ranches within years, since some of the data were not available on some of the ranches during the entire period of this study. The sums of squares of the respective variances of the pooled ranches were then pooled over the five years. From these pooled sums of squares the expected component for sires and dams within sires was computed. The heritability estimate of maternal effect was then computed by intra class correlation. This was multiplied by 4 since the correlation between genetic values of half-sibs is .25 under conditions of random mating.

The other design was set up to partition the variance between sires, using the average of three records of the various daughters by the different sires.

Since unequal number of observations per sire is present in this design also, the method described by Snedecor (1956) for samples of unequal size was used to estimate the average number of observations per sire. The differences between sires, computed on a within-ranch basis and then pooled over ranches, were partitioned from the ranch-sire-dam combinations, after the variances between ranches had been subtracted. The remainder was the variance between dams within sires within ranches. The estimate of heritability for maternal effects was then computed, using the same method described for the first design.

The second design permitted an estimate of repeatability for weaning weight and weaning score, as each dam's performance, on the different ranches, was measured for three consecutive years. The intra class correlation as described by Snedecor (1956) was used for this estimate.

RESULTS AND DISCUSSION

Heritability estimates for maternal effects were computed from intra class correlations of calves by paternal half-sisters. It is recognized that these intra class correlations could also include a transmitted influence of genes for growth transmitted from the sire through his daughters to their offspring. To this extent an estimate of heritability from the above intra class correlation would be an overestimate of maternal effects. Maternal effects embrace that part of the offspring's life from conception to weaning. These effects influence the offspring's development by the amount of nutrients provided for the developing fetus, the amount of desirable milk provided from birth to weaning, the amount of protection, and desirable environment provided from birth to weaning by the offspring's dam.

The heritability estimates of maternal effects derived from the pooled sums of squares in the hierarchical classification are shown in Table IV. These estimates are .19 and .30 for weaning weight and weaning score, respectively.

The heritability estimates derived from the pooled sums of squares in the cross classification are shown in Table V. These estimates are .22 and .40 for weaning weight and weaning score, respectively. In other studies

TABLE IV

ANALYSIS OF VARIANCE AND HERITABILITY ESTIMATES OF MATERNAL EFFECTS FOR PATERNAL HALF-SISTERS USING A HIERARCHICAL CLASSIFICATION (POOLED FROM ALL HERDS).

(Weaning weight)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Heritability estimate
Between sires	112	4,732.98	$\sigma_e^2 + 5.14\sigma_s^2$	186.19	.0469	.1876
Dams in sires	550	3,775.92	σ_e^2	3,775.92		

(Weaning score)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Heritability estimate
Between sires	112	9.93	$\sigma_e^2 + 5.14\sigma_s^2$	.566	.0746	.2984
Dams in sires	550	7.02	σ_e^2	7.02		

TABLE V

ANALYSIS OF VARIANCE AND HERITABILITY ESTIMATES OF MATERNAL EFFECTS FOR PATERNAL HALF-SISTERS USING A CROSS-CLASSIFICATION (POOLED FROM ALL HERDS).

(Weaning weight)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Heritability estimate
Sires in ranches	13	8,885.71	$\sigma_e^2 + 10.41\sigma_s^2$	329.17	.056	.22
Dams in sires in ranches	46	5,459.00	σ_e^2	5,459.00		

(Weaning score)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Heritability estimate
Sires in ranches	13	20.06	$\sigma_e^2 + 10.41\sigma_s^2$	1.04	.102	.408
Dams in sires in ranches	46	9.10	σ_e^2	9.10		

Dawson *et al.* (1954) reported an estimate of .19 for weaning weight from intra class correlation. Koch and Clark (1955c) reported estimates of total genetic value, which took into account the genetic value for direct response in the calf and the gene value for maternal environment. Heritability estimates of total genetic value were .19, and .16 for weaning weight and weaning score, respectively. These estimates were obtained indirectly from parent-offspring correlations. Chambers *et al.* (1958) used 159 daughters from 46 different dams to estimate the heritability of beef cow productivity. They reported a heritability estimate of .28 for weaning weight. Kieffer (1959) reported a heritability estimate of .39 and .04 for weaning weight and weaning score, respectively. These estimates were computed from the pooled sums of squares of several herds using the intra class correlation method.

The repeatability of production was estimated to be .29 and .12 for weaning weight and weaning score, respectively. This estimate was computed by the intra class correlation method as shown in Table VI. Koger and Knox (1947), in their investigation of repeatability of weaning weights and grades of calves from range cows, found the average correlation between the weights of adjacent calves to be .49. Koch (1951) noted that differences between cows accounted for 52 per cent of the variance in the calves' corrected weaning weights. Botkin and Whatley (1953) reported estimates of repeatability for weaning weight as .43, for birth weight as .18, and for gain from birth to

TABLE VI

REPEATABILITY ESTIMATES FOR WEANING WEIGHT AND WEANING SCORE BY INTRA-CLASS CORRELATION IN A CROSS-CLASSIFICATION DESIGN

(Weaning weight)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Repeatability estimate
Dams in sires in ranches	46	5,459.00	$\sigma_e^2 + 3\sigma_d^2$	1,002.89	.29	.29
Calves in dams in sires in ranches	124	2,450.33	σ_e^2	2,450.33		

(Weaning score)

Sources of variation	D/F	Mean square	Expected mean square	Expected component	Intra-class r	Repeatability estimate
Dams in sires in ranches	46	9.10	$\sigma_e^2 + 3\sigma_d^2$	.90	.12	.12
Calves in dams in sires in ranches	124	6.39	σ_e^2	6.39		

weaning as .58. Koch and Clark (1955a) reported repeatability estimates for birth weight, 0.26; weaning weight, 0.34; gain from birth to weaning, 0.34; for weaning score, 0.22. Chambers *et al.* (1956) estimated the repeatability of weights of calves by the same cow as approximately 0.30 by two methods for 112 and 210 day weights.

SUMMARY AND CONCLUSIONS

The data for this study consisted of weaning weights and weaning scores of calves from 5 different herds located in northeastern Oklahoma. All analyses were made on an intra-herd basis. The data were corrected for age of dam, age of calf, and sex of calf. Three ranches creep-fed the calves and two ranches did not, but the calves on each ranch were treated alike. On the hierarchical design all analyses were made on an intra-herd basis. On the cross classification the variances between ranches were partitioned from the ranch-sire-dam combinations, and thus there was no need to adjust for creep feeding or other treatment differences.

The inheritance of maternal effect on weaning weight and weaning score was estimated from the intra class correlations of the average performance of calves produced by paternal half-sisters. Estimates of repeatability of production for weaning weight and weaning score were made from intra class correlation by using 3 production records of each dam.

The records of calves produced by a total of 680 paternal half-sisters were utilized for the heritability estimates of maternal effects obtained by the paternal half-sib correlation method. The 680 paternal half-sisters were sired by 130 different bulls. Estimates of heritability obtained from the sums of squares pooled over all herds and years were .19 for weaning weight and .30 for weaning score from the hierarchical design with a single classification. Estimates of heritability obtained from the cross classification design using 3 records by the same cow, and where the sums of squares of sire differences were pooled over all herds was .22 for weaning weight and .40 for weaning score. Estimates of repeatability of production by daughters of the different sires was .29 for weaning weight and .12 for weaning score.

LITERATURE CITED

Albaugh, Reuben, Horace T. Strong, and F. D. Carrol. 1956. A guide for beef cattle improvement programs. Calif. Agri. Exp. Sta. and Extension Service Cir. 451.

Anderson, David E. and Doyle Chambers. 1957. Genetic aspects of cancer eye in cattle. Okla. Agri. Exp. Sta. Misc. Pub. 48:28.

Bogart, Ralph. 1959. Improvement of Livestock. First Printing. The Macmillan Company. New York.

Botkin, M. P. and J. A. Whatley Jr. 1953. Repeatability of production in range cows. Jour. Ani. Sci. 12:552.

Burgess, J. B., Nellie L. Londblon, and H. H. Stonaker. 1954. Weaning weights of Hereford calves as affected by inbreeding, sex and age. Jour. Ani. Sci. 13:843.

Chambers, Doyle, M. P. Botkin, and J. A. Whatley Jr. 1953. Weaning weight of calf as a measure of mothering ability of the beef cow. Okla. Agri. Exp. Sta. Misc. Pub. 31:10.

Chambers, Doyle, Dale Hoover, J. A. Whatley Jr., and D. F. Stephens. 1956. Productivity of beef cows as appraised by 112 and 210 day calf weights. Okla. Agri. Exp. Sta. Misc. Pub. 45:30.

Chambers, Doyle, Gary Conley, and J. A. Whatley Jr. 1957. Reproductive efficiency of range beef cows. Okla. Agri. Exp. Sta. Misc. Pub. 48:23.

Chambers, Doyle, Nat M. Kieffer, and L. S. Pope. 1958. Inheritance of Productivity of beef cows. Okla. Agri. Exp. Sta. Misc. Pub. 51:69.

Dawson, W. M., E. H. Vernon, A. L. Baker, and E. J. Warwick. 1954. Selection for increased weights of six-month-old beef calves in a Brahman-Angus population. Jour. Ani. Sci. 13:556.

Dickerson, G. E. and L. N. Hazel. 1944. Effectiveness of selection on progeny performance as a supplement to earlier culling in livestock. Jour. of Agri. Res. 69:459-476.

Dinkel, C. A. and A. L. Musson. 1956. Beef cattle breeding research in South Dakota. S. Dakota Agri. Exp. Sta. Cir. 130.

Drewry, K. J., C. J. Brown, and R. S. Honea. 1959. Relationships among factors associated with mothering ability in beef cattle. Jour. Ani. Sci. 18:938.

Fisher, R. A., F. R. Immer, and Olof Tedin. 1932. The Genetical interpretation of statistics of the 3rd degree in the study of quantitative inheritance. Genetics. 17:107-124.

Gregory, Keith E., Cecil T. Blunn, and Marvel L. Baker. 1950. A study of some of the factors influencing the birth and weaning weights of beef calves. Jour. Ani. Sci. 9:338.

Guilbert, H. R. and G. H. Hart. 1957. California Beef Production. Manual 2. Calif. Agri. Exp. Sta. and Extension Service. Sec. II: 24-42.

Hazel, L. N., M. L. Baker, and C. F. Reinmiller. 1943. Genetic and environmental correlations between the growth rate of pigs at different ages. Jour. Ani. Sci. 3:143.

Hazel, L. N. and Clair E. Terrill. 1945. Heritability of weaning weight and staple length in range Rambouillet lambs. Jour. Ani. Sci. 4:347.

Hazel, L. N. 1949. Problems techniques and experimental designs in animal investigations, breeding and genetics. Jour. Ani. Sci. 8:610 (abstract).

Kieffer, Nat Mathan. 1959. Inheritance of certain maternal traits in Beef Cattle. Ph.D. Thesis. Okla. State. Univ.

Knapp, Bradford Jr., and A. W. Nordskog. 1946. Heritability of growth and efficiency in beef cattle. Jour. Ani. Sci. 5:62.

Knapp, Bradford Jr., and R. L. Clark. 1950. Revised estimates of heritability of economic characteristics in beef cattle. Jour. Ani. Sci. 9:582.

Knox, J. H. and M. Koger. 1945. Effect of age on the weight and production of range cows. New. Mex. Agri. Exp. Sta. Press Bul. 1004.

Koch, Robert M. 1951. Size of calves at weaning as a permanent characteristic of range Hereford cows. Jour. Ani. Sci. 10:768.

Koch, Robert M. and R. T. Clark. 1955a. Genetic and environmental relationships among economic characters in beef cattle. I. Correlations among paternal and maternal half-sibs. Jour. Ani. Sci. 14:775.

Koch, Robert M. and R. T. Clark. 1955b. Genetic and environmental relationships among economic characters in beef cattle. II. Correlations between offspring and dam and offspring and sire. Jour. Ani. Sci. 14:786.

Koch, Robert M. and R. T. Clark. 1955c. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. Jour. Ani. Sci. 14:979.

Koch, Robert M. and R. T. Clark. 1955d. Influence of sex, season of birth and age of dam on economic traits in range cattle. Jour. Ani. Sci. 14:386.

Koch, Robert M., K. E. Gregory, J. E. Ingalls, and R. L. Arthaud. 1959. Evaluating the influence of sex on birth weight and preweaning gain in beef cattle. Jour. Ani. Sci. 18:738.

Koger, Marvin and J. H. Knox. 1945a. The effect of sex on weaning weight of range calves. Jour. Ani. Sci. 4:15.

Koger, Marvin and J. H. Knox. 1945b. A method for estimating weaning weights of range calves at a constant age. Jour. Ani. Sci. 4:285.

Koger, Marvin and J. H. Knox. 1947. The repeatability of the yearly production of range cows. Jour. Ani. Sci. 6:461.

Lindley, C. E., G. T. Easley, J. A. Whatley Jr., and Doyle Chambers. 1958. A study of the reproductive performance of a purebred Hereford herd. Jour. Ani. Sci. 17:336.

Lush, J. L. 1935. The inheritance of productivity in farm Livestock. Part 5. Discussion of preceding contributions. Emp. Jour. of Exp. Agri. 3:25.

Lush, J. L. 1936. Genetic aspects of the Danish system of progeny testing swine. Iowa Agri. Exp. Sta. Res. Bul. 204.

Lush, J. L. and Floyd Arnold. 1937. Differences between records, real productivity and breeding values of dairy cattle. Jour. Dairy Sci. 20:440.

Lush, J. L. 1940. Intra-sire correlations or regressions of offspring on dam as a method of estimating heritability of characteristics. Am. Soc. An. Prod. Proc. p. 293-301.

Lush, J. L., H. W. Norton, and Floyd Arnold. 1941. Effects which selection of dams may have on sire indexes. Jour. Dairy Sci. 24:695.

Lush, J. L. 1945. Animal Breeding Plans 3rd Ed. The Iowa State College Press, Ames, Iowa.

Lush, J. L. 1948. The Genetics of Populations. Ames, Iowa. (mimeographed).

Marlowe, Thomas J., Charles M. Kincaid, and George W. Litton. 1958. Virginia Beef Cattle Performance Testing Program. Va. Agri. Exp. Sta. Bul. 489.

Nelms, G. E. and Ralph Bogart. 1956. The effect of birth weight, age of dam and time of birth on suckling gains of beef calves. Jour. Ani. Sci. 15:662.

Nordskog, A. W., R. E. Comstock, and L. M. Winters. 1944. Heredity and environmental factors affecting growth in swine. Jour. Ani. Sci. 3:257.

Rollins, W. C. and H. R. Guilbert. 1954. Factors affecting the growth of beef calves during the suckling period. Jour. Ani. Sci. 13:517.

Rollins, W. C. and K. A. Wagnon. 1956. A genetic analysis of weaning weights in a range beef herd operated under optimum and sub-optimum nutritional regimes. Jour. Ani. Sci. 15:125.

Shelby, C. E., R. T. Clark, and R. R. Woodward. 1955. The heritability of some economic characteristics of beef cattle. Jour. Ani. Sci. 14:372.

Snedecor, G. W. 1956. Statistical Methods. 5th Ed. The Iowa State College Press, Ames, Iowa.

Snyder, Laurence H. 1946. The Principles of Heredity. 3rd Ed. D. C. Heath and Company, Boston.

Stonaker, H. H. 1958. Breeding for beef. Colo. State Univ. Exp. Sta. Bul. 501-S.

Whatley, J. A. Jr. 1942. Influence of heredity and other factors on 180-day weights in Poland China Swine. Jour. of Agri. Res. 65:249-264.

Wright, Sewall. 1921. Systems of Mating. I. The biometric relations between parent and offspring. Genetics. 6:114.

Wright, Sewall. 1921. Correlation and Causation. Jour. Ani. Res. 20:557.

A P P E N D I X

APPENDIX A

METHOD OF COMPUTING N_o VALUES

The value of N_o is the corrected number of offspring per sire. This formula given by Snedecor (1956) is needed to correct averages for samples of unequal size.

$$N_o = \frac{1}{A-1}\left(N. - \frac{\Sigma n_i^2}{n.}\right)$$

A = the number of sires

N. = the total number of observations.

n_i = the number of observations per sire.

The N_o values computed in the hierarchical and cross-classification designs are given below.

Hierarchical

$$\frac{1}{130-1}\left(680 - \frac{8384}{680}\right) = 5.14$$

Cross-Classification

$$\frac{1}{17-1}\left(189 - \frac{4167}{189}\right) = 10.41$$

APPENDIX B

The sums of squares pooled within ranches for years, for weaning weight from the hierarchial design.

Sources of Variation	df	ss
Year 1955		
Between Sires	5	4,626.4
Dams in Sires	35	179,192.4
Year 1956		
Between Sires	21	71,618.6
Dams in Sires	83	253,160.7
Year 1957		
Between Sires	37	230,456.6
Dams in Sires	153	717,373.6
Year 1958		
Between Sires	39	190,247.0
Dams in Sires	191	680,849.7
Year 1959		
Between Sires	10	33,145.9
Dams in Sires	88	246,184.0

The sums of squares pooled over years

Sources of Variation	df	ss	ms
Between Sires	112	530,094.5	4,732.98
Dams in Sires	550	2,076,760.0	3,775.92

APPENDIX C

The sums of squares pooled within ranches for years, for weaning score from the hierarchial design.

Sources of Variation	df	ss
Year 1955		
Between Sires	5	62.3
Dams in Sires	35	452.9
Year 1956		
Between Sires	21	322.8
Dams in Sires	83	746.8
Year 1957		
Between Sires	37	343.0
Dams in Sires	153	1,367.5
Year 1958		
Between Sires	39	316.2
Dams in Sires	191	976.0
Year 1959		
Between Sires	10	68.1
Dams in Sires	88	321.6

The sums of squares pooled over years

Sources of Variation	df	ss	ms
Between Sires	112	1,112.4	9.93
Dams in Sires	550	3,864.8	7.02

APPENDIX D

Analysis of variance of paternal half-sibs, as measured by weaning weight of calves, in a cross-classification.

(Weaning weight)

Sources of Variation	df	ss	ms
Totals	188	899,282.11	
Years	2	5,480.61	
Ranch-sire-dam combinations	62	589,960.11	
Ranches	3	223,331.65	
Sires in ranches	13	115,514.28	8,885.71
Dams in sires in ranches	46	251,114.18	5,459.00
Calves in dams in sires in ranches (interaction)	124	303,841.39	2,450.33

APPENDIX E

Analysis of variance of paternal half-sibs, as measured by weaning score of calves, in a cross-classification.

(Weaning score)

Sources of Variation	df	ss	ms
Totals	188	2,161.63	
Years	2	12.70	
Ranch-sire-dam combinations	62	1,355.63	
Ranches	3	675.78	
Sires in ranches	13	260.85	20.06
Dams in sires in ranches	46	419.00	9.10
Calves in dams in sires in ranches (interaction)	124	793.30	6.39

VITA

Charles A. Pratt

Candidate for the Degree of

Master of Science

Thesis: INHERITANCE OF MATERNAL EFFECTS IN BEEF CATTLE

Major Field: Animal Breeding

Biographical:

Personal data: Born near Oklahoma City, Oklahoma, July 20, 1922, the son of Charles S. and Mary Pratt.

Education: Received the Bachelor of Science degree from Oklahoma State University, with a major in Animal Husbandry in June, 1947.

Experiences: Entered the United States Army in 1942 and was separated in 1945; from 1954 to 1961 have served as Assistant County Agent, Associate County Agent, Agent at Large, and as Acting Associate Livestock Specialist.

Date of Final Examination: July, 1961.