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**A GENETIC ANALYSIS OF ECONOMIC CHARACTERISTICS
OF RANGE BEEF HEIFERS**

By

Keith O. Zoellner

This thesis is approved by a qualified, independent investigation
by a committee for the degree master of science, and acceptable as
meeting the thesis requirements for the degree; but without implying
that the conclusions reached by the candidate are necessarily the
conclusions of the major department.



A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science at South Dakota
State College of Agriculture
and Mechanic Arts

August, 1957

OF GE BE E

This thesis is approved as a creditable, independent investigation by a candidate for the degree, Master of Science, and acceptable as meeting the thesis requirements for this degree; but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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INTRODUCTION

The beef cattle industry is one of the major sources of rural income in South Dakota. According to the South Dakota Crop and Livestock Reporting Service (1955), there were 1,492,000 beef cows and yearling beef heifers on the farms and ranches in South Dakota as of January 1, 1957. They also reported that sales from cattle and calves amounted to approximately 34.6 percent of the gross farm and ranch income in the state. Since the beef cattle industry is a major source of the farm and ranch income in South Dakota, any improvement in the performance of beef cattle will also improve the economy of the state.

In the past, most of the selection of beef replacement heifers has been based on breed type. As a result of this selection, improvement in type has occurred in the beef breeds. However, a comparable improvement in gaining ability does not seem to have occurred. Since the majority of the beef cattle are sold by weight, it appears that it should be a factor considered when selecting replacement heifers.

The purpose of this study then is to obtain a workable selection method which the breeders would be able to adopt. According to Hazel and Lush (1942), the selection for a total score or index of net desirability is much more efficient than selection for one trait at a time. Before a selection index can be constructed the heritability of each trait and the genetic correlations between the traits must be established. Therefore, reliable estimates need to be obtained for these genetic values. First, however, adjustments must be made for the sources of environmental and other variations that are known to account for some

of the differences among animals. The sources of variation investigated here are the effects of age on 18-month weight and the effects of inbreeding on weaning weight, 18-month weight and 18-month type score.

There is a significant effect on the weight of the animal. Birth dates of calves usually have a range of one to three months from calving season. This variation in birth date may have an effect on the animal's 18-month weight. Partially data including variations of age and are adjusted by the use of correction factors. However, age correction factors for 18-month weight of beef cattle, that have been reported in the literature are limited. However, this study has developed several methods that have been used successfully.

Bywaters and Wilkins (1935) working with pre-market weights in calves, developed a formula for estimating the growth rate of pigs at a constant age. They found that by fitting straight lines to growth curves, the lines intersect the age axis of the age-weight curve at nearly the same age. The authors concluded that the individual pig's weight divided by his age, less 21 days, gives a relatively accurate estimate of the pig's growth rate during the pre-market period.

Shaller and Smith (1937) following the procedure of Bywaters and Wilkins (1935) substituted a set of factors for adjusting wean weights to a constant age of 21 days. Their intra-farm regression coefficient of weight on age was 0.72 pounds per day. The regression they developed for the age was 14.3 days. This formula was used throughout the study. The authors also reported that the regression coefficient of weight on age was 0.72 pounds per day. The regression they developed for the age was 14.3 days. This formula was used throughout the study.

REVIEW OF LITERATURE

Age Correction Factors

Studies by previous workers have shown that the age of an animal does have a significant effect on the weight of the animal. Birth dates of calves normally have a range of two to three months each calving season. This variation in birth date may have an effect on the animal's 18-month weight. Normally data containing variations of this kind are adjusted by the use of correction factors. However, age correction factors for 18-month weight of beef cattle, that have been reported in the literature are limited. Workers with swine have developed several methods that have been used successfully.

Bywaters and Willham (1935) working with pre-market weights in swine, developed a formula for estimating the growth rate of pigs at a constant age. They found that by fitting straight lines to growth curves, the lines intersect the age axis of the age-weight charts at nearly the same age. The authors concluded that the individual pig's weight divided by his age, less 65 days, gives a relatively accurate estimate of the pig's growth rate during the pre-market period.

Whatley and Quaife (1937) following the procedures of Bywaters and Willham (1935) calculated a set of factors for adjusting swine weights to a constant age of 56 days. Their intra-farm regression coefficient of weight on age was 0.72 pounds per day. The regression line intercepted the age axis at 14.9 days. This intercept was used

in the equation as follows:

$$\text{Corrected Weight} = \text{Actual Weight} \times \frac{\text{Standard Age} - 15 \text{ days}}{\text{Actual Age} - 15 \text{ days}}$$

Lush and Kincaid (1943) developed a set of correction factors for adjusting weights of pigs to 154 days based on a quadratic equation. They assumed that the daily gain in pounds increases by a constant amount each day, instead of the rate of gain being constant. When the growth curve was expressed as a quadratic equation, the following data were used: The average pig gained 1.39 and 1.75 pounds per day at 126 and 182 days of age respectively. The average weight at 154 days of age was 142.5 pounds. Assuming the daily gain in pounds increases by a constant amount each day, between the age of 126 and 182 days, the differential of weight with respect to age is:

$$\frac{Y - 1.75}{X - 182} = \frac{1.75 - 1.39}{182 - 126}$$

Where X = age in days, Y = daily gain in pounds. After integrating and solving for the constant by substituting weight (W) = 142.5 when X = 154 the following equation is obtained:

$$W = .0032143X^2 / .58X - 23$$

The equation for adjusting weight to an age of 154 days becomes:

$$\hat{W} = Z \frac{142.5}{.0032143X^2 / .58X - 23}$$

where Z is the actual weight at age X, and \hat{W} is adjusted weight.

Koger and Knox (1945) working with weaning weights of range calves found that the regression coefficient of weight on age was positively correlated with the weaning weight. This made the use of a variable regression coefficient necessary. The authors used the following equation

for correcting weight to a standard age: $W = w / db$, where W is the corrected weight, w the weight at weaning, d is the standard age minus the age at weighing and b the regression coefficient. The authors state that this method adjusts for differences in birth dates as well as for age and is felt to be more satisfactory for some purposes than methods which do not take into account seasonal influence on growth.

Dinkel (1953) reported an age correction factor for 18-month weight of range beef heifers, raised in western South Dakota. In his study, the data included 110 heifers from two substations, taken in four different years. The analysis of weights was made by using the method of least squares. The regression of weight on age was .97 pound per day of age. The regression line intercepted the age axis at -150 days. The correction factors were calculated by using the method developed by Whatley and Quaife (1937).

Studies in central Oregon by Hitchcock, et al. (1955) at the Squaw Butte-Barney Experiment Station showed that the age of the heifer had a significant effect on her yearling weight. Their studies included records of 157 grade Hereford cows and their 376 offspring from 1936 through 1951. They found a partial linear regression of 1.09 pounds per day for growth rate during the dry fall months on sagebrush-bunch grass range.

Inbreeding Effects

Inbreeding generally has resulted in reduced vigor as exhibited by slower growth, smaller size, greater mortality and lower production

and fertility. The effects of inbreeding on Holstein calves at the Iowa Agricultural Experiment Station were reported by Nelson and Lush (1950). They found an intra-sire regression of -0.72 pound for each one percent of inbreeding on the sixth month weight of dairy calves. The inbreeding coefficients ranged from 0 to 28 percent, with an average of five percent for the 176 Holstein calves used in their study.

Krch (1951) reported the effects of inbreeding on weaning weights of the Line 1 Herefords at the U. S. Range Livestock Experiment Station at Miles City, Montana. His data included records from 745 calves from 180 cows having two or more calves during the period 1938-1948. The average inbreeding of the calves was 12.4 percent. The regression of weaning weight due to the inbreeding of calf in his study was -0.48 pound for each one percent of inbreeding.

In a study of the weaning weights of purebred Herefords at the San Juan Basin Experiment Station, Fort Lewis A and M College, Hesperus, Colorado, Burgess, et al. (1954) found a deviation from the average weaning weights of -1.75 pounds per one percent inbreeding of the calf. Their analysis was confined to 546 conventional type Hereford calves out of conventional type Hereford dams. The calves were dropped during the period 1946-1951, inclusive. The percent of inbreeding of the calves in this study ranged from 0 to 50, with about three-fourths of the calves falling in the 0 to 20 range. They investigated the possibility of curvilinearity for the effects of inbreeding on weaning weights and found a significant deviation from linearity.

Reports have not been made on the effects of inbreeding on 18-month weight of beef heifers. However, Nelson and Lush (1950) working with dairy cattle indicated that the shape of the growth curve changes as the intensity of inbreeding changes. They further indicated that inbreeding slows the rate of growth at early age, but permits rapid growth to continue longer, so that mature size is not decreased and may even be increased. They concluded that increased inbreeding resulted in a smaller size at least to two years of age.

Nelson and Lush (1950) also reported the effects of inbreeding on dairy type. Their data were the classification scores of 215 individuals raised at the Iowa Agricultural Experiment Station. The average inbreeding of the group was 4.6 percent. They reported a non-significant regression of -0.04 for type on inbreeding.

Heritability Estimates

Weaning Weight

Heritability estimates that have been published for weaning weight of the beef calf vary considerably. One of the first investigations on the heritability of weaning weight was by Knapp and Nordskog (1946). They studied the records of 177 steer calves from 23 sires at the U. S. Range Livestock Experiment Station at Miles City, Montana. The authors used two methods to obtain their heritability estimates: The intra-sire correlation obtained by analysis of variance, and the sire-progeny regression obtained by covariance analysis. They reported estimates of zero by the sire-progeny regression method and 12 percent by intra-sire correlation.

These estimates were later revised by Knapp and Clark (1950) to 28 percent by half-sib correlations.

Gregory, et al. (1950) reported heritability estimates for weaning weights of calves raised at the North Platte and Valentine Substations of the Nebraska Agricultural Experiment Station. Since their data were from experiments designed primarily to determine the effects of different wintering rations on the performance of breeding cows, the analysis was made on an intra-year intra-lot basis. Due to the management differences at the two stations, paternal half-sib correlations were determined for each station. The authors reported a heritability estimate of 26 percent for the weaning weights of the 270 calves raised at the North Platte station and 52 percent for the 69 calves at the Valentine station.

Shelby, et al. (1955) studied weaning weight records of 635 steers raised at the U. S. Range Livestock Experiment Station at Miles City, Montana. The steers were from grade Hereford cows mated to 88 sires. Their estimate of heritability for weaning weight by paternal half-sib correlation was 23 percent, which is in close agreement with the estimate of 26 percent that Gregory, et al. (1950) reported at their North Platte station.

One of the most comprehensive investigations on economic characteristics in beef cattle was conducted by Koch and Clark (1955a) on Hereford calves raised at the U. S. Range Livestock Experiment Station at Miles City, Montana. The data available for their paternal half-sib analysis were the records of 4553 weaning weights. The weaning weights

were accumulated over the period 1929-1951 from 137 different sires. They reported a heritability estimate of 24 percent for weaning weights of beef calves computed from the paternal half-sib analysis.

Koch and Clark (1955b) in another extensive study at Miles City, used the method of regression of offspring on dam to obtain heritability estimates of weaning weights. In this study records on 4234 calves and their 1231 dams were available. The year effects and the age of dam effects were eliminated by grouping the pairs into subclasses according to the years the cows were born and the years the calves were born. In this study they found a heritability estimate of 11 percent for weaning weight. In another section of the same study the regression of offspring on sire was used to estimate heritability of weaning weight. The records from 85 sires and their offspring were used. The data were grouped into subclasses according to the year the sire was born and the year the calves were born. Their estimate of 25 percent heritability for weaning weight, when the progeny averages were regressed on the sires records, is in agreement with most recently published heritability estimates for weaning weight.

Working with data collected through the South Dakota Extension Service in cooperation with breeders throughout the state, Dinkel and Musson (1956) reported that about 36 percent of the individual differences in weaning weights are inherited. Their data included weaning weights on 646 calves sired by 62 bulls on eleven ranches. Since the authors found large environmental differences from year to year and ranch to ranch the analysis was made by comparing sires in the same year on

each ranch.

18 Month Weight

The estimates of heritability reported for 18-month weight of range beef heifers are very limited. Knapp and Nordmark (1946) gave an estimate of 61 percent heritability for 18-month weight of range beef heifers raised at the U. S. Range Livestock Experiment Station at Miles City, Montana. The half-sib correlation method was used to obtain their estimate.

Further studies on data collected at Miles City, Montana, were conducted by Koch and Clark (1955a) on the heritability of fall yearling weights of range Hereford heifers. Their data included 169 $\frac{1}{2}$ fall yearling weights that were accumulated over the period 1929-1951, from 137 different sires. They reported the heritability of fall yearling weight as 47 percent by the paternal half-sib correlation method.

Additional studies at Miles City, Montana, by Koch and Clark (1955b), were conducted to determine the heritability of fall yearling weight of beef heifers by parent-offspring regression. In their regression of offspring on dam study, records from 1623 heifers and their 822 dams were used. An estimate of 43 percent was reported for the heritability of fall yearling weight. This estimate and the one reported previously (47 percent) (1955a) indicate that fall yearling weight is highly heritable and probably above 40 percent.

18-Month Type Score

The heritability of fall yearling type scores of range beef heifers was reported as 27 percent by Koch and Clark (1955a). Their estimate was obtained from the paternal half-sib correlation among 1483 heifers sired by 124 different bulls. These heifers were raised at the U. S. Range Livestock Experiment Station at Miles City, Montana over the years 1936-1951.

Koch and Clark (1955b) reported the heritability of fall yearling type score obtained by the offspring-dam regression method. Their data included the records of 797 heifers and 443 dams carried at the range station at Miles City, Montana. An estimate of 14 percent heritability was obtained in this study.

McCormick, et al. (1956) listed an estimate of 15 percent for heritability of type score for yearling heifers at the end of feedlot tests. Their estimate was obtained by paternal half-sib correlation and included 148 purebred Polled Hereford heifers. These heifers were raised under farm conditions at the Georgia Coastal Plain Experiment Station in South Georgia. This estimate and the ones reported by Koch and Clark (1955a) (1955b) indicate that fall yearling type score is moderately heritable, in the range of 14-27 percent.

Genetic and Environmental Correlations

Knapp and Clark (1951) calculated genetic and environmental correlations between type score at weaning time and gains in the feedlot using data from 613 Hereford steers. A genetic correlation of .300 and an

environmental correlation of -0.304 were obtained. The authors indicated that apparently there are some genetic factors which determined both scores and gains, but that this is not observable in phenotypic correlations because of the negative influence of the environmental factors on scores and gains. The authors suggest that the negative environmental correlation may have been due to some compensating increased gains in the feedlot for the relatively poorer conditions of environment before weaning, or that negative correlation may exist between milk production and gains.

Genetic and environmental correlations between several characteristics of range beef heifers were reported by Koch and Clark (1955a). Their data included records of 4553 calves raised at the U. S. Range Livestock Experiment Station at Miles City, Montana. They reported a genetic correlation of $.49$ between yearling weight and yearling score, and an environmental correlation of $.61$ between the same characteristics. The genetic and environmental correlations between weaning weight and yearling weight were $.54$ and $.46$, respectively. They listed values of $.23$ and $.27$ for genetic and environmental correlations between yearling score and weaning weight. The authors suggest that the reason for the quite large genetic correlations between gains and scores would be that the better-doing calves would show more desirable beef characteristics than the unthrifty or slow-gaining calves.

SOURCE OF DATA

The data in this study were obtained from 303 unselected heifers raised by the South Dakota Agricultural Experiment Station under a co-operative project with the North Central States' Regional Beef Cattle Breeding Project. The heifers were from purebred Hereford cows carried on three outlying stations--the Antelope Range Field Station, Buffalo; the Range Field Station, Cottonwood; and the Reed Ranch, Presho.

The Antelope Range Field Station summer range is of the mixed prairie type with the medium height grasses dominating over the short grasses. The dominant medium height grasses are western wheat grass, green needlegrass, and needle-and-thread. The short grasses and grass-like plants found are blue grama grass, threadleaf sedge, needleleaf sedge, and buffalo grass. The Antelope Range lies in the Chestnut soil zone, composed principally of the sandy loam type. The average annual precipitation is 14 inches per year.

The summer range at the Cottonwood Range Field Station may be best described as a mixed prairie, consisting principally of short and medium height grasses. The dominant short grasses and grasslike plants are blue grama, buffalo grass, threadleaf sedge, needleleaf sedge, and sandberg blue grass. Among the dominant medium height grasses are western wheat grass, green needlegrass, needle-and-thread, sidecoats grama, and little bluestem. The soil is heavy, ranging in texture from a silty clay loam to a heavy clay. The climate is dry with an annual precipitation of about 15 inches, with about 60 percent of this falling during the months April to September.

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The vegetation at the Reed Ranch is a mixed short and tall grass, generally consisting of blue grama, buffalo grass, and western wheat grass, with green needlegrass, needle-and-throat, sideoats grama, cheat, and little bluestem grass intermixed. The soil is classified in the Promise and Pierre series, in the Chestnut soil zone. The climate is characteristically continental and subhumid, with frequent extended periods of drought. Precipitation averages 17.5 inches per year with about 65 percent of it falling during the months April to September.

The beef cattle breeding project was originally started in 1947. At this time the Antelope Range beef breeding herd was obtained on a lease program. The cows were leased by the Experiment Station from cattle breeders in the state. Most of these original cows were purchased by the Experiment Station in 1949. Originally the cow herd at the Range Field Station at Cottonwood was used for both the range management studies and the breeding studies. Since 1951 the two projects have been separated in order to prevent confounding of the data with respect to the primary objectives of both studies.

The present inbred lines were formed in 1952. Four one-sire lines and one control line were originally started at the Antelope Range Station. Three inbred lines and one control were started at the Reed Ranch, and one inbred line at Cottonwood. Two inbred lines at Reed Ranch were subsequently moved to the Antelope station.

The calves are weighed at weaning about the end of October or first of November. Prior to the 1952 calf crop, the heifers were wintered and summer grazed at the ranches where they were born, with the exception

that the 1951 heifer calves born at Antelope were summer grazed at the Newell substation. Since 1951, the heifer calves from all stations have been moved to Cottonwood for wintering and summer grazing. The plane of nutrition for wintering the heifers allows a gain of approximately one to one and one-half pounds per day. The wintering ration for the calves dropped during the period 1951 to 1954, inclusive, was five pounds oats, one pound 40 percent cottonseed cake, and prairie hay free choice. The 1955 calf crop received two pounds of cottonseed cake and prairie hay free choice. The heifers are placed on pasture about the first of May and do not receive any supplement during summer grazing. The heifers are removed from summer grazing around the middle of October and at this time are weighed and typed scored. The type scoring is conducted by a committee of three judges, each judge working independently and using the following scoring system:

Score	Code	
17	17	
1	16	Suitable type for show prospect
1-	15	
2	14	
2	13	Suitable type to be used in purebred herds
2-	12	
3	11	
3	10	Average range heifers
3-	9	
4	8	
4	7	Heifers of this grade and lower are not recommended for use
4-	6	
5	5	
5	4	
5-	3	

Tables I and II list the mean 18-month weight, weaning weight and 18-month type score by years, ranches and sires. In the case of 18-month weights, the weights are adjusted to a common age of 550 days and to the basis of a heifer from a six year old dam. The weaning weights presented are adjusted to a 190 day basis from a six year old dam. Corrections for the effects of inbreeding on weaning weight were made.

Table I. Year and Ranch Means

Year of Birth	No. of Progeny	18-Month Weight (lbs.)	No. of Progeny	Weaning Weight (lbs.)	No. of Progeny	18-Month Type Score
1948	20	681	20	379	20	11.2
1949	27	653	27	363	27	10.9
1950	16	779	19	394	19	10.7
1951	30	669	32	411	32	10.5
1952	41	763	44	388	44	11.1
1953	41	763	41	457	41	10.6
1954	60	758	60	434	60	10.5
1955	49	754	49	434	49	10.4
Ranch						
Reed	44	705	49	374	49	10.5
Cotton-wood	108	705	109	396	109	10.7
Antelope	132	768	134	446	134	10.7

The means in Table I show that the 18-month weight of the heifers did vary from year to year, as indicated by the mean of 779 pounds for heifers born in 1950 and the mean of 653 pounds for the 1949 heifers. Weaning weights varied from a high of 457 pounds in 1953 to a low of 363 pounds in 1949. The 18-month type scores varied from 11.2 in 1948 to 10.4 in 1955. The table also indicates that the heifers born at the Antelope Range Field Station had heavier weaning and 18-month weights than the heifers born at the other two stations. The means for type scores at the three stations show little variation as indicated by the mean of 10.5 for heifers born at Reed Ranch and 10.7 for the Cottonwood and Antelope heifers.

Differences in ability of sires to produce heavier heifers at 18-month of age is shown in Table II. The means vary from a high of 865 pounds for sire 022, to a low of 630 pounds for sire 011. Considerable variation is also indicated for weaning weights, with a range from 362 to 472 pounds. Little difference in the means for type score is found, with the exception of sire 011 whose heifers averaged 7.5.

Table II. Sire Means

Sire	No. of Progeny	18-Month Weight (lbs.)	No. of Progeny	Weaning Weight (lbs.)	No. of Progeny	18-Month Type Score
022	2	865	2	446	2	10.5
xx3	2	820	3	441	3	11.7
012	18	810	18	472	18	10.5
233	10	784	10	470	10	9.8
101	40	779	42	445	42	10.4
436	7	776	7	451	7	10.3
219	10	772	10	423	10	11.3
030	5	766	5	411	5	10.8
014	14	759	14	452	14	11.0
339	4	751	4	362	4	10.8
228	13	750	13	448	13	10.8
920	12	746	12	420	12	11.8
433	10	743	10	406	10	10.8
132	5	738	5	443	5	10.4
028	9	725	9	393	9	10.4
027	5	723	5	374	5	10.4
032	10	717	10	408	10	10.9
321	8	714	8	418	8	10.6
502	8	712	8	388	8	10.6
013	2	712	2	414	2	11.0
402	8	705	9	428	9	11.2
015	6	702	6	368	6	10.3
026	18	701	18	388	18	9.9
x08	17	677	17	364	17	12.1
601	23	676	23	369	23	10.7
xx4	3	666	3	377	3	11.3
023	7	650	10	390	10	10.3
011	2	630	2	356	2	7.5

The effects of sire on the 18-month weight, weaning weight and 18-month type score were determined by using the least squares method of estimation of multiple regression with orthogonal contrast. The results are shown in Table II (1954), Table III (1955), Table IV (1956) and Table V (1957).

STATISTICAL ANALYSIS

Age Correction Factors for 18-Month Weight

In order to measure the effect of age on 18-month weight, the regression coefficient for weight on age was calculated. One hundred and thirty-one heifers from 15 sires were used for this study. The data included heifers from three ranches dropped during the period 1948 to 1952, inclusive, using the non-inbred animals only. In the analysis of variance, year and ranch effects were avoided by analyzing the data on an intra-year, intra-ranch basis. The sums of squares and cross-products were then pooled to obtain the regression coefficient for 18-month weight on age. The intercept of the regression line on the age axis was determined for use in the equation developed by Whatley and Quaife (1937):

$$Y = \frac{S - I}{A - I},$$

where Y is the correction factor, S is the standard age, I is the intercept and A is the actual age.

Effects of Inbreeding

The effects of inbreeding of an animal on its weaning weight, 18-month weight and 18-month type score were determined by using the least squares method of estimation of multiple classifications with nonorthogonal data. This method was studied and discussed by Yates (1934), Crump (1946), (1951), Eisenhart (1947) and Henderson (1953).

The inbreeding study included records from 143 heifers raised at three ranches during the period 1953 to 1955, inclusive. The data for all animals were adjusted to a common age. The weaning weights were corrected to 190 days by using the correction factors obtained by Johnson and Dinkel (1951). The 18-month weight age correction factors developed by Dinkel (1953) were used. The inbreeding coefficients were determined by using the methods outlined by Wright (1922) and Baik and Terrill (1949).

The first step in this method is to form a mathematical model describing the manner in which the observations are influenced by the sources of variation. The following mathematical model was assumed for this study.

$$Y_{ijklm} = \mu + a_{ijk} + I_m + e_{ijklm}$$

Y_{ijklm} = 18-month weight in the i th year from the j th line at the k th ranch, with m inbreeding and of the o th individual.

μ = the effect common to all calves.

a_{ijk} = the effect common to all calves born in the i th year from the j th line at the k th ranch.

I_m = the effect common to all calves from the m th inbreeding group.

e_{ijklm} = sum of all other things which cause that individual observation to vary.

Constants were then fitted for each independent variable. In this study constants were fitted for 25 sire-ranch-year groups, and six inbreeding classifications.

In solving the least squares equations, the zero inbreeding classification was deleted, making the equations independent. The estimates obtained for each remaining inbreeding classification are deviations from the zero classification.

Heritability Estimates and Genetic Correlations

Lush (1940) lists several methods for estimating heritability. The two methods that he lists that appear to lend themselves to this data are the paternal half-sib correlation and the intra-sire regression of offspring on dam.

Paternal Half-sib Correlations

The data available for the paternal half-sib analysis included the records from 126 heifers, raised during the period 1948 to 1952, inclusive. Fifteen sires were represented. The weaning and 18-month weights were adjusted to a constant age by using the correction factors obtained by Johnson and Dinkel (1951) and Dinkel (1953), respectively. The correction factors for age of dam, Koch and Clark (1955a), were used to adjust the weaning and 18-month weights. The data were analyzed on an intra-year, intra-ranch basis. Some sires were used in more than one year, however, each yearly sample would be an unbiased estimate of the sire differences. In the analysis the between and within sire sums of squares were pooled to obtain estimates of the components of variance.

The methods used here for estimating the components of variance and covariance have been studied and discussed by Hazel, et al. (1943), Knapp and Clark (1947), (1951), Henderson (1953) and Snedecor (1956).

A number of factors may affect both weight and score of an animal. Since each source of variation is quantitative, or partially so, estimates of each source can be made. The weight of the heifer, X , is the sum of two variables, (1) a genetic source (G), composed of the average effects of all genes which influence the characteristics; (2) a residual effect (E), including the effects of the dominance, epistasis and environmental factors peculiar to the individual heifer. This is also true for any other characteristic. Then the weight or score of an animal can be defined by the following equation:

$X = G + E + 2Cov_{GE}$. Since the data were analyzed on an intra-year intra-ranch basis there is no reason to suspect that a correlation exists between G and E , and it is assumed therefore to be zero. The variance in weight or score may then be defined as follows: $V(X) = V(G) + V(E)$. To obtain the components of variance the intra-year intra-ranch variance must be broken down into two mean squares; between sire groups and within sire groups. Under the conditions of random mating, half-sibs each receive a sample half of their sire's inheritance; hence the genetic value of half-sibs would be correlated by one-fourth, dominance deviations are uncorrelated, and epistatic deviations are correlated by a small but undetermined amount. If the environmental correlations between half-sibs have been adequately removed and epistasis is negligible, the expected value of the sire

component is, $V_s = \frac{1}{4} V(G)$, under random mating. The expected value for the within sires mean square is $V = 3/4 V(G) + V(E)$. Based on these assumptions the genetic and environmental variances may be calculated as follows:

$$V(G) = 4V_s$$

$$V(E) = V - 3V_s$$

In an infinite population, the sum of $V + V_s$ is the total or population variance. The fraction $\frac{V_s}{V + V_s}$ is the intraclass correlation among half-sib groups and when multiplied by four represents the theoretical additive genetic portion of the total variance or heritability (h^2).

The fiducial limits for the paternal half-sib correlation estimates of heritability were computed by following the method outlined by Knapp and Nordskog (1946). The procedures for obtaining the limits are as follows: The significance of the mean square is first obtained by dividing it by its appropriate error mean square. The resulting ratio is F . In terms of mean square components $F = \frac{V}{kV_s}$ which is equal to $(1 + k \frac{V_s}{V})$. V_s is therefore equal to $\frac{(F - 1)V}{k}$ for n and n' degrees of freedom. Since h^2 is equal to $\frac{4V_s}{V + V_s}$ substituting $\frac{(F - 1)V}{k}$ for V_s in the equation, the following equation expresses the sampling error of $h^2 = 0$, $E_h = \frac{4(F - 1)}{k + F - 1}$. In order to calculate chance deviation from true heritability (h^2 is greater than zero) it is necessary to employ Fisher's z for which the upper and lower limits may be obtained for a given level of probability.

By converting the fiducial limits of z in terms of F and substituting into the formula: $\frac{4(F - 1)}{k / F - 1}$ the fiducial limits of h^2 are obtained.

Genetic and Environmental Correlations

The genetic and environmental correlations can be obtained from the components in a paternal half-sib analysis of variance and covariance. The procedures for this study were discussed by Hazel, et al. (1943) and Knapp and Clark, (1947), (1951), and the data were those used in the paternal half-sib analysis.

The covariance components can be calculated in the same manner as the variance components. The variance in weight or score was defined as due to two sources of variation; that due to genetic source (G), and the other due to residual (E), which included dominance, epistasis and environment. The covariance, between any two traits can likewise be divided into:

$$\text{Cov}_{X_1X_2} = \text{Cov}_{G_1G_2} / \text{Cov}_{E_1E_2},$$

provided each source is statistically independent of the other source. The expected covariance value for the sire component of covariance would be the same as in the variance analysis and would be $\text{Cov}_{S_1S_2} = \frac{1}{4}\text{Cov}_{G_1G_2}$, under random mating. The expected value for the within sire mean square would be $\text{Cov} = \frac{3}{4}\text{Cov}_{G_1G_2} / \text{Cov}_{E_1E_2}$. Based on these assumptions the genetic and environmental covariance between two traits may be calculated as follows:

$$\text{Cov}_{G_1 G_j} = 4 \text{ Cov}_{S_1 S_j},$$

$$\text{Cov}_{E_1 E_j} = \text{Cov} - 3 \text{ Cov}_{S_1 S_j}.$$

From these equations and the ones from the half-sib analysis, the correlation of the effect of one source of variation (either G or E) between one trait and another may be calculated as follows:

$$r_{G_1 G_j} = \text{Cov}_{G_1 G_j}$$

$$\sqrt{V(G_1) \cdot V(G_j)}$$

Regression of Offspring on Dam

The data suitable for the intra-sire regression of offspring on dam consisted of records from 113 heifers and their dams for weaning weight, 110 pairs for 18-month weight and 132 pairs for 18-month type score. The heifers were born during the period 1951-1955, inclusive, and included animals from the one-sire inbred lines. The weaning and 18-month weights were adjusted to a constant age by using the corrections obtained by Johnson and Dinkel (1951) and Dinkel (1953), respectively. The age of dam corrections obtained by Koch and Clark (1955a) were used. Corrections for the effect of inbreeding on weaning weights were made by using the estimates obtained from the inbreeding study.

The method of analysis used here was outlined and discussed by Hazel and Terrill (1945). The data were analyzed on an intra-sire intra-year basis. The estimates of the phenotypic variance and covariance for the traits were obtained from the pooled sums of squares and cross-products, within sire subclasses. In analyzing non-inbred

populations the formula for estimating heritability from the intra-sire regression of offspring on dam is $\frac{2 \text{ cov } (b)}{B'}$, where $\text{Cov } (b)$ is the covariance between a dam and her offspring within the sire group and B' represents the variance between dams mated to the same sire. In one-sire inbred lines, the dams are related to each other and also to the sire, necessitating the modification of the formula for heritability. The formula for estimating heritability from one-sire inbred lines is as follows:

$$\frac{2}{1 + f' - 2f} \cdot \frac{\text{cov}(b)}{B' + 2 \frac{(2f - f') \text{ cov } (b)}{1 + f' - 2f}}, \text{ Hazel and Terrill}$$

(1945). f' and f are the inbreeding coefficients for parents and offspring, respectively.

The standard error of the heritability estimate would also be biased by the inbreeding. The formula for estimating the standard error would be:

$$\frac{2}{1 + f' - 2f} \cdot \sqrt{\frac{B B' - \text{cov } (b)^2}{(B')^2 (nk - n - 1)}}, \text{ Hazel and}$$

Terrill (1945). The component B represents the variance between heifers by the same sire, n the number of sires and k is the number of calves per sire.

Comparisons of Selection Methods

The effectiveness of the selection program is an important consideration in any range beef operation. This effectiveness can

be measured by the use of a selection differential. Selection differential is defined here as the difference between the average of those selected to be parents and the average of the whole population in which they were born. Selection differentials were determined for weaning weight, 18-month weight and 18-month type score for each method of selection used. The methods of selection used were based on the following traits and combinations of traits:

<u>Selection Method</u>	<u>Trait or Traits Involved</u>
1	Weaning weight, 18-month weight and 18-month type score
2	Weaning weight and 18-month weight
3	Weaning weight and 18-month type score
4	18-month weight and 18-month type score
5	Weaning weight
6	18-month weight
7	18-month type score

The data used in this study consisted of records from 254 pure-bred Hereford heifers born during the period 1948-1954, inclusive. The weaning and 18-month weights were corrected to a constant age by using the factors obtained by Johnson and Dinkel (1951) and Dinkel (1953), respectively. The weaning weights were corrected for age of dam by using the factors obtained by Koch and Clark (1955a).

The index of net desirability of an animal was determined by combining the credits or penalties of each trait considered in a selection method. The credit or penalty to be placed on each trait

was determined by dividing the deviation from the yearly average by the standard deviation of the trait. This would place equal emphasis on each trait considered in a selection method. The standard deviations used were obtained from the total variance of the population and are as follows: weaning weight 53, 18-month weight 92, and 18-month type score 1.6.

Forty percent of each yearly heifer crop was selected as replacement on the basis of the index of net desirability in each selection method. The totals of the weights or type scores for each year's selected group were combined and averaged to obtain the average of the selected group. The difference between the average of the selected group and the average of the whole population, for each trait would be the average selection differential.

The overall genetic progress that could be made with each method of selection was determined by combining the selection differentials for the various traits after each was weighted by its heritability and its economic importance.

The economic value assigned to a trait was the relative effect this trait is assumed to have on profit when it varies one unit. The average price of 100 pounds of Good to Choice beef heifer calves sold at the Omaha, Nebraska market was \$17.00, during the months of August to November, inclusive, in 1955 and 1956. For the same period of time and at the same market Choice yearling beef heifers were selling for \$17.70 per hundred, and Medium to Good yearling heifers were selling for \$14.32. The economic value for type score was determined by

considering Choice heifers would score in the Type two range and the Medium to Good would be in the Type three range. The average difference in sale price for adjacent classes is \$.84 per hundred. The average 18-month weight of heifers in this study was 716 pounds, therefore, an increase in one-third of a type score would be an increase of \$6.01 in income. These estimates were based on data presented by Market News (1956). The relative economic values obtained from the above considerations and used in the study are: weaning weight .17, 18-month weight .18, and 18-month type score 6.01.

The heritability estimates used were obtained from estimates reported by other workers. The estimate of 25 percent was used for weaning weight which is in agreement with estimates reported by most workers. The heritability estimate for 18-month weight used was 47 percent, Koch and Clark (1955a) and the estimate for 18-month type score was 27 percent from the same study.

Selection Indexes

It has been shown that selection for at least the additive genetic portion of variation, when considering more than one trait per individual, can be done most efficiently by selecting for the traits simultaneously, Hazel and Lush (1942). The index of net desirability of an animal is constructed by combining into one figure the credits and penalties given each animal according to its superiority or inferiority of each trait. The methods for constructing selection indexes have been discussed by Hazel (1943) and used by

Karam, et al. (1953) and Bernard, et al. (1954).

The goal toward which selection will be directed should be considered in the first step in constructing an index. Therefore, the aggregate genetic value of an animal is defined as:

$$H = a_1G_1 + a_2G_2 + a_3G_3$$

where G_1 , G_2 , and G_3 are the genetic values for weaning weight, 18-month weight and 18-month type score, respectively, and a_1 , a_2 and a_3 are the relative economic values of these traits.

The index is a linear function of the observed records,

$$I = b_1X_1 + b_2X_2 + b_3X_3,$$

where the X 's represent the phenotypic performance for the traits, and the b 's are multiple regression coefficients, designed to make r_{IH} as large as possible. These regression coefficients may be calculated from simultaneous equations:

$$B_1 + B_2r_{X_1X_2} + B_3r_{X_1X_3} = r_{X_1H}$$

$$B_1r_{X_1X_2} + B_2 + B_3r_{X_2X_3} = r_{X_2H}$$

$$B_1r_{X_1X_3} + B_2r_{X_2X_3} + B_3 = r_{X_3H}$$

where $B_i = b_i \frac{\sigma_{X_i}}{\sigma_H}$ and r_{X_iH} is the correlation between H and the i th phenotypic measurement. The standard deviation of the breeding value (σ_H) is as follows:

$$\sigma_H = \sqrt{a_1^2\sigma_{G_1}^2 + a_2^2\sigma_{G_2}^2 + \dots + 2a_1a_2\sigma_{G_1}\sigma_{G_2}r_{G_1G_2} + \dots},$$

where $\sigma_{G_i}^2 = h_i^2\sigma_{X_i}^2$, h^2 is the heritability estimate of the X_i trait. The correlation between H and the i th phenotypic measurement

is as follows:

$$^H X_{1H} = r_{G_1 X_1} \left\{ d_1 r_{G_1 G_1} + d_2 r_{G_2 G_1} + d_3 r_{G_3 G_1} \right\},$$

where $d_1 = a_1 \frac{\sigma_{G_1}}{\sigma_H}$, and $r_{G_1 X_1}$ is the correlation between genotype and phenotypic performance for each trait.

Genetic improvement will be proportional to the multiple correlation between the index and H , (r_{IH}). This correlation provides a means of comparing the accuracy of the indexes.

The data available from the South Dakota Experiment Station records did not furnish all the estimates required for the construction of the indexes. With the help of statistics reported by other workers, the construction of the indexes was possible.

Table III gives the test of significance for the analysis of variance and covariance for 15-month weight and 15-month age. The F -test indicates that the effect of the sow's age on her 15-month weight is highly significant. The regression coefficient of weight on age was 1.18. The standard error for the regression coefficient was 1.33. The regression line intersected the age axis at -42 days. Using the method outlined by Weather and Quigley (1917) the approximate factor is as follows:

$$CF = \frac{1.18}{\text{Actual age} - (-42)}$$

The age correction factors for the 15-month weight obtained from the analysis of variance and covariance are listed in Table IV. The twelve and thirty-two sows were used in this study. With these limited data the correction factors should be considered only

RESULTS

Age Correction Factors

The relationship between 18-month weight and age, expressed in days, is shown in Figure I. The range in age varied from 459 days to a maximum of 593 days. The mean age was 542 days. The dots represent the averages of all weights available for each day of age. The x's represent the average weights of all heifers within successive 10 day periods. The straight line drawn in the figure is the linear regression of weight on age. The figure shows that the growth from about 490 days to 580 days is practically an additive effect, however, the observations within each day class vary considerably.

Table III gives the test of significance for the analysis of variance and covariance for 18-month weight and 18-month age. The F-test indicates that the effect of the heifer's age on her 18-month weight is highly significant. The regression coefficient of weight on age was 1.18. The standard error for the regression coefficient was $\pm .22$. The regression line intercepted the age axis at -42 days. Using the method outlined by Whatley and Quaife (1937) the correction factor is as follows:

$$CF = \frac{592}{\text{Actual age} - (-42)}$$

The age correction factors for the 18-month weight obtained from the analysis of variance and covariance are listed in Table IV. One hundred and thirty-one animals were used in this study. With these limited data the correction factors should be considered only

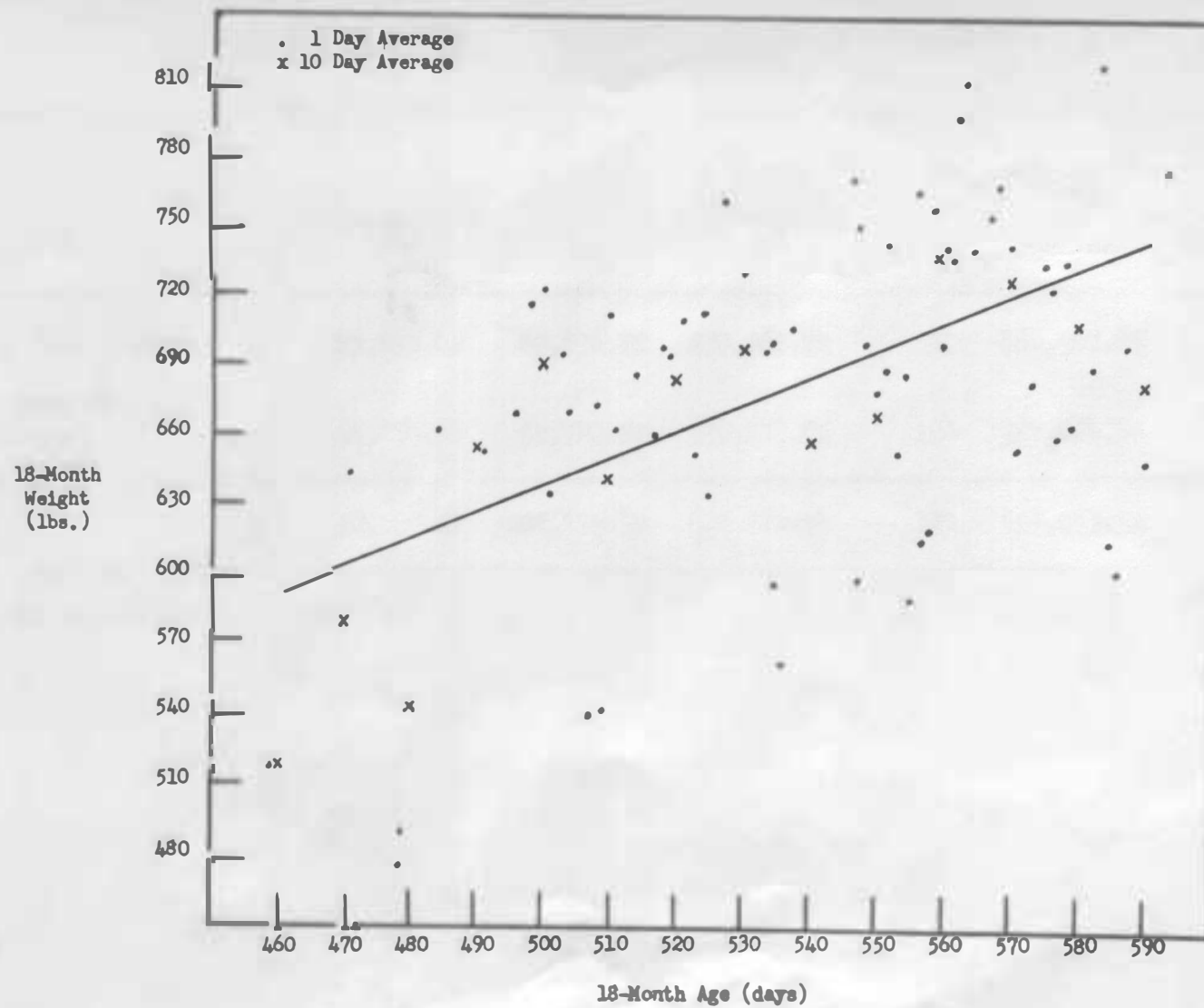


Figure I. Relation of 18-Month Weight to 18-Month Age

Table III. Analysis of Variance and Covariance for 18-Month Age
and 18-Month Weight

Source of Variance	df	18-Month Age Sz^2	Sxz	18-Month Wt. Sx^2	Residuals		
					df	Sums of Squares	Mean Squares
Between Sire Groups	17	25,695.09	49,596.72	270,965.72	17	184,398.86	10,846.99**
Within Sire Groups (Error)	105	44,854.98	52,982.87	370,248.02	104	307,664.46	2,958.31
T / E	122	70,550.07	102,579.59	641,213.74	121	492,063.32	

** Highly Significant ($P < .01$)

Table IV. Age Correction Factors for 18-Month Weight of Range Heifers
Standard Age = 550 days

Actual Age	Correction Factor	Actual Age	Correction Factor
441-	1.23	514-518	1.06
442-445	1.22	519-524	1.05
446-449	1.21	525-529	1.04
450-453	1.20	530-535	1.03
454-457	1.19	536-541	1.02
458-461	1.18	542-547	1.01
462-466	1.17	548-552	1.00
467-470	1.16	553-558	.99
471-475	1.15	559-565	.98
476-479	1.14	566-571	.97
480-484	1.13	572-577	.96
485-488	1.12	578-584	.95
489-493	1.11	585-591	.94
494-498	1.10	592-597	.93
499-503	1.09	598-604	.92
504-508	1.08	605-610	.91
509-513	1.07	611-	.90

Table V shows the comparison of corrected weights when two different methods were used to adjust the 18-month to a constant age. The correction factors for Method I, were determined by Dinkel (1953), from a solution of least squares simultaneous equations. The second method is from the analysis of variance and covariance just outlined. The standard errors indicate a slight favor for the Method II correction factors. The "t" test indicates that the difference between the two methods is non-significant.

Table V. Comparisons of Two Methods for Correcting 18-Month Weight to a Constant Age of 550 days

Actual Weight	Corrected Weights		Actual Weight	Corrected Weights	
	Method I	Method II		Method I	Method II
880	880	880	788	788	780
680	680	680	768	814	822
852	861	861	694	715	715
776	807	807	822	814	814
790	782	774	754	746	739
788	788	788	726	726	726
768	760	753	706	727	734
742	735	727	678	692	698
728	721	721	814	822	822
806	798	798	822	822	814
772	772	772	700	700	707
746	753	753	636	661	661
640	698	710	716	709	695
736	788	795	794	818	826
592	633	639	762	800	800
658	678	678	720	727	727
664	664	664	760	760	768
822	814	806	742	749	749
770	770	770	700	742	749
746	739	739	714	707	707
746	739	731	704	704	704
832	815	815	778	786	786
721	714	714	638	702	708
610	683	702	720	720	727
741	734	726	722	744	744
519	555	566	Totals	44,502	44,529
768	774	783	n	60	60
718	711	711	Means	741.70	742.15
618	612	612	Standard		
753	738	738	Error	± 7.68	± 7.55
749	742	742	t = .5895		
660	660	653	.05 for 59 d.f. = 2.0008		
753	753	745			
722	744	744			
717	710	710			

Effects of Inbreeding

The estimates of the effects of inbreeding on weaning weight, 18-month weight and 18-month type score are presented in Table VI. In solving the least squares equations in this analysis, the zero inbreeding classification was deleted, making the equations independent. Therefore, the estimates presented in Table VI are deviations from the zero classification. For example, a heifer that is 25 percent inbred would be expected to weigh 57 pounds less at 18-months than a non-inbred. The effects of inbreeding on weaning weight and 18-month weight were curvilinear, as indicated by the irregular decrease in the weights as inbreeding approached 25 percent. However, the increased inbreeding had very little effect on type score, as indicated by the reduction of only one-third of a grade in the 16 to 20 percent inbreeding classification and less than one-third of a grade in the 21 to 25 percent classification.

Table VI. Estimates of the Inbreeding Effects

Percent Inbreeding	Number Animals	18-Month Weight	Weaning Weight	18-Month Type Score
0	25	0	0	0
1 - 5	19	-23.30	-22.77	0.27
6 - 10	39	-28.44	-38.56	0.26
11 - 15	36	-25.89	-33.86	-0.20
16 - 20	12	-55.55	-43.40	-1.01
21 - 25	12	-56.62	-52.66	-0.85

Table VII. Analysis of Variance for 18-Month Weight

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F-Value
Total	142	79,180,227.000	-	-
Total reduction due to (a,1)	30	78,905,998.952	-	-
Due to year-line-ranch (a)	25	78,884,132.835	-	-
Due to inbreeding (1)	5	21,866.117	4,373.2234	1.79
Remainder	112	274,228.048	2,448.4647	

The analysis of variance for 18-month weight is shown in Table VII. The difference between the levels of inbreeding for the reduction in 18-month weight was not significant.

The total reduction in sum of squares due to fitting constants for the year-line-ranch and inbreeding classifications is 78,905,998.952. This reduction was obtained by summing the products of the estimates and their corresponding right hand sides in the original matrix. The sums of squares due to the inbreeding classification were obtained by subtracting from the total reduction, the reduction due to fitting all but the inbreeding classifications. The error term used in the analysis is the remainder shown in Table VII.

Table VIII shows the analysis of variance for weaning weight. The analysis was carried out in the same manner as the analysis for 18-month weight. A significant difference, at the .05 level of probability, was found between the levels of inbreeding.

Table VIII. Analysis of Variance for Weaning Weight

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F-Value
Total	142	24,440,125.000	-	-
Total reduction due to (a, 1)	30	24,291,443.995	-	-
Due to year-line-ranch (a)	25	24,272,557.989	-	-
Due to inbreeding (1)	5	18,886.006	3,777.2012	2.85*
Remainder	112	148,681.005	1,327.5090	

* Significant ($P < .05$)

Table IX. Analysis of Variance for 18-Month Type Score

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F-Value
Total	142	16,190.000	-	-
Total reduction due to (a, 1)	30	15,995.677	-	-
Due to year-line-ranch (a)	25	15,981.111	-	-
Due to inbreeding (1)	5	15.566	3.1132	1.80
Remainder	112	193.323	1.7261	

A non-significant difference was found between the levels of in-breeding for 18-month type score. This is indicated by the analysis of variance given in Table IX.

Heritability Estimates and Genetic Correlations

Paternal Half-sib Analysis

Table X gives the mean squares and covariance terms that were obtained from the pooled paternal half-sib analysis of variance and covariance. No significant difference was found between sire groups for weaning weight. However, the difference between sire groups for 18-month weight was significant at the .01 level of probability. Significance at the .05 level was found for differences between sire groups for 18-month type score.

The non-significant difference between sire groups for weaning weight, and the highly significant difference between sire groups for 18-month weight, is confusing. With weaning weight being a large component of 18-month weight it would be expected that the two traits would react similarly. Since the data from the Cottonwood station taken in 1948 to 1951, inclusive, included records from heifers on the rate of grazing study, it was felt that this would magnify the within sire differences for weaning weight. If this were so, a non-significant difference between sire groups might occur. However, when the data were analyzed on an intra-year intra-pasture treatment basis a non-significant difference was still found between sire groups for weaning weight, as shown by the pooled analysis of variance in Table XI.

Table X. Analysis of Variance and Covariance for Weaning Weight (X),
18-Month Weight (Y) and 18-Month Type Score (Z)

Source of Variance	df	Theoretical Composition	Mean Squares			Cross-products		
			X	Y	Z	XY	XZ	YZ
Between Sire Groups ^{a/}	16	B / kA	1,835.28	14,041.37**	4.76*	2,818.96	10.35	19.17
Within Sire Groups	102	B	1,866.89	3,095.08	2.38	1,320.55	2.70	9.52

a/ Within year-ranch groups

** Highly Significant (P < .01)

* Significant (P < .05)

Table XI. Analysis of Variance for Weaning Weight and 18-Month Weight

Source of Variance	df	Mean Squares	
		Weaning Weight	18-Month Weight
Between Sire Groups ^{a/}	20	1,528.41	7,467.69**
Within Sire Groups	77	1,763.80	3,089.13

^{a/} Within year-ranch-pasture treatment groups

** Highly Significant ($P < .01$)

Table XII. Components of Variances and Covariances for Weaning Weight (X), 18-Month Weight (Y) and 18-Month Type Score (Z)

Source of Variance	Weaning Weight X	XY	18-Month Weight Y	18-Month Type Score Z		
				YZ	Z	XZ
Sire Variance (A)	-6.10	289.27	2,113.18	1.86	.46	1.48
Within Sire (B)	1,866.89	1,320.55	3,095.08	9.52	2.38	2.70

The components of variance and covariance for weaning weight, 18-month weight, and 18-month type score are given in Table XII.

The half-sib estimates of heritability for weaning weight, 18-month weight and 18-month type score are given in Table XIII. Probably the best estimate for heritability of weaning weight from these data would be zero. An extremely high estimate of 1.62 was found for the heritability of 18-month weight. The fiducial limits estimate the

sampling error of these heritability estimates, and indicate that one of the probable causes for the large range of heritability estimates would be that the population is too restricted to give reliable estimates.

Table XIII. Heritability Estimates Computed from the Paternal Half-sib Analysis

	Weaning Weight	18-Month Weight	18-Month Type Score
Heritability	-.01	1.62	.65
95 percent fiducial limits			
Upper	.71	2.52	1.57
Lower	-.38	.92	.09

The genetic, environmental and phenotypic components of variance and covariance among paternal half-sibs are given in Table XIV. The negative genetic component of variance for weaning weight is due to the greater variance within sire groups than between sire groups. The larger between sire component of variance, compared to the within sire component, for 18-month weight would cause the negative environmental component for 18-month weight. The environmental variance was determined by the formula $V(E) = V - 3V_s$, where V is the within sire variance component and V_s is the sire variance component. Consequently a large sire variance component would cause a negative environmental component.

The genetic, environmental and phenotypic correlations that were available in these data are presented in Table XV. The negative components of variance that appear in Table XIV, make it impossible to obtain some of

Table XIV. Genetic, Environmental and Phenotypic Components of Variance and Covariance among Paternal Half-sibs^{a/}

		Weaning Weight	18-Month Weight	18-Month Type Score
Weaning Weight	Genetic	-24.40	1,157.08	5.92
	Environ.	1,885.19	452.74	-1.74
	Pheno.	1,860.79	1,609.82	4.18
18-Month Weight	Genetic		8,452.72	7.44
	Environ.		-3,244.46	3.94
	Pheno.		5,208.26	11.38
18-Month Type	Genetic			1.84
	Environ.			1.00
	Pheno.			2.84

^{a/}Variance on main diagonal; covariance off main diagonal.

Table IV. Genetic, Environmental and Phenotypic Correlations among Paternal Half-sibs

		18-Month Weight	18-Month Type Score
Weaning Weight	Genetic	---	---
	Environ.	---	-.04
	Pheno.	.52	.06
18-Month Weight	Genetic		.06
	Environ.		---
	Pheno.		.09

the correlation coefficients. The formula used to obtain the correlation coefficients was as follows:

$$r_{X_i X_j} = \frac{\text{Cov}(X_i X_j)}{\sqrt{V(X_i) \cdot V(X_j)}},$$

where the X's can represent G, E or P. Consequently, when conflicting signs appear in the denominator it is impossible to obtain the correlation coefficient. Low genetic and phenotypic correlations (.06) and (.09) were found between 18-month weight and 18-month type score. A phenotypic correlation of .52 was found between weaning weight and 18-month weight. The phenotypic correlation between weaning weight and 18-month type score was .06, with a negative environmental correlation of -.04.

Regression of Offspring on Dam Analysis

The heritability estimates obtained from the intra-sire regression of offspring on dam are presented in Table XVI. The negative heritability obtained for weaning weight is due to the negative cross-product term obtained within sires. One of the possible causes for the negative cross-product would be if the cows with heavier weaning weights produced calves with lighter weaning weights and those cows with light weaning weights produced calves with heavier weaning weights. The 18-month weight estimate of heritability is .19 and the estimate for 18-month type score is .26. The standard errors for the heritability estimate of weaning weight are below the range that would be necessary to bring the estimate above zero, even though true heritability can never be negative.

Table XVI. Heritability Estimates Computed from Regression of Offspring on Dam

	Weaning Weight	18-Month Weight	18-Month Type Score
Heritability	-.26	.19	.26
Standard error	$\pm .24$	$\pm .14$	$\pm .22$

Table XVII. Mean Squares and Covariances for Weaning Weights of 113 Dams and Daughters

Source of Variance	df	Mean Squares		Cross-products Dams and Daughters	Constants
		Dams	Daughters		
Between Sires ^{a/}	23	3,051.74*	7,877.32**	-149.14	$r' = .004$
Within Sires	85	1,657.24	1,313.60	-182.34	$r = .092$

^{a/} Within birth year groups of daughters

** Highly Significant ($P < .01$)

* Significant ($P < .05$)

The mean squares and covariances for weaning weights are given in Table XVII. A highly significant difference was found between sires for their daughters' weaning weights. A significant difference at the .05 level of probability was found between sires for the weaning weights of the dams.

The difference between sires for 18-month weight of heifers was found significant at the .01 level of probability as indicated in Table XVIII. A non-significant difference was found between sires for 18-month weight of the dams.

The mean squares and covariances for 18-month type score are given in Table XIX. No significant difference was found between sire groups for type score of their daughters.

Table XVIII. Mean Squares and Covariances for 18-Month Weights of 110 Dams and Daughters

Source of Variance	df	Mean Squares		Cross-products Dams and Daughters	Constants
		Dams	Daughters		
Between Sires ^{a/}	24	10,525.72	6,598.18**	-978.03	$r' = .005$
Within Sires	81	8,435.51	2,223.39	684.35	$r = .088$

^{a/} Within birth year groups of daughters

** Highly Significant ($P < .01$)

Table XIX. Mean Squares and Covariances for 18-Month Type Scores of 132 Dams and Daughters

Source of Variance	df	Mean Squares		Cross-products Dams and Daughters	Constants
		Dams	Daughters		
Between Sires ^{a/}	24	4.15*	3.03	0.225	$r' = .006$
Within Sires	103	2.38	2.01	0.271	$r = .085$

^{a/} Within birth year groups of daughters

* Significant ($P < .05$)

Comparisons of Several Methods of Selection

Table XX shows the improvement, in the three traits, that would be made above the average of the population in which the heifers were born had selection been made by each of the various methods. The intensity of selection used in this study was 40 percent of each yearly heifer crop. The table, rather clearly, shows that when a breeder selects his replacement heifers on 18-month type (Method #7), he is sacrificing increased weaning weight and 18-month weight for a slight improvement in type score. It also shows that when selection is made on weight alone (either weaning or 18-month) a slight improvement in type score is made.

Table XX. Average Selection Differentials for Weaning Weight (X),
18-Month Weight (Y) and 18-Month Type Score (Z)
by Several Methods of Selection

Method of Selection	Traits Involved	Weaning Weight (X) (lbs.)	18-Month Weight (Y) (lbs.)	18-Month Type Score (Z)
1	XYZ	33.42	45.40	1.02
2	XY	39.54	54.47	.25
3	XZ	32.94	31.06	1.15
4	YZ	20.19	49.77	.97
5	X	44.10	36.97	.21
6	Y	27.33	62.53	.33
7	Z	12.42	20.87	1.35

The progress that could be made with each method of selection is presented in Table XXI. The progress per generation was determined by combining the selection differentials for the various traits after

each was weighted by its heritability and its economic importance. The heritability estimates used were: weaning weight 25 percent, 18-month weight 47 percent and 18-month type score 27 percent. The relative economic values used were: weaning weight .17, 18-month weight .18 and 18-month type score 6.01. The total progress column indicates the relative value of each method of selection. The table indicates that the most efficient method of selection for the breeder would be on the basis of all three traits, however, almost equal progress could be made by selecting for 18-month weight alone. Selection on the basis of 18-month type score would result in the least progress.

Table XXI. Progress per Generation^{a/} for Several Methods of Selection

Method of Selection	Traits Involved	Weaning Weight (X)	18-Month Weight (Y)	18-Month Type Score (Z)	Total Progress
1	XYZ	1.42	3.93	1.65	7.01
2	XY	1.68	4.61	.41	6.79
3	XZ	1.40	2.63	1.87	5.90
4	YZ	.85	4.21	1.57	6.64
5	X	1.87	3.13	.34	5.34
6	Y	1.15	5.29	.54	6.99
7	Z	.53	1.77	2.19	4.49

a/ Selection differentials weighted by heritability estimates and economic value.

Selection Indexes

Table XXII presents the statistical information required for the construction of an index based on two or more traits. The heritability estimates and the genetic and phenotypic correlations were obtained by

Koch and Clark (1955). The phenotypic standard deviations were obtained from the analysis of the data in this study. The relative economic values used here were discussed in Comparisons of Selection Methods in the Statistical Analysis section.

Table XXII. Statistical Information Required for Construction of the Indexes

Trait	Econ. Value	Std. Dev.	Heritability	Correlations			
				Phenotypic		Genetic	
				Y	Z	Y	Z
Weaning Wt. (X)	.17	40	.25	.47	.26	.54	.23
18-Month Wt. (Y)	.18	53	.47		.56		.49
Type Score (Z)	6.01	1.48	.27				

Seven indexes were calculated and correlations between each of them and H were compared. The same H value, aggregate genetic value, was used in the correlation with each of the seven indexes. The regression coefficients and r_{IH} , the multiple correlation between each index and the aggregate genetic value are given in Table XXIII for each index. Values for the equations were calculated by substituting the statistics from Table XXII.

The amount of genetic progress expected when a given index is used is proportional to r_{IH} . Therefore, these values provide a means for choosing an index. Comparison of the correlation between each of the seven indexes and the aggregate genetic value shows that the first

index consisting of weaning weight, 18-month weight and 18-month type score has little advantage over selecting on the basis of 18-month weight alone. Comparisons of the correlations also indicate that weaning weight or 18-month type score contributes very little to an index that includes 18-month weight.

Table XXIII. Comparisons of Indexes

Traits	Indexes						
	I ₁	I ₂	I ₃	I ₄	I ₅	I ₆	I ₇
Weaning Wt. (X)	.018	.018	.076		.010		
18-Month Wt. (Y)	.125	.131		.132		.138	
Type Score (Z)	.383		2.488	.382			3.024
r_{IH}	.628	.627	.458	.626	.342	.624	.383

DISCUSSION AND CONCLUSIONS

The purpose of this study was to investigate the factors which phenotypically and genotypically influence economic characteristics of range beef heifers and to construct an index for selecting range beef heifers. The sample studied is probably large enough to obtain reliable phenotypic estimates but not large enough to give precision to the genotypic estimates.

The analysis of the data has shown that the age of a heifer does have a significant effect on her 18-month weight. The linear regression coefficient found was 1.18. This is larger than those obtained by Dinkel (1953) and Hitchcock, et al. (1955). The regression coefficient of weight on age that Dinkel obtained was .97. Hitchcock, et al. found a partial regression coefficient of 1.09 for yearling weight on yearling age and concluded that the growth rate is linear for range beef heifers around the 520 day weigh period.

The adjustment of weights along a straight line requires the assumption that growth rate is linear over the period the weights were taken. To actually check the correction factors, weights would have had to be taken on the actual 550th day. This has not been done. However, Figure 1 indicates that the growth rate of the heifers in this investigation has a linear tendency. The standard error also indicates that the departure, if any, from linearity would be slight.

The regression of weight on age obtained in this study and the one obtained by Dinkel, were taken from the same data, over the same period of years, with the exception that the analysis in this investigation

included heifers born in 1952. The two correction factors, Dinkel's and the one obtained from this study, were compared by correcting the weights of 60 randomly selected heifers. No significant difference was found between the two methods. The correction factors for 18-month weight obtained by Dinkel were used to make the needed adjustments in this study. These factors obtained by solution of simultaneous equations should have an advantage in that the sources of variation, other than age, would be more adequately removed.

In agreement with previous research this study indicates that the weaning weight of a calf is significantly influenced by inbreeding. Koch (1951) found that the regression of weaning weight on inbreeding of the calf was -0.48 pound for each one percent of inbreeding. The mean inbreeding in Koch's study was 12.4 percent. The findings of Burgess, et al. (1954) with higher inbreeding (mean of 30 percent), were considerably larger, -1.75 pounds per one percent of inbreeding of the calf. In this study the estimates of reduction in weaning weight due to inbreeding are larger than reported by Koch (1951), but correspond to Burgess, et al. (1954), when expressed in terms of a linear regression. The linear reduction in the present study was -1.75 pounds per one percent inbreeding. The analysis in this investigation was designed to take into consideration the possibility of curvilinearity, while the estimates of Koch (1951) and Burgess, et al. (1954) were expressed as linear regression coefficients. The curvilinearity noticed in the estimates are in support of the findings of Burgess, et al. (1954), when they reported a significant deviation from linearity for

the effect of the calf's inbreeding on weaning weight.

The estimates obtained for the effect of the heifer's inbreeding on her 18-month weight appear to have about the same curvilinearity as found for weaning weight. The reduction of 18-month weight appears to be less than would be expected, when compared to the estimates for weaning weight. The reduction between the levels of inbreeding was not significant. Nelson and Lush (1945) with dairy cattle found that the regression coefficient increased up to two years, then decreased until five years, at which time maximum weight was reached. That this is the case with range beef heifers is not known, but the indications are that the effects of inbreeding on weight are still of the same magnitude at 18-months of age as they were at weaning. Apparently the inbred animals are gaining as rapidly from weaning to 18-months of age as the non-inbreds. In view of this it seems possible that the inbred heifers will attain a mature weight comparable to the non-inbred heifers.

The reduction in type score between inbreeding levels was not significant. At the lower levels of inbreeding, a slight improvement over the non-inbred heifers was noticed. However, a reduction of one-third of a grade was found at the higher levels of inbreeding. Nelson and Lush (1945) suggested a slight but not significant tendency for inbreeding to be detrimental to type rating in dairy cattle.

This study indicates that inbreeding does have a curvilinear depressing effect on weaning weight, 18-month weight and 18-month type score for range beef heifers. With the limited numbers represented in some of the inbreeding classifications the estimates obtained for the

effects of inbreeding should not be considered sufficiently reliable for general use. However, the estimates do represent the effects of inbreeding as found in these data and may be useful in subsequent studies.

The cause (or causes) for the wide range in heritability estimates is not known. The estimates are probably affected by the lack of enough animals in the study. Indications that the population is too restricted in size to give reliable heritability estimates is found in the wide ranges of fiducial limits and standard errors.

The estimates from the parent-offspring regression would normally be expected to yield larger values than the half-sib estimates, due to the added maternal environment included in the parent-offspring regression estimates. However, this is not the case in this study. The parent-offspring estimates could be subject to two other biases; one being that the dams' records were not necessarily made on the same ranch as their daughters' records, and second, that the year the dams were calved was not considered in the analysis. If the year and place of birth of dams had been included in the analysis the number of subclasses would have increased and the size of the subclasses decreased. This would result in the loss of a large portion of the data. To avoid the loss of too many animals in the study the year and place of birth of the dams were disregarded. Disregarding either or both year of birth and place of birth could increase the variation of the dams, resulting in biasing the estimates of heritability in the negative direction.

The negative estimate of heritability for weaning weight from the parent-offspring analysis is due to the negative cross-product in the within sire group. Since the year of birth of the dams was not considered in the analysis, the negative cross-product term might arise if dams heavier at weaning were heavier because of an advantageous year effect and subsequently had daughters lighter at weaning because of a detrimental year effect. The converse of this would also have to be true. These contradictory relationships between dams and daughters would have to be paired nearly perfect within a sire group; this seems unlikely with the more or less random nature of year effects affecting both dams and daughters.

The estimate of heritability for 18-month weight, obtained from the regression of offspring on dam in this study, is much lower than the estimates reported by other workers. Knapp and Nordskog (1946) reported an estimate of 61 percent by the paternal half-sib correlation method. By the same method, Koch and Clark (1955a) listed an estimate of 47 percent from the records of 1694 heifers. The same authors (1955b) listed an estimate of 43 percent by the regression of 1023 heifers on 822 dams. The estimate found in the present study was 19 percent. The estimates reported by Koch and Clark are supported by a much greater volume of data and are felt to present a more reliable estimate of heritability for 18-month weight.

The heritability estimate (25 percent) obtained for 18-month type score, by the offspring-dam analysis, is in agreement with the one reported by Koch and Clark (1955a). These authors reported an estimate

of 27 percent for yearling heifers, by the paternal half-sib analysis. Both of these estimates are larger than those reported by Koch and Clark (1955b), 14 percent and McCormick, et al. (1956), 15 percent.

The paternal half-sib correlation estimates for heritability of weaning weight (-.01) and 18-month weight (1.62) are theoretically impossible. The negative estimate for weaning weight is caused by the much larger variation within sire groups than between sire groups. One of the reasons for the small between sire variance for weaning weight might be the lack of genetic variability among the sires used. This seems improbable in view of the apparent difference between sires for weaning weights of their daughters.

In the half-sib analysis, it is difficult to understand why there should be a small between sire variance for weaning weight, but for 18-month weight an extremely large between sire variance. Since weaning weight is a large component of the 18-month weight this wouldn't be expected. Koch and Clark (1955c) suggested that selection on the basis of gain from weaning to yearling age would increase the genetic value for yearling gain, but will cause a small loss in genetic value for milking ability. If there is a negative relationship between 18-month weight and milking ability and the sires with the genotypes most favorable for rapid growth by chance were mated to the cows heaviest at 18-months, then this situation may come about. With so many assumptions involved this seems unlikely but is a possible explanation.

The most probable reason for the wide ranges in heritability estimates, found in this study, is that the population is too restricted to yield reliable estimates. An estimate of these sampling errors is indicated in the fiducial limits. It is apparent from the estimates obtained, that the paternal half-sib estimates of heritability are subject to large sampling errors.

The genetic correlations between 18-month weight and 18-month type score (.06), found is much lower than the correlation (.49) that Koch and Clark (1955a), reported. However, the genetic correlations in this study would be subject to the sampling errors that appeared in the half-sib estimates of heritability. With these sampling errors present, it is felt that the genetic correlations found are unreliable.

Selection of beef heifers on the basis of weaning weight, 18-month weight and 18-month type score showed the greatest increase in selection differentials for the methods of selection used. When the three factors were considered, increases of 21 pounds for weaning weight and 25.5 pounds for 18-month weight were found as compared to selection by 18-month type score alone. Selection for all three traits simultaneously resulted in a decrease of .33 of one-third of a grade in type score below the level attained by selection for type score alone. This would amount to only .33 of the difference between a 2 and a 2 $\frac{1}{2}$, which is so small that it would not be apparent to the eye.

Selection on the basis of 18-month weight alone, increased weaning weight 14.9 pounds and 18-month weight 41.7 pounds, above the selection by 18-month type score alone. The gain in type score was one-third of a grade less than when selection was by type score alone.

It is apparent from this study that in order to make maximum improvement in beef cattle herds, selection methods should include weight records as well as type score and that considerations of weight for age are more important for progress in economic traits than type score.

Comparisons of the correlations between each of the seven indexes, developed in this study, and the aggregate genetic value, shows that the first index, which included weaning weight, 18-month weight and 18-month type score, should provide the greatest gains. Index 1, can estimate the genetic value of the animal .626 as accurately as if the genetic constitution of each animal were completely known. However, the index that used 18-month weight alone predicts the aggregate genetic value of an animal almost equally as efficient, as indicated by $r_{IGH} = .624$. The importance of 18-month weight was also shown in the Selection Methods section when total progress by selecting for 18-month weight was 6.99 and 7.01 when weaning weight, 18-month weight and 18-month type score were used. Hence, the sixth index (18-month weight alone) is indicated by this study to be equivalent in practical value to Index 1. In many herds this will resolve itself to selecting the heifers on 18-month weight alone. It is fortunate that this is so because the heifers would have to be weighed once and wouldn't have to be typed scored. Disregarding type score is to an advantage because of the subjective basis for type score classification and the highly arbitrary nature of the decision as to the relative economic value for type score used in this study.

The most efficient method for selecting range beef heifers obtained in this study would be Index 1. For easier application this index may be simplified to:

$$I_1 = .18X + 1.25Y + 3.83Z,$$

where, X is the weaning weight at 190 days, Y represents the weight at 550 days and Z the 18-month type score based on a scoring system of 15 classifications. However, the selection index that would be used, would probably vary from breeder to breeder. One breeder may be interested in improving his herd in weaning weight, 18-month weight and 18-month type score, while another may be interested in only weaning weight and type score. The opportunity, need and desire to improve these characteristics will vary, and personal preference, variation in the herds, the selection intensity for replacement needs, economic changes and time trends will determine the amount of progress made. The important thing is to set a goal as to what characteristics will mean greater dollar returns for improvement in them. Then once the goal is set, a selection index is the most effective way of achieving it.

The data included results from 903 heifers raised by the North Dakota Agricultural Experiment Station during the period 1940 to 1959. The heifers were from purebred Hereford cows raised at Dickinson in western North Dakota. The results are as follows:

(1) The age of a heifer does have a significant effect on

her weaning weight. The linear regression coefficient

SUMMARY

The purpose of this study was to investigate the factors that genotypically and phenotypically influence economic characteristics of range beef heifers and to develop a selection index that would be adaptable by beef cattle breeders. The characteristics studied were weaning weight, 18-month weight and 18-month type score. Correction factors were determined for adjusting 18-month weight to a constant age. Corrections were also determined for the depressing effects that inbreeding has on weaning weight, 18-month weight and 18-month type score. Heritability estimates were determined for the various traits by the methods of paternal half-sib analysis and intra-sire regression of offspring on dam. Genetic correlations were obtained from the paternal half-sib analysis of variance and covariance. The effectiveness of several methods of selection based on the traits of economic importance were investigated. Selection indexes for range beef heifers were developed and the accuracy of each index for predicting the aggregate genetic value of an animal was determined.

The data included records from 303 heifers raised by the South Dakota Agricultural Experiment Station during the period 1948 to 1955, inclusive. The heifers were from purebred Hereford cows carried at substations in western South Dakota. The results are as follows:

- (1) The age of a heifer does have a significant effect on her 18-month weight. The linear regression coefficient

- (1) found was 1.18 pounds per day.
- (2) The study indicates that the weaning weight of a calf is significantly influenced by its inbreeding. Curvilinearity was found for the effects of inbreeding on weaning weight.
- (3) The effects of the inbreeding of heifers on their 18-month weights have a similar curvilinear effect as found for weaning weights. However, the reduction in 18-month weight between the levels of inbreeding was non-significant.
- (4) The 18-month type score reduction between the levels of inbreeding was non-significant.
- (5) The heritability estimates obtained from the intra-sire regression of offspring on dam are as follows: weaning weight -26 percent, 18-month weight 19 percent and 18-month type score 26 percent.
- (6) The heritability estimates and genetic correlations for weaning weight, 18-month weight and 18-month type score obtained from the paternal half-sib analysis are believed unreliable, due primarily to the restricted population and the limited number of sires represented.
- (7) Selection of 40 percent of each yearly heifer crop on the basis of weaning weight, 18-month weight and 18-month type score resulted in an increase of 21 pounds for weaning weight and 25.5 pounds for 18-month weight, over the increases that were made when selection was by type score alone. This resulted in a gain slightly less (.33 of one-third of a grade) than was made by selection by type score alone.

- (8) The most efficient selection index for range beef halfers would be one that included; weaning weight, 18-month weight and 18-month type score. The precision of predicting the aggregate genetic value of an animal by this index was .628.

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