TB 1323 (1965) USDA TECHNICAL BULLETINS UPDATA
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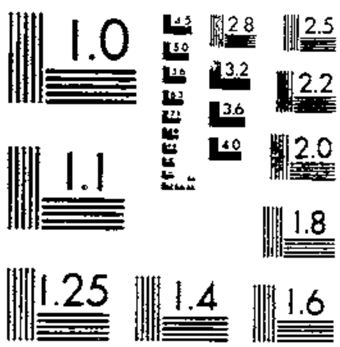

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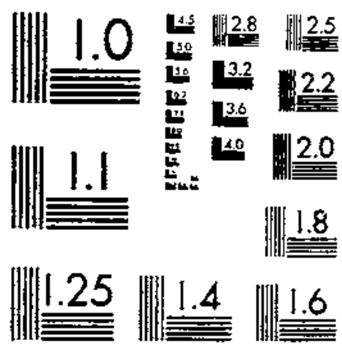

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EVALUATION OF RESPONSE TO SELECTION AND INBREEDING IN A CLOSED LINE OF HEREFORD CATTLE

Technical Bulletin No. 1323

Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE
in cooperation with
Montana Agricultural Experiment Station

Acknowledgment

The authors acknowledge the service of J. R. Quesenberry who was Superintendent of the United States Range Livestock Experiment Station, Miles City, Mont., during the entire period covered by this study and under whose supervision the data were obtained. Acknowledgment is made to the following scientists who were instrumental in planning and carrying out the breeding program and in collecting and processing the data: A. L. Baker (deceased) and Bradford Knapp, Jr., animal husbandmen, and R. R. Woodward and F. J. Rice, geneticists, Agricultural Research Service, U.S. Department of Agriculture; and to F. S. Willson, head, Department of Animal Science and Range Management, Montana State College, Bozeman, Mont.

Washington, D.C. Issued March 1965

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 Price 15 cents

Contents

EVALUATION OF RESPONSE TO SELECTION AND INBREEDING IN A CLOSED LINE OF HEREFORD CATTLE [1]

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INTRODUCTION

Selection is the process, either natural or artificial, that allows individuals of differing phenotypes to differ in rate of reproduction. Man has practiced selection in animals since their domestication in his attempt to improve performance and to breed animals that conform to his ideals.

The theoretical aspects underlying changes in populations expected from artificial selection have been extensively explored. Much of the theory has been checked through actual experimentation. This is especially true of laboratory animals, where generation intervals are short and the environment can be controlled to a greater extent than with large animals. Chapman (1951) [2] cites a number of selection experiments on laboratory animals. More recent studies include those of Falconer (1953, 1955), Bell et al. (1955), Robertson (1955), Clayton et al. (1957), Clayton and Robertson (1957), and Thoday and Boam (1961). Kojima and Kelleher (1963) discuss some of the more recent selection studies in laboratory animals. Several studies concerning the intensity and effectiveness of selection on poultry have been published by Lerner and Dempster (1951), Dempster et al. (1952), Dickerson (1955), Oliver et al. (1957), and Yamada et al. (1958). The results of these studies vary with the species and traits and with the nature of variation controlling the traits. In general, however, these studies have shown fairly rapid improvement for the highly heritable selected traits in the early stages of the experiment. This has been followed by a steady decline in the effectiveness of selection and eventually a plateaued population even though the genetic variability appeared to remain high. Possible explanations for this situation have been discussed by Lush (1951a), Dickerson et al. (1954), Lerner (1954), Dickerson (1955), and other scientists.

Relatively few studies have evaluated the response to selection in large animals. Most of these studies have dealt with time trends, which could not be accurately partitioned into the respective genetic and environmental components owing to inadequate environmental controls. However, much information can be obtained from the

[1] This study was conducted at the U.S. Range Livestock Experiment Station, Miles City, Mont., in cooperation with the Montana Agricultural Experiment Station, under Western Regional Project W-1, The Improvement of Beef Cattle Through the Application of Breeding Methods.

[2] Names followed by year or years in parentheses refer to Literature cited, p. 34.

analyses of time trends, and Lush (1951b) presents evidence that several important traits of livestock have improved steadily through the years.

Most of the studies that evaluated selection in large animals have been on swine. Lush (1936) analyzed time trends on the Danish Landrace and found that several characteristics had changed markedly in the period studied. Other studies on the effectiveness of selection in swine include those by Comstock and Winters (1944), Krider et al. (1946), Dickerson and Grimes (1947), Kottman et al. (1948), Fine and Winters (1952, 1953), Rempel and Winters (1952), Dickerson et al. (1954), Damon and Winters (1955), and Smith (1962, 1963). These studies have shown varying degrees of response to selection, depending on the characters studied and breeding systems followed. Dickerson et al. (1954) worked with data from several experiment stations and reported that selection in mildly inbred lines apparently failed to improve measurably the genetic merit for traits associated with growth and litter size even after adjusting for the effects of inbreeding. Selection apparently has been effective in producing large changes in body dimensions and carcass composition where heritability was higher and previous selection had been mild and had changed directions frequently (Dickerson, 1951). Studies on sheep by Terrill (1951) and by Peters et al. (1961) and on dairy cattle by Van Vleck and Henderson (1961) indicate that selection has been at least partially effective in improving the traits studied. Flower et al. (1964) reported estimates of positive genetic trends for birth weight and weaning weight in closed lines of Hereford cattle.

The purpose of the present analysis was to study the intensity and effectiveness of selection for several economic traits in a closed Hereford line over a 25-year period of concurrent inbreeding and selection. The effects of inbreeding are determined and discussed in relation to the response to selection. The expected and the actual responses to selection are compared and discussed.

EXPERIMENTAL PROCEDURE

Source and Description of Data

The data used in this study were obtained from a single inbred line (Line 1) that was founded in 1933 by purchasing two half brothers, Advance Domino 54th and Advance Domino 20th, and mating them to a select group of registered cows that had been produced at the United States Range Livestock Experiment Station. The first calves were dropped in 1934, and the line has remained closed to outside breeding since that time. A list of the sires used and the number of progeny they contributed is given in table 1. A detailed description of the origin of Line 1 was reported by Knapp et al. (1951).

Management practices and facilities have remained fairly constant over the entire period; the same station superintendent has been in charge. Management factors such as breeding and weaning dates, levels of wintering, bull feeding rations, and housing facilities for individual feeding have not changed materially during the period of study.

TABLE 1.—*Sires used in Line 1*

Name of bull	Bull number	Birth year of bull	Birth year of progeny	Number of progeny weaned
Advance Domino 20th	1	1931	1934–40 and 1942	180
Advance Domino 54th	2	1932	1935–40 and 1942	151
Prairie Domino	6	1934	1940–44	124
Chief Domino 1st	8	1935	1941	23
Alton Domino	22	1939	1943–46	98
Clayton Domino	28	1939	1943–47	87
L1B Domino 1st	43	1940	1946	13
L1B Domino 2d	44	1940	1944–47	65
A–A Domino 2d	57	1941	1945–46	43
Adam's Domino	104	1944	1947–50	83
Albion Domino	114	1944	1948	30
Carroll Domino	130	1944	1948	22
Carson Domino	152	1945	1948–51	84
Chase Domino	153	1945	1947–48	44
Chico Domino	157	1945	1947	24
L1 Domino 10	196	1947	1949–54	142
L1 Domino 29th	215	1947	1951–52	37
L1 Domino 35th	241	1948	1952	27
L1 Domino 67	292	1949	1953–56	86
L1 Domino 72	297	1949	1952	11
L1 Domino 73	298	1949	1953–54	42
L1 Domino 94	339	1950	1953–54	52
L1 Domino 112	390	1951	1955–56	51
L1 Domino 115	393	1951	1953–54	46
L1 Domino 122	400	1951	1956	21
L1 Domino 168	547	1953	1959	23
L1 Domino 171	550	1953	1955 and 1957–58	64
L1 Domino 181	560	1953	1955–59	109
L1 Domino 220	637	1954	1956–58	70
L1 Domino 253	716	1955	1957–59	62
L1 Domino 284	791	1956	1958–59	46
L1 Domino 286	793	1956	1958–59	44
L1 Domino 311	866	1957	1959	22

Cows were grazed on native range throughout the year. They were moved to winter pasture around January 1 each year, and varying amounts of protein supplement were fed. Hay was provided when heavy snow prevented normal grazing. Cows were placed in the calving pastures around the middle of March and remained there until placed in the smaller, single-sire breeding pastures around June 1. The bulls were turned in with the cows on June 15 for a period of 45 days, after which cows and calves were placed on summer range. Calves were weaned late in October at an average age of about 180 days, after which the cows were moved to fall range. After weaning, the selected bull calves were individually fed for 196 days. Heifer calves were wintered at headquarters and were fed to gain approximately one-half pound per day. Yearling heifers were grazed on native range and provided with some supplemental feed during the second winter. All heifers were bred to calve at 3 years of age.

Selection practiced within the line has been on the basis of performance—primarily weights and gains. Some emphasis was placed on conformation. No specific index was used. Bulls used in the line were selected on the basis of weaning weight and score, performance during a 196-day postweaning test, and in most instances a progeny test. Sequential culling was practiced; some culling took place at each of the three stages. Approximately the top half of the male weanling calves were selected for the postweaning performance test each year. From 1939 through 1957, the male calves were sorted around September 1, and the top bull calves were selected on the basis of conformation and weight per day of age. The remaining calves were castrated. All calves were returned to the range with their mothers until weaning time.

Since 1958 the top bull calves were selected late in October at weaning time, and preweaning castration was not practiced. The selected bull calves were placed on feed about November 1 and were given a 2-week warmup period before going on test. Bulls were individually fed for 196 days. A more detailed report of the feeding and management practices is given by Knapp et al. (1951), Shelby et al. (1960), and Brinks et al. (1962a). The top yearling bulls, on the basis of the performance test and weaning weight and score, were then mated to a tester group of about 20 cows each. From 2 to 10 bulls were progeny tested each year. The top-performing bulls based on the progeny test were retained for use within the line. Occasionally, outstanding yearling bulls were used in the line without benefit of a progeny test. Bulls that produced outstanding progeny within the line were used several years.

Selection among females was practiced on the basis of 18-month weight and score, fertility, age, and production as measured by the weaning weights of their calves. Cows that failed to produce a calf for 2 consecutive years were culled. All cows were culled after they reached an age of 10 years.

Characters Studied

Several characters of economic importance have been recorded and used as selection criteria through the years. To facilitate analysis, these criteria were divided into three different categories: (1) birth and weanling traits, (2) postweaning performance of bulls, and (3) postweaning performance of females. The birth and weanling traits studied in this analysis were birth weight, weaning weight, gain from birth to weaning, and weaning score. The postweaning traits studied on bulls were 196-day gain and final weight off test. Postweaning characters studied on the females were gain from weaning to 12 months, 12-month weight, gain from 12 to 18 months, 18-month weight, 18-month score, mature spring weight, mature fall weight, and most probable producing ability. Weaning and 18-month scores were expressed as percentages on a scale on which the ideal animal would be scored 100. The deviation from the line average in most probable producing ability was computed by use of the formula:

$$\frac{nr}{1+(n-1)r} \times \frac{\Sigma(\text{cow's record minus sire–year average})}{n}$$

where n is the number of records per cow, and r is repeatability.

The cow's record refers to the ratio of her calf's adjusted 180-day weaning weight to the adjusted sire-year subclass mean for weaning weight. The sire-year average was set equal to 1.00 in each case. The value of 100 was then added to the deviation so cows with values over 100 were above the population mean and cows below 100 were below the mean.

In addition, coefficients of inbreeding were calculated for all animals in order to determine the effects of inbreeding on performance and to ascertain whether selection had favored or discriminated against homozygosity.

Adjustment Factors

To have a basis of comparison, the data were adjusted for some of the known sources of environmental variation. The adjustment factors are shown in table 2. The additive factors for age of dam for the birth and weanling traits are those reported by Koch and Clark (1955), which were derived from data from the same station as the present study. The multiplicative factors for sex are those reported by Brinks et al. (1961) and also are based on data from the same station. The weaning weights and gains from birth to weaning were adjusted to 180 days of age using the calf's own average daily gain during that period.

The adjustment factors for postweaning traits were calculated separately for each sex. The adjustment factors for bulls are those reported by Brinks et al. (1962b). Final weight of the bulls was adjusted to 376 days of age. Adjustment factors for 12- and 18-month heifer weights were taken from a previous analysis, and the weights were adjusted to 365 and 545 days, respectively. Adjustment factors for mature spring and fall cow weights were previously reported by Brinks et al. (1962a).

Means and Variation

The adjustment factors in table 2 were applied to the data, and the resulting means, standard deviations, and coefficients of variation are given in table 3. All standard deviations were computed within sire-year subgroups after the adjustments had been made. Records on foundation animals are not included in these values except for inbreeding of dam.

The means for inbreeding of calf and dam were 16.1 and 11.7 percent, respectively, and they reflect the mild inbreeding practiced in the selection program. Inbreeding increased slowly from about 1 percent in the initial years to around 20 percent in the later years. The coefficients of variation for inbreeding of calf and dam were fairly high, amounting to 26.7 and 39.3 percent, respectively.

The adjusted means for the birth and weanling traits are very similar to the unadjusted means because the data were adjusted upward to a mature-dam equivalent and downward to a heifer basis. The postweaning weights are slightly larger than the unadjusted means because the data were adjusted to a mature-dam or age-of-cow basis. Coefficients of variation for weights ranged from 5.5 percent for final weight off test in the selected population of bulls to 10.4 percent for weaning weight.

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TABLE 2.—*Adjustment factors for various traits*

Source of variation	Birth and weaning traits			Postweaning traits					
				Males		Females			
	Birth weight	Weaning weight	Weaning score	196-day gain	Final weight off test	12-month weight	18-month weight	Mature spring weight	Mature fall weight
Age of dam or cow:	*Lb.*	*Lb.*	*Pct.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*
3 years	4	41	0.6	2	34	32	30	129	100
4 do	2	18	.3	−7	9	19	20	66	41
5 do	0	6	.2	1	5	8	8	7	−2
6 do	0	0	0	0	0	0	0	−24	−20
7 do	0	3	0	−3	−4	1	0	−41	−27
8 do	0	6	.1	0	−2	4	3	−46	−38
9 do	0	12	.2	1	3	5	1	−46	−29
10+ do	2	24	.4	−5	1	9	6	−42	−25
Sex:									
(Multiplicative)									
Heifers	0	0							
Bulls	.934	.941							
Steers	.934	.949							
Regression on age				.0410	1.8894	1.6545	1.4991		

TABLE 3.—*Means and variation for performance traits and for inbreeding of calf and dam*

Trait	Number of records	Mean	Standard deviation	Coefficient of variation
Calf and dam:				
Inbreeding of calf____percent__	2027	16.1	4.3	26.7
Inbreeding of dam_____do____	2027	11.7	4.6	39.3
Calf:				
Birth weight________pounds__	2027	76.8	7.4	9.6
180-day gain__________do____	2027	328	40	12.2
Weaning weight_______do____	2027	405	42	10.4
Weaning score______percent__	1815	76.5	6.8	8.9
Bulls:				
196-day gain________pounds__	459	448	39	8.7
Final weight off test____do____	459	901	50	5.5
Females:				
Gain from weaning to 12 months___________pounds__	933	89	32	36.4
12-month weight_______do____	933	493	46	9.4
Gain from 12 to 18 months pounds__	933	246	34	13.8
18-month weight______do____	933	738	59	8.0
18-month score______percent__	904	73.5	6.4	8.7
Mature spring weight pounds__	[1] 1770	1155	105	9.1
Mature fall weight_____do____	[1] 1770	1152	114	9.9
Most probable producing ability______________percent__	546	100	4.6	4.6

[1] The same cow is included each time she produced a calf.

EXPERIMENTAL RESULTS AND DISCUSSION

Effects of Inbreeding

The means and ranges for the coefficients of inbreeding of calf and dam by years for animals used in the birth and weanling analysis are shown in table 4. The average rate of increase in inbreeding of calf and dam was slightly under 1 percent per year. The level of inbreeding was stable in the initial years because foundation cows were mated to the two original sires. From 1937 through 1940 there were a few times in which the two foundation sires were mated to daughters of the other. The first calves by a sire produced within the line were dropped in 1940. The inbreeding level increased sharply from 1940 to 1941, when all sires used were produced within the line, and most of the foundation cows had been replaced. From 1941 through 1951 the inbreeding level increased gradually, after which time it remained almost constant.

The average range of inbreeding of calf and dam per year was 7.2 to 26.5 percent and 3.1 to 22.7 percent, respectively. The ranges over all years were 0.3 to 55.2 and 0 to 40.4 percent, respectively. The within sire-year subclass standard deviations were 4.3 and 4.6 percent, respectively. Thus, the opportunity for selection for or against homozygosity in any one year was fairly substantial.

TABLE 4.—*Means and ranges of coefficients of inbreeding of calf and dam by years*

Year	Number of records	Inbreeding of calf		Inbreeding of dam	
		Mean	Range	Mean	Range
		Percent	*Percent*	*Percent*	*Percent*
1934	23	0.7	0.3- 1.2	1.1	0- 3.2
1935	37	1.0	.3- 2.6	3.2	0-25.7
1936	35	1.0	.3- 5.4	1.7	0-14.7
1937	47	1.5	.3- 7.9	2.8	0-25.4
1938	55	2.9	.4-26.3	3.8	0-26.0
1939	48	5.9	.3- 8.7	1.3	0- 8.4
1940	61	7.9	.9-17.7	1.6	.3- 8.4
1941	58	15.7	13.8-17.7	1.3	.3- 7.9
1942	69	11.7	4.5-21.0	2.8	.3- 8.7
1943	90	16.8	4.6-33.5	4.1	.3-14.2
1944	102	15.4	4.5-21.2	6.0	.3-17.7
1945	72	14.6	4.6-25.6	6.8	.3-21.0
1946	68	16.0	8.4-33.8	8.7	.3-21.0
1947	94	17.4	11.0-34.4	10.3	.4-21.0
1948	118	18.6	10.3-26.2	11.7	.4-21.0
1949	63	16.1	9.1-25.4	15.4	5.8-21.1
1950	54	16.1	9.1-26.7	14.5	4.6-21.0
1951	75	20.1	11.0-40.4	15.4	5.6-30.8
1952	75	21.6	9.6-37.6	16.6	5.6-30.8
1953	119	20.6	11.1-38.3	16.7	5.6-30.8
1954	114	21.6	11.8-40.2	17.1	5.6-30.8
1955	85	21.4	13.9-40.4	17.1	5.6-33.4
1956	117	17.3	12.4-27.1	18.5	10.4-37.3
1957	91	18.9	10.6-55.2	19.6	9.1-35.9
1958	131	19.3	12.0-38.5	19.1	9.1-40.4
1959	126	21.6	11.4-34.9	19.2	10.5-33.4
Total or average	2027	16.1	7.2-26.5	11.7	3.1-22.7

The partial regressions in actual units and in standard measure of traits on the inbreeding of calf and dam by sex classes are shown in table 5. The partial regressions were computed within sire-year subclasses on the adjusted data. The effect of inbreeding on the birth and weanling traits was found to be markedly different for the two sexes and are, therefore, presented separately.

In general, inbreeding of calf and dam had a marked detrimental effect on the birth and weanling traits. Inbreeding of calf had a more pronounced effect on females than on males. The partial regressions were over three times as large for females for birth weight, preweaning gain, and weaning weight. Stonaker (1963) reported that heterosis in female beef calves for 260-day weaning weight was much greater than in males when inbreds were compared with their half-sib linecross contemporaries. He reported the ratio of linecross/inbred males and females to be 1.08 and 1.15, respectively. The reason for this marked difference of inbreeding on the performance between the two sexes is not readily apparent.

TABLE 5.—*Partial regressions of performance traits on inbreeding of calf and dam in actual and standard measure*

Trait	Number of records	Partial regression on inbreeding of calf		Partial regression on inbreeding of dam	
		b	β	b	β
Birth weight:					
Males	1041	−0.1279	−0.0762	0.0091	0.0058
Females	986	−.4012	−.2189	.0961	.0570
180-day gain:					
Males	1041	−.4643	−.0489	−1.8872	−.2133
Females	986	−1.7082	−.1850	−.4308	−.0507
Weaning weight:					
Males	1041	−.5922	−.0596	−1.8781	−.2026
Females	986	−2.1094	−.2173	−.3347	−.0375
Weaning score:					
Males	929	.0939	.0623	−.3156	−.2133
Females	886	−.3663	−.2297	.0252	.0166
Bulls:					
196-day gain	459	−1.6748	−.1877	.1981	.0222
Final weight off test	459	−2.2957	−.2027	−.8654	−.0764
Females:					
Gain from weaning to 12 months	933	−1.2463	−.1609	.1868	.0255
12-month weight	933	−3.0447	−.2734	−.2165	−.0205
Gain from 12 to 18 months	933	−1.7851	−.2169	.2715	.0348
18-month weight	933	−4.8298	−.3381	.0550	.0041
18-month score	904	−.5459	−.3482	.0376	.0258
Mature spring weight [1]	536	−2.8441	−.1322		
Mature fall weight [1]	536	−3.2766	−.1403		
Most probable producing ability [1]	536	−.1846	−.1591		

[1] Regression of trait on inbreeding instead of partial regression.

Stonaker (1963) has discussed the hypothesis that genetic differences between the two sexes may exist owing to differences in the sex chromosomes. A second hypothesis discussed by Brinks et al. (1963) is that essentially the same genotypes show a differential response in an environment that is actually different for the two sexes in proportion to their potential for growth during the weanling period. The effects of maternal environment could mask the response to inbreeding, especially in the male calves.

In contrast, inbreeding of dam had a more detrimental effect on preweaning gain, weaning weight, and weaning score of bulls than of heifers. Bulls, having a greater growth potential, are probably held back more than heifers by the decreased milk supply of their mothers that is associated with increased inbreeding of dam. It appears that inbreeding of dam had a negligible effect on birth weight because the partial regressions for both sexes were slightly positive.

Inbreeding of calf had a sizable detrimental effect on postweaning gain and final weight off test in the selected population of bulls.

There was some compensation in gain during the postweaning period for the detrimental effect of inbreeding of dam during the preweaning period. This was not enough to compensate fully, and the partial regression of final weight off test on inbreeding of dam was still – 0.8654 of a pound.

Inbreeding of calf continued to have a large detrimental effect on postweaning weights and gains among females. In fact, the effect of inbreeding of calf was greater as age increased to 18 months in both actual units and standard measure. The effect of inbreeding on mature weight is less than on weight at 18 months but is still a very sizable effect. Mature weight, as used here, was an average of all weights taken from 3 to 10 years of age adjusted for age-of-cow and year effects. Therefore, it cannot be determined if the effect of inbreeding diminishes at the older ages.

After studying a mildly inbred herd of Holsteins, Nelson and Lush (1950) concluded that increased inbreeding resulted in smaller size at least to 2 years of age and for some of the later maturing measurements up to 4 years of age. They reported a tendency for larger size with increased inbreeding at 5 years of age. Nutritional environment may be a factor that influences the magnitude and persistence of the effects of inbreeding on growth.

The female population also showed some compensation during the postweaning periods for the small detrimental effect of inbreeding of dam during the preweaning period. Compensation for the effect is evident from weaning through 18 months of age; the partial regression of 18-month weight on inbreeding of dam was 0.0550 of a pound. This indicates that full compensation for the poorer preweaning environment had taken place.

The within sire-year correlation between inbreeding of calf and inbreeding of dam was 0.23 when all 2,027 calf-dam records were used, and it ranged from 0.22 to 0.25 in the subpopulations studied.

Intensity of Selection

Selection Differentials

Selection intensity is shown as annual selection differentials—the average performance of those who became parents minus the average performance of the unselected group in which they were born, divided by the average age of the parents when the offspring are born. Selection differentials were computed separately for sires and dams for comparison purposes and were then combined to obtain overall annual selection differentials. The formulas used were essentially the same as those presented by Dickerson et al. (1954) and were as follows:

$$\Delta S = \frac{n_1^s s_1 + n_2^s s_2 + \ldots + n_p^s s_p}{N\overline{A}},$$

$$\Delta D = \frac{n_1^d d_1 + n_2^d d_2 + \ldots + n_q^d d_q}{N\overline{A}}, \text{ and}$$

$$\Delta P = \frac{\Delta S + \Delta D}{2}$$

where n_i^s and n_j^d are the number of progeny by a particular sire and dam, respectively, in a given year; s_i and d_j are the superiority or inferiority of a particular sire and dam measured as the deviation from the mean of the unselected group in which they were born; N is the number of progeny in a given year; and $\overline{A}=\frac{\Sigma n_i^s A_i^s + \Sigma n_j^d A_j^d}{2N}$ or the average age of the parents when the offspring are born.

The annual selection differentials for inbreeding and the birth and weanling traits along with the annual average age of the parents are listed in table 6. Listed at the bottom of table 6 are the average annual and generation selection differentials in both actual and standard deviation units and the percent of the population the selected animals are representative of under truncation selection. Selection differentials are not presented for 1934 through 1942 since many of the parents were foundation animals, and performance information was not available in all cases. Parents of all progeny born after 1943 were produced within the line, and complete information was available.

The average age of the parents when the offspring were born, or generation interval, was 4.93, or slightly under 5 years. Replacement rates were faster on the sire side—4.31 years compared with 5.55 years on the dam side.

There was some selection against homozygosity as indicated by the small but fairly consistent negative selection differentials for inbreeding of calf and dam. Selection pressure was somewhat greater against inbreeding of calf than against inbreeding of dam resulting in average annual selection differentials of −0.20 and −0.08 percent, respectively. The selection differentials per generation of −0.99 and −0.39 percent indicate the average selection pressure actually practiced each year, and they represent the lower 88 and 96 percent of the population for levels of inbreeding of calf and dam, respectively. No direct attention was given to level of inbreeding when animals to be retained in the herd were selected. Therefore, some selection against homozygosity is expected because performance decreased as inbreeding increased (table 5).

Since there was some selection against homozygosity, the computed coefficients of inbreeding may be biased somewhat from actual homozygosity existing within the line. Selection for heterozygosity per se, or for allelic combinations that exhibit overdominance, would cause actual inbreeding values to be less than computed values. Selection and concurrent inbreeding should exert positive selection pressure for advantageous homozygous combinations and negative pressure for disadvantageous homozygous combinations. If the decline in performance associated with increases in inbreeding is due to the accumulations of disadvantageous homozygous combinations or to deleterious recessives, the number of disadvantageous combinations must be greater or have a larger average effect than advantageous combinations because inbreeding was shown to have a detrimental effect on all traits studied.

Selection differentials for birth and weanling traits averaged positive on both the dam and sire side over the years. Selection on the sire side was much more intense than on the dam side, being about five times as great for 180-day preweaning gain and for weaning weight.

TABLE 6.—*Annual selection differentials for levels*

[Selection differential symbols are ΔD for dams,

Year of birth	Number of progeny	Average age			Inbreeding of calf			Inbreeding of dam		
		Dam	Sire	$\bar{A}$	ΔD	ΔS	ΔP	ΔD	ΔS	ΔP
		Yr.	*Yr.*	*Yr.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*
1943	90	4. 80	5. 50	5. 15	−0. 08	−0. 08	−0. 08	−0. 10	0. 17	0. 04
1944	102	5. 37	5. 67	5. 52	−. 11	−. 05	−. 08	−. 07	. 13	. 03
1945	72	5. 67	5. 07	5. 37	−. 13	−. 20	−. 17	−. 15	. 04	−. 06
1946	68	5. 75	6. 03	5. 89	−. 10	−. 17	−. 14	−. 12	−. 12	−. 12
1947	94	5. 63	3. 50	4. 57	−. 20	−. 09	−. 15	−. 22	−. 85	−. 54
1948	118	5. 77	3. 65	4. 71	−. 13	−. 23	−. 18	−. 15	−. 47	−. 31
1949	63	4. 70	3. 61	4. 16	. 02	−. 31	−. 15	−. 12	−. 36	−. 24
1950	54	5. 39	4. 37	4. 88	−. 25	−. 39	−. 32	−. 29	−. 16	−. 23
1951	75	5. 24	4. 59	4. 92	−. 18	. 12	−. 03	−. 08	. 45	. 19
1952	75	5. 19	4. 35	4. 77	−. 00	−. 82	−. 41	−. 08	−. 15	−. 12
1953	119	5. 76	3. 73	4. 75	−. 02	−. 95	−. 49	−. 02	. 29	. 14
1954	114	5. 96	4. 81	5. 39	−. 02	−. 87	−. 45	−. 06	. 28	. 11
1955	85	6. 38	3. 41	4. 90	−. 10	−. 43	−. 27	−. 08	−. 24	−. 16
1956	117	5. 66	4. 29	4. 98	−. 08	−. 16	−. 12	−. 08	−. 52	−. 30
1957	91	5. 89	3. 18	4. 54	−. 04	. 37	. 17	. 09	−. 18	−. 05
1958	131	5. 63	5. 43	4. 53	−. 24	. 24	. 00	−. 04	. 31	. 14
1959	126	5. 52	4. 05	4. 79	−. 04	. 06	. 01	. 02	. 40	. 21
Total or mean	1594	5. 55	4. 31	4. 93	------	------	------	------	------	------
Mean selection differential per year in actual units					−0. 17	−0. 23	−0. 20	−0. 09	−0. 06	−0. 08
Mean selection differential per year in standard units					−. 04	−. 05	−. 05	−. 02	−. 01	−. 02
Mean selection differential per generation in actual units					−. 84	−1. 13	−. 99	−. 44	−. 30	−. 39
Mean selection differential per generation in standard units					−. 20	−. 26	−. 23	−. 10	−. 07	−. 08
Corresponding value for percent saved under truncation selection using standardized selection differentials per generation					90	86	88	95	97	96

The selection differential per generation in standard units on the sire side of 1.07 for weaning weight indicates that selection was fairly intense for this trait. The selected animals were representative of the top 34 percent of the population. Although birth weight was not selected for directly, positive selection differentials were obtained for this trait because of its positive relationship with weights later in life.

The selection differentials on the sire side, ΔS, for postweaning traits of bulls are presented in table 7. The average age of the parents is very similar to that presented in the weanling data, there having been some tendency to select bulls from older dams. Selection pressure was positive and fairly consistent over the years. The annual selection differentials averaged 8.5 and 14.4 pounds for 196-day gain and *of inbreeding and for birth and weanling traits*

ΔS for sires, and ΔP average for both parents]

Birth weight			180-day gain			Weaning weight			Weaning score		
ΔD	ΔS	ΔP	ΔD	ΔS	ΔP	ΔD	ΔS	ΔP	ΔD	ΔS	ΔP
Lb.	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Pct.*	*Pct.*	*Pct.*
0.15	[illegible]	0.38	0.2	5.5	2.9	0.3	6.1	3.2	0.14	0.16	0.15
.04	.53	.29	.4	3.6	2.0	.4	4.1	2.3	.13	.11	.12
.13	.54	.34	1.5	3.4	2.5	1.6	3.9	2.8	.11	.48	.30
.20	.62	.41	1.2	6.8	4.0	1.4	7.4	4.4	.12	.58	.35
.02	2.14	1.08	2.3	11.1	6.7	2.3	13.1	7.7	.22	1.58	.90
.19	1.59	.89	2.5	12.3	7.4	2.6	13.8	8.2	.32	1.87	1.10
.37	1.73	1.05	3.0	19.0	11.0	3.3	20.6	12.0	.55	2.28	1.42
-.03	1.11	.54	3.7	16.2	10.0	3.6	17.2	10.4	.64	1.86	1.25
.27	.78	.53	2.2	13.1	7.7	2.5	13.7	8.1	.41	1.67	1.04
-.06	.14	.04	2.2	3.7	3.0	2.2	3.8	3.0	.27	.69	.48
-.01	1.87	.93	2.0	7.8	4.9	2.1	9.7	5.9	.02	1.07	.55
.08	1.61	.85	1.7	6.9	4.3	1.8	8.5	5.2	.22	.89	.56
.42	1.19	.66	1.2	7.1	4.2	1.3	8.3	4.8	.10	1.65	.88
.18	2.08	1.13	.7	6.4	3.6	.9	8.5	4.7	.24	1.55	.90
.02	.76	.39	1.4	6.9	4.2	1.5	7.7	4.6	.31	.88	.60
.01	1.03	.51	.9	3.4	2.2	.9	4.5	2.7	.26	.84	.55
.00	.90	.45	2.1	3.0	2.6	2.1	3.9	3.0	.31	.58	.45
0.10	1.13	0.62	1.7	8.0	4.9	1.8	9.1	5.5	0.26	1.40	.68
.01	.15	.08	.04	.20	.12	.04	.22	.13	.04	.16	.10
.49	5.57	3.06	8.4	39.4	24.2	8.9	44.9	27.1	1.28	5.42	3.35
.07	.75	.41	.21	.99	.61	.21	1.07	.65	.19	.80	.49
97	54	76	89	39	63	89	34	60	90	50	70

final weight off test, respectively. In standard units per generation, this amounts to 1.10 and 1.46 standard deviations, and corresponds to selecting the top 32 and 18 percent of the population. Considering that selection was not for any one trait and that culling was practiced for fertility, obvious conformation defects, and nonregistrable color markings, the overall selection pressure on the sire side was fairly intense.

The annual selection differentials for the postweaning traits for females and the average age of the parents are listed in table 8. The average age of the parents, or generation interval, was again nearly the same as in the larger population for weanling traits. Again, there was some tendency to select heifers from the somewhat older dams, as it was in the case for bulls.

TABLE 7.—*Annual selection differentials for postweaning traits for males*

Year of birth	Bulls	Average age			196-day gain ΔS	Final weight ΔS
		Dam	Sire	$\bar{A}$		
	Number	*Years*	*Years*	*Years*	*Pounds*	*Pounds*
1943	5	5.43	4.00	4.72	4.1	0.6
1944	24	6.16	4.71	5.44	6.8	3.6
1945	16	5.50	4.94	5.22	9.8	10.1
1946	16	6.31	6.31	6.31	4.6	6.8
1947	25	6.04	3.64	4.84	10.3	19.4
1948	27	6.67	3.56	5.12	9.2	18.0
1949	17	5.18	3.59	4.39	12.6	28.0
1950	17	5.47	4.71	5.09	10.1	23.4
1951	24	5.79	4.67	5.23	9.5	17.2
1952	21	5.57	4.24	4.91	10.9	9.6
1953	34	5.79	3.65	4.72	9.0	16.8
1954	32	5.94	5.31	5.63	9.7	15.9
1955	27	6.44	2.67	4.56	6.4	17.6
1956	35	5.51	4.37	4.94	6.1	15.6
1957	23	6.65	3.17	4.91	7.5	14.4
1958	38	5.74	3.55	4.65	10.7	16.7
1959	32	5.28	4.22	4.75	7.8	11.6
Total or mean	413	5.85	4.19	5.02		
Mean selection differential per year in actual units					8.5	14.4
Mean selection differential per year in standard units					.22	.29
Mean selection differential per generation in actual units					42.7	72.3
Mean selection differential per generation in standard units					1.10	1.46
Corresponding value for percent saved under truncation selection using standardized selection differentials per generation					33	18

Selection was not intense for any of the postweaning traits in females and amounted essentially to zero for gain in weight from weaning to 12 months, for mature weight, and for producing ability. Although small, there was consistent positive selection pressure placed on 12-month weight, gain in weight from 12 to 18 months, and 18-month weight and score. The cows that actually had female offspring that reached these ages correspond to about the top 90 percent of the female population for these traits. The selection differentials, ΔD, per generation in standard measure for 18-month weight and score are almost identical with the corresponding selection differentials for weaning weight and score, respectively.

Besides the direct selection differentials discussed in this section, there was some selection pressure exerted on the basis of a topcross progeny test of sires. Sires that performed well within the line were retained as herd sires longer than those with poorer progeny. Although only a limited number of sires were progeny tested and used, the actual selection pressure for weights, gains, and scores is probably underestimated somewhat.

TABLE 8. *Annual selection differentials for postweaning traits for females*

Year of birth	Number of progeny	Average age			Gain from weaning to 12 months	12-month weight	Gain from 12 to 18 months	18-month weight	18-month score	Mature spring weight	Mature fall weight	Producing ability
		Dam	Sire	A	ΔD	ΔD	ΔD	ΔD	ΔD	ΔD	ΔD	ΔD
		Yr.	*Yr.*	*Yr.*	*Lb.*	*Lb.*	*Lb.*	*Lb.*	*Pct.*	*Lb.*	*Lb.*	*Pct.*
1943	45	4.96	5.56	5.26	0.3	0.4	0.5	0.9	0.24	−1.5	−1.4	−0.04
1944	38	5.16	5.74	5.45	.8	.9	.6	1.5	.15	.9	.6	.15
1945	35	6.03	4.94	5.49	.4	1.6	.9	2.5	.23	2.0	.5	.11
1946	32	5.72	6.09	5.90	.4	1.9	.8	2.7	.16	−.6	−.1	.15
1947	45	5.60	3.60	4.60	−.9	1.1	1.4	2.5	.19	.6	−1.2	.16
1948	60	5.33	3.68	4.51	−.5	1.4	1.2	2.6	.23	.7	.0	.02
1949	31	4.68	3.58	4.13	−1.2	.9	.8	1.7	.06	−1.4	−1.7	−.19
1950	27	5.37	4.26	4.82	−2.1	1.3	1.9	3.2	.27	−.1	.3	.14
1951	31	5.26	4.58	4.92	−.1	1.7	1.4	3.1	.29	−.6	.7	.01
1952	39	5.42	4.58	5.00	−.6	.5	1.4	1.9	.26	−1.5	−.2	−.01
1953	67	6.10	4.00	5.05	−.1	1.5	.5	2.0	.19	−1.0	−.1	.00
1954	54	6.09	4.63	5.36	.1	1.6	.4	2.0	.15	.6	.7	.07
1955	37	6.59	3.73	5.16	1.2	2.3	.4	2.7	.34	−1.5	−.4	.34
1956	47	5.87	4.32	5.10	1.0	1.8	1.3	3.1	.32	−.2	.0	−.03
1957	52	6.28	3.31	4.80	−.8	1.5	.5	2.0	.18	−3.6	−3.1	−.06
1958	59	5.85	3.24	4.55	.3	1.6	2.5	4.1	.35	.2	.5	.02
1959	34	5.50	4.03	4.77	−.7	2.3	.9	3.2	.31	.6	.3	.19
Total or mean	733	5.64	4.35	5.00								
Mean selection differential per year in actual units					−0.1	1.4	1.1	2.5	0.23	−0.4	−0.3	0.06
Mean selection differential per year in standard units					−.003	.030	.032	.074	.036	−.004	−.003	.013
Mean selection differential per generation in actual units					−.5	7.0	5.5	12.5	1.15	−2.0	−1.5	.30
Mean selection differential per generation in standard units					−.016	.152	.162	.212	.180	−.019	−.013	.065
Corresponding value for percent saved under truncation selection using standardized selection differentials per generation					99	93	92	89	91	99	99	97

Selection Indices Actually Practiced

Dickerson et al. (1954) have shown that the index actually used may be calculated in retrospect when the selection differentials and phenotypic correlations are known for all traits that were considered in selection. Harvey and Bearden [3] have demonstrated this method in correlation matrix form and have presented tables on expected genetic progress in each of two traits with varying genetic parameters and intensities of selection.

Although all traits that receive some emphasis through both natural and artificial selection would probably never be included in an index in actual practice, those that were given primary consideration—weights, gains, scores, and producing abilities—are considered here. The phenotypic correlations and selection differentials for males per generation in standard measure are given in table 9. These may be regarded as equations with the correlations being the independent variable and the selection differential the dependent variable. The phenotypic correlations were reported previously by Brinks et al. (1962b) on the male population in the Miles City herd that were fed in a postweaning test and included inbred lines other than Line 1, although Line 1 made up the bulk of the data. Preweaning and postweaning gains were not used in calculating the index since these are fully described by the various weights.

TABLE 9.—*Phenotypic correlations and selection differentials for males used to calculate selection index in retrospect*

Trait	BW	WW	WS	FW	Selection differential (ΔS)
Birth weight (BW)	1.00	0.30	0.13	0.39	0.75
Weaning weight (WW)	.30	1.00	.50	.62	1.07
Weaning score (WS)	.13	.50	1.00	.37	.80
Final weight off test (FW)	.39	.62	.37	1.00	1.46

Solving the equations, the resulting index in standard measure actually practiced on the average was:

$$I_S = 0.2083\ (BW) + 0.1324\ (WW) + 0.2629\ (WS) + 1.1994\ (FW).$$

This index indicates that final weight off test received much more emphasis than weights or scores taken previous to final weight.

The selection differential in standard measure for the index actually practiced on the sire side is given by:

$$\Delta I_S = (a_1 s_1 + a_2 s_2 + \ldots a_n s_n)^{1/2} \text{ (Harvey and Bearden)}$$

$$= [(0.2083)\ (0.75) + (0.1324)\ (1.07) + (0.2629)\ (0.80) + (1.1994)(1.46)]^{1/2}$$

$$= 1.50$$

[3] Harvey, W. R., and Bearden, G. D. Tables of expected genetic progress in each of two traits. U.S. Dept. Agr. Agr. Res. Serv., ARS 20-12. 1962.

where a_i is the relative weight expressed as standard partial regression coefficient, and s_i is the selection differential in standard measure.

The phenotypic correlations and selection differentials for the females are listed in table 10. The phenotypic correlations involving weights and scores only were reported by Brinks et al. (1964a) and those involving producing ability were reported by Brinks et al. (1964b). All correlations were derived from the female population in the Miles City herd.

TABLE 10.—*Phenotypic correlations and selection differentials for females used to calculate selection index in retrospect*

Trait	BW	WW	WS	12W	18W	18S	SW	FW	PA	Selection differential (ΔD)
Birth weight (BW)	1.00	0.41	0.13	0.42	0.43	0.17	0.35	0.35	0.07	0.07
Weaning weight (WW)	.41	1.00	.51	.73	.66	.25	.45	.45	.09	.21
Weaning score (WS)	.13	.51	1.00	.36	.28	.35	.19	.22	.01	.19
12-month weight (12W)	.42	.73	.36	1.00	.82	.36	.57	.57	.15	.15
18-month weight (18W)	.43	.66	.28	.82	1.00	.46	.67	.67	.20	.21
18-month score (18S)	.17	.25	.35	.36	.46	1.00	.29	.29	.06	.18
Mature spring weight (SW)	.35	.45	.19	.57	.67	.29	1.00	.87	.17	−.02
Mature fall weight (FW)	.35	.45	.22	.57	.67	.29	.87	1.00	.01	−.01
Producing ability (PA)	.07	.09	.01	.15	.20	.06	.17	.01	1.00	.07

The resulting index in standard measure actually used on the average was:

$$I_D = -0.0068\ (BW) + 0.1353\ (WW) + 0.1054\ (WS) - 0.1612\ (12W) + 0.3942\ (18W) + 0.0758\ (18S) - 0.2034\ (SW) - 0.1093\ (FW) + 0.0337\ (PA).$$

The trait receiving the most emphasis in the index was 18-month weight, which was the time when some culling took place on the female side. The selection differential for the index actually practiced on the females in standard measure was calculated in the same manner as given previously for the males and is:

$$\Delta I_D = [(-0.0068)(0.07) + (0.1353)(0.21) + (0.1054)(0.19) + (-0.1612)(0.15) + (0.3942)(0.21) + (0.0758)(0.18) + (-0.2034)(-0.02) + (-0.1093)(-0.01) + (0.0337)(0.07)]^{1/2} = 0.36.$$

Expected Progress

The expected genetic progress (ΔG_i) in each of the traits can be calculated directly from the relative weights in standard measure (a_j), the genetic correlations ($r_{g_i g_j}$), and square roots of the heritability values (g_i) as:

$$\Delta G_i = \sum a_j\, r_{g_i g_j}\, g_i g_j \text{ (Harvey and Bearden)}$$

The genetic correlations and square roots of heritability values were taken from the same studies as cited in the previous section for the phenotypic correlations used in calculating the indices (Brinks et al. 1962b, 1964a, 1964b). The genetic correlations and square roots of heritability values for the males are listed in table 11. It is interesting to note that there are no negative correlations that would tend to retard improvement. Correlations of traits with final weight are fairly high.

TABLE 11. *Genetic correlations and square roots of heritability for males used to estimate genetic progress*

Trait	BW	WW	WS	FW	Square root of heritability (g_i)
Birth weight (BW)	1.00	0.21	0.20	0.75	0.59
Weaning weight (WW)		1.00	.72	.67	.49
Weaning score (WS)			1.00	.48	.42
Final weight off test (FW)				1.00	.69

The expected genetic progress, ΔG_i, can be obtained from matrix multiplication of $A'G$ where A' is the row vector of the relative weights in standard measure and G is the genotypic variance-covariance matrix in standard measure. The diagonal elements in the G matrix become the heritability values, and the off diagonal elements are calculated from $r_{g_i g_j}\, g_i g_j$.

$$A'G=[(0.2083\ 0.1324\ 0.2629\ 1.1994)]\begin{bmatrix}0.3500 & 0.0607 & 0.0496 & 0.3053\\ .0607 & .2400 & .1482 & .2265\\ .0496 & .1482 & .1800 & .1391\\ .3053 & .2265 & .1391 & .4800\end{bmatrix}$$

The resulting ΔG_S values obtained upon multiplication are listed in table 12. The ΔG_S values are the expected genetic progress per generation in standard measure resulting from selection among bulls. These values must be averaged with the ΔG_D, the expected genetic progress per generation in standard measure resulting from selection among females, or halved if no corresponding trait is available on the female side, to estimate the overall genetic progress expected from selection. Genetic progress resulting from sire selection was expected for all traits under study, with the largest improvement expected in final weight off test.

TABLE 12.—*Expected genetic progress per generation in standard measure from selection among males*

Item	Birth weight	Weaning weight	Weaning score	Final weight off test
ΔG_S [1]	0.4602	0.3550	0.2441	0.7059

[1] Expected genetic progress resulting from selection among sires.

TABLE 13.—*Genetic correlations and square roots of heritability for females used to estimate genetic progress*

Trait	BW	WW	WS	12W	18W	18S	SW	FW	PA	Square root of herita-bility (g_i)
Birth weight (BW)	1.00	0.60	0.05	0.56	0.60	0.23	0.61	0.68	−0.11	0.62
Weaning weight (WW)		1.00	.27	.71	.75	.07	.59	.51	0	.66
Weaning score (WS)			1.00	−.19	−.08	.10	.10	.09	.10	.53
12-month weight (12W)				1.00	.90	.21	.66	.62	.14	.64
18-month weight (18W)					1.00	.62	.84	.74	.25	.71
18-month score (18S)						1.00	.28	.20	−.09	.36
Mature spring weight (SW)							1.00	.93	.09	.72
Mature fall weight (FW)								1.00	−.19	.75
Producing ability (PA)									1.00	.67

The genetic correlations and square roots of the heritability values for traits measured on the females are listed in table 13. A few small negative correlations were obtained involving weaning score and producing ability. Correlations involving weights and gains during various periods of an animal's life were generally quite large.

The values in table 13 were then used to compute the ΔG_D for females using the same matrix multiplication procedure previously outlined for the males. The resulting ΔG_D values for females are listed in table 14.

TABLE 14.—*Expected genetic progress per generation in standard measure from selection among females*

Item	Birth weight	Wean-ing weight	Wean-ing score	12-month weight	18-month weight	18-month score	Mature spring weight	Mature fall weight	Produc-ing ability
ΔG_D[1]	0.0131	0.0733	0.0316	0.0387	0.0594	0.0470	0.0067	−0.0204	0.0564

[1] Expected genetic progress resulting from selection among dams.

The ΔG_D for females again would need to be averaged with the ΔG_S for males or halved if no corresponding trait in the males was available in order to predict overall expected genetic progress. Although small, some genetic progress was expected from selection among females in all traits except mature fall weight.

The same traits were measured on both sexes from birth through weaning and, therefore, the ΔG_S and ΔG_D need only to be averaged to predict overall genetic progress. The ΔG_S and ΔG_D, converted into actual units by multiplying by the respective standard deviations listed in table 3, are shown in table 15 along with their average.

TABLE 15.—*Expected genetic progress per generation in birth and weaning traits in actual units by sires, dams, and average*

Trait	ΔG_S[1]	ΔG_D[2]	$\frac{\Delta G_S + \Delta G_D}{2}$
Birth weight ....pounds..	3.41	0.10	1.75
Gain from birth to weaning..........do....	11.50	2.98	7.24
Weaning weight......................do....	14.91	3.08	8.99
Weaning score....................percent..	1.66	.21	.94

[1] Expected genetic progress resulting from selection among sires.
[2] Expected genetic progress resulting from selection among dams.

Most of the expected genetic progress resulted from selection on the sire side as has been shown previously. The expected progress in gain from birth to weaning was taken as the difference between birth and weaning weights. Some additional phenotypic improvement would also be expected in weaning weight and in gain from birth to weaning resulting from genetic improvement in producing ability. However, this would be expected to amount to only about 1.66 pounds per generation.

Calculating the expected genetic progress in the postweaning traits is more difficult because the two sexes were managed differently, and different traits were measured. Because selection pressure was relatively minor on postweaning traits in females, a fairly accurate estimate of expected genetic improvement in final weight off test for bulls may be obtained simply by halving the ΔG_S for final weight off test of bulls. In converting the expected progress of 0.7059 standard deviation units in final weight to actual units, one obtains 35.30 pounds. Dividing this figure by two yields an estimate of 17.65 pounds per generation as the expected genetic improvement.

This estimate of improvement is probably biased down somewhat because there was some positive selection pressure for increased weight among the females. If one assumes that one standard deviation of selection pressure for 18-month weight in females is equal to one standard deviation in final weight off test for bulls, the expected improvement per generation in final weight would rise to 19.13 pounds. Because the genetic correlation between final weight off test of bulls and the 18-month weight of heifers would be less than 1, this estimate would be biased upwards somewhat. The actual expected improvement would probably be between 17.65 and 19.13 pounds per generation.

Most of the selection pressure for increased weights and gains was on the sire side and, therefore, simply halving the ΔG_D for postweaning traits in the females would undoubtedly underestimate the expected genetic progress in traits measured in the females. Because the 18-month weight in heifers and the final weight off test in bulls described about the same stage of development, and since both traits appear to have nearly the same estimate of heritability and indicate similar genetic correlations with weights and gains recorded earlier in life, it was decided to set one standard deviation of selection pressure in final weight off test of bulls equal to one standard deviation of selection pressure in 18-month weight of heifers. Although this procedure will probably bias upward somewhat the expected genetic improvement, it should yield a reasonable maximum estimate of the amount of improvement expected.

The 1.46σ selection differential for final weight of bulls was set equal to 1.46σ of 18-month weight of heifers, and the expected direct response in 18-month weight and expected correlated responses in other postweaning traits in females were calculated. The ΔG_S for postweaning traits in females are listed in table 16 along with the ΔG_D and their averages.

TABLE 16.—*Expected genetic progress per generation in postweaning traits of females in actual units by sires, dams, and average*

Trait	ΔG_S [1]	ΔG_D [2]	$\frac{\Delta G_S + \Delta G_D}{2}$
Gain from weaning to 12 months..pounds..	7.44	−1.30	3.07
12-month weight..do....	27.46	1.78	14.62
Gain from 12 to 18 months..do....	15.61	1.73	8.67
18-month weight..do....	43.07	3.51	23.29
18-month score..percent..	1.20	.30	.75
Mature spring weight..pounds..	50.78	.70	25.74
Mature fall weight..do....	49.48	−2.33	23.58
Producing ability..percent..	.55	.26	.41

[1] Expected genetic progress resulting from selection among sires.
[2] Expected genetic progress resulting from selection among dams.

The expected progress in the gain periods was taken as the difference between the weights in question. On the assumption specified above that selection pressure for increased final weight off test of bulls would result in equivalent selection pressure in 18-month weight of heifers, it is evident that sizable genetic progress is expected in all weights and gains in the female population. To the extent that the genetic correlation between weights of bulls and heifers is not unity, these estimates of expected progress are biased upward.

Response to Selection

It was shown in the preceding section that considerable selection pressure was applied and that a positive response from selection is expected in all traits under consideration. Conversely, it has been shown that increased inbreeding is associated with a decline in performance, and that a downward trend from this effect is expected with increased inbreeding over the years. This part of the report presents information on changes in performance in a population where these two opposing forces are operating concurrently.

Since planned control populations were not carried, separation of the phenotypic change into its respective genetic and environmental components is difficult. However, inspection of the data revealed a sizable number of repeat matings, and this information has been used in an attempt to gain some insight on the amount of genetic and environmental changes that have been made on birth and weanling traits. Useful information also can be obtained from phenotypic time trends over the years. The results and discussion in this part of the report are divided into: (1) phenotypic time trends and (2) estimation of genetic and environmental time trends for birth and weanling traits from repeat mating information.

Phenotypic Time Trends

The means of the performance traits by years and the phenotypic regressions on years are listed in table 17. Only animals that were

TABLE 17.—*Means for performance traits*

Year [1]	Birth and weanling traits						Postweaning traits: Males		
	Number of records	Birth weight	180-day gain	Weaning weight	Number of records	Weaning score	Number of records	196-day gain	Final weight off test
		Lb.	*Lb.*	*Lb.*		*Pct.*		*Lb.*	*Lb.*
1934–36	95	68.6	277	345					
1937	47	67.0	281	348					
1938	55	76.2	292	368					
1939	48	77.9	334	412	40	74.7	8	359	878
1940	61	78.5	325	404	60	76.9	7	369	808
1941	58	76.6	334	411	58	78.2	7	336	797
1942	69	77.5	316	394	69	76.2	15	332	764
1943	90	73.8	300	374	90	71.8	7	432	868
1944	102	76.4	312	389	101	77.2	31	420	857
1945	72	79.9	324	404	71	77.8	16	456	913
1946	68	78.8	371	450	68	72.0	16	461	936
1947	94	79.1	322	402	94	74.4	25	431	879
1948	118	77.9	339	416	117	77.1	27	382	813
1949	63	68.4	233	301	63	63.3	17	462	810
1950	54	70.1	327	397	54	78.9	17	486	945
1951	75	79.5	359	439	75	76.2	24	468	920
1952	75	75.8	316	392	75	74.1	21	471	931
1953	119	81.3	358	439	119	79.4	34	477	960
1954	114	78.7	366	444	113	76.9	32	469	949
1955	85	77.7	353	431	85	78.2	27	461	934
1956	117	79.0	352	431	116	75.6	35	478	924
1957	91	78.5	325	404	91	76.4	23	484	917
1958	131	78.7	334	413	131	79.5	38	438	881
1959	126	76.7	343	419	125	82.4	32	490	929
bp [2]		0.223	2.154	2.368		0.178		6.296	5.831
ΔP [3]		5.3	52	57		3.7		132	122

[1] Denotes year of birth for all traits except mature weights of females. For this trait it denotes year in which the weight was taken.

[2] Denotes phenotypic regression on years.

[3] $\Delta P = bp \times$ number of years.

produced within the line are included, and foundation animals have been excluded. A weighted average of the traits is presented for the years 1934 through 1936 because the same foundation sires and dams were used during this period, and no offspring came into production until 1937. The birth and weanling information was pooled over sexes even though inbreeding effects were found to be markedly different, since it was found that the differences due to sex remained nearly constant over the years. Apparently the net effect of both inbreeding of calf and inbreeding of dam was nearly the same for both sexes.

All traits show a sizable increase over the years although the trend is highly variable due to large year effects (table 17). At the bottom of the table are shown the average trend for the various traits indicated

by years and phenotypic regressions on years

Postweaning traits—Continued								
Females								
Number of records	Gain weaning to 12 months	12-month weight	Gain, 12–18 months	18-month weight	18-month score	Number of records	Mature spring weight	Mature fall weight
	Lb.	*Lb.*	*Lb.*	*Lb.*	*Pct.*		*Lb.*	*Lb.*
44	114	468	164	631	75.8	--------	--------	--------
20	113	450	264	714	72.0	2	998	1000
28	69	437	253	690	76.9	6	1032	1099
22	116	525	220	745	70.9	32	1077	1072
35	121	526	215	741	76.3	40	1149	1076
28	109	523	199	723	73.0	58	1180	1161
23	95	491	213	704	66.8	68	1122	1138
45	120	490	209	699	69.4	88	1061	1102
38	73	466	201	667	75.4	102	1054	1121
35	60	472	270	742	70.2	71	1104	1115
32	−2	452	264	715	71.2	68	1123	1091
45	39	427	316	743	68.6	92	1131	1109
60	29	449	179	628	69.6	116	1095	1145
31	112	415	290	705	78.5	61	1068	968
27	114	508	293	801	76.9	50	1078	1167
31	61	495	269	764	73.1	74	1194	1190
39	126	504	268	771	72.1	73	1189	1170
67	111	547	268	815	74.6	115	1245	1228
54	109	546	290	836	74.5	113	1209	1202
37	82	512	268	780	76.8	83	1219	1208
47	99	535	251	785	73.6	116	1222	1212
52	86	489	250	738	71.1	89	1178	1194
59	87	498	247	745	79.2	129	1211	1155
34	125	554	240	794	75.7	124	1183	1165
--------	−0.042	2.290	2.394	4.671	0.114	--------	7.599	6.261
--------	−1	55	57	112	2.7	--------	175	144

by the phenotypic regression on years and the estimate of the total change, which is computed by multiplying the regression by the number of years.

The regression of birth weight on years was 0.223 of a pound per year or an estimated increase of 5.3 pounds over the years. Birth weight appears to be affected less by yearly differences than does preweaning gain and weaning weight. The phenotypic regressions of preweaning gain and weaning weight of 2.154 and 2.368 pounds per year indicate an increase over the years amounting to 52 and 57 pounds, respectively. The regressions of birth weight and preweaning gain sum to the regression for weaning weight except for rounding errors. The regression of weaning score on years of 0.178 also indicates an upward trend amounting to 3.7 percent over the years. Differences among scorers over the years would add to the environmental component of this trend.

Postweaning performance of bulls also shows a considerable increase through the years. amounting to an estimated increase of 132 and 122 pounds on 196-day gain and final weight, respectively, over the 21-year period. The phenotypic regressions of 6.296 and 5.831 pounds per year appear extremely large. Inspection of the annual means shows a large increase in 1943 and thereafter over previous years, which could account for the large regression coefficients.

The phenotypic regressions on years for postweaning traits in females also indicate substantial increases over the years except for gain from weaning to 12 months, which shows almost no change. The average gain during this period over the 24 years was 89 pounds or about 0.5 pound per day. The estimated total change in 12-month weight is about the same as that for weaning weight, and the phenotypic regressions on years of weaning weight and gain from weaning to 12 months nearly sum to the regression of 12-month weight on years. This indicates that the small loss in number of females between weaning and 12 months had very little effect on the regressions.

The phenotypic regressions of gain from 12 to 18 months and 18-month weight of 2.394 and 4.671 per year indicate a substantial increase over the years. The estimated total increase in gain from 12 to 18 months of 57 pounds is the same as the estimated total increase in weaning weight over the same period. Eighteen-month score of heifers showed a phenotypic increase of 2.7 percent over the years, which is slightly less than the phenotypic increase in weaning score.

Estimated phenotypic change in mature weight of cows indicated substantial increases in both spring and fall weights amounting to 175 and 144 pounds, respectively, over the years. The regressions of mature cow weights on years appear to be exceptionally high. Inspection of the annual means shown in table 17 indicates that the average mature cow weights were markedly lower in the first few years when numbers were small. It is probable that these regressions overestimate the actual genetic improvement, and that some of the change is due to sampling error and abrupt environmental changes. Only cows that weaned a calf in the fall were included. Cow weights were adjusted to a 6-year-old basis, and each cow's record appears in every year she produced a calf. The differences in phenotypic increases between 18-month weight and spring and fall mature weights were 63 and 32 pounds, respectively. The differences between the amounts of estimated increases at various weights indicate that positive phenotypic changes took place at all stages except from weaning to 12 months of age.

Genetic and Environmental Time Trends

Repeat matings from all inbred lines raised at the U.S. Range Livestock Experiment Station were used to estimate the environmental trend over the years for the birth and weanling traits. Although the sampling error is probably high for any one 2-year comparison, the average regression over a fairly long period of time should yield some idea of the environmental trend. The existence of interactions involving sire, dam, year, sex, and age-of-dam effects could cause a bias in this method of estimating environmental trends.

Separate adjustments for age-of-dam effect were made in this analysis using age-of-dam differences from repeat observations on the same cow, as computed by method B in the work of Koch and Clark (1955). These age-of-dam adjustment factors are biased because of confounding with the effects of culling of cows based on performance of their calves. However, using these adjustments, one adjusts for the effects of age of dam and effects of culling simultaneously. The assumptions must be made that the amount of culling among cows on performance in the repeat matings is the same as in the data from which the adjustments were derived, and that a fairly constant culling intensity was practiced each year. Deviations in culling intensity from year to year may have little effect on the overall environmental regression on years, but a consistent bias in one direction may lead to misleading results over a period of years.

As described previously, the environmental difference between any 2 consecutive years was taken as the difference of adjusted calf weights produced by repeat matings after adjustment had been made for age of dam. In years when repeat matings were not available, the environmental change was taken as the phenotypic change with the genetic change for that year being set to zero. This would bias downward somewhat the estimated genetic change if genetic progress was actually being made.

The environmental year to year deviations computed from the repeat matings were added and accumulated to obtain yearly means that would indicate the environmental trend and also correspond to the method used to calculate the phenotypic regression on years (table 18). The base point was taken as the weighted mean for 1934–36.

The environmental regression of —0.184 for birth weight indicates a negative trend that amounts to —4.4 pounds over the 24-year period. The environmental regression on years of gain from birth to weaning and weaning weight was positive, indicating that environmental conditions for faster preweaning gain improved over the years.

The genetic regressions on years, obtained by subtracting the environmental regressions from the phenotypic regressions, are shown in table 19 along with the estimates of total genetic change over the

TABLE 18.—*Environmental trend for birth and weaning traits by years and environmental regressions on years*

Year	Number of repeat matings [1]	Trait			
		Birth weight	180-day gain	Weaning weight	Weaning score
		Pounds	*Pounds*	*Pounds*	*Percent*
1934–36		68.6	276	345	
1937	89	66.5	278	345	
1938	[2] 0	75.7	289	365	
1939	[2] 0	77.4	337	409	74.7
1940	69	79.1	330	409	75.4
1941	11	77.9	341	419	75.0
1942	27	77.5	330	408	72.7
1943	60	75.2	324	399	68.8
1944	52	75.3	326	401	74.4
1945	11	74.0	331	405	71.7
1946	[2] 0	72.9	378	451	66.1
1947	[2] 0	73.[illegible]	330	403	71.0
1948	39	73.2	346	419	70.3
1949	[2] 0	64.5	248	313	56.4
1950	48	66.9	318	385	70.4
1951	80	74.5	356	431	68.9
1952	75	71.9	332	404	70.9
1953	76	72.8	332	405	70.4
1954	145	69.1	345	414	68.0
1955	91	72.2	335	407	70.0
1956	41	74.1	329	403	66.9
1957	28	74.1	322	396	70.2
1958	29	69.1	340	409	74.0
1959	50	67.5	327	395	75.4
bE [3]		−0.184	1.286	1.135	−0.135
ΔE [4]		−4.4	31	27	−2.8

[1] Figures given are for matings in a particular year, which are repeats of matings made the previous year or group of years as in the period 1934–36.

[2] There were no repeat matings available in these years and the environmental change was set equal to the phenotypic change with the genetic change equal to zero.

[3] Denotes environmental regression on years.

[4] $\Delta E = bE \times$ number of years.

years. All birth and weanling traits studied indicate that substantial genetic improvement was made over the years. The estimated total genetic increase of 9.7 pounds in birth weight over the 24-year period is more than one standard deviation. The estimated genetic increase from 1936 through 1959 in preweaning gain and weaning weight amounts to 21 and 30 pounds, respectively. These values indicate that about half of the phenotypic increase in weaning weight may be attributed to a genetic increase. The genetic change in weaning score also appears to be in a positive direction and amounts to 6.5 percent over the 21-year period or approximately one standard deviation.

Partitioning the phenotypic trend into the genetic and environmental components was not attempted for postweaning traits owing to the small number of repeat matings in each of the sex subclasses.

TABLE 19.—*Estimated genetic regressions on years and total genetic response*

Item	Trait			
	Birth weight	180-day gain	Weaning weight	Weaning score
	Pounds	*Pounds*	*Pounds*	*Percent*
bG [1]	0.407	0.867	1.234	0.313
ΔG [2]	9.7	21	30	6.5

[1] bG is difference when environmental regression is subtracted from phenotypic regression.
[2] $\Delta G = bG \times$ number of years.

Comparison of Expected and Actual Response

The expected and actual amounts of response to selection in the various traits have been presented in the previous two sections. The discussion and comparison of these results are in this part of the report.

Since the expected progress was calculated from selection differentials during the period 1943 through 1959, phenotypic, environmental, and genetic regressions on years were recalculated to correspond to this same period for comparison purposes. The regressions on years were calculated in the same manner as described previously from the annual means in tables 17 and 18. The phenotypic regression on years for birth weight, gain from birth to weaning, weaning weight, and weaning score were 0.148 of a pound, 2.091 pounds, 2.216 pounds, and 0.374 percent, respectively. The corresponding environmental regressions on years were —0.228 of a pound, 0.054 of a pound, —0.162 of a pound, and 0.153 percent; and the genetic regressions were 0.376 of a pound, 2.037 pounds, 2.378 pounds, and 0.220 percent, respectively.

The expected genetic response and estimates of the average genetic and phenotypic responses per generation are listed in table 20. The phenotypic and estimated genetic responses per generation were obtained by multiplying the generation interval of 4.93 years by the corresponding regression on years.

The data indicate that genetic progress was expected in all traits studied. The values obtained for the estimated genetic response and average phenotypic changes indicate that improvement was made in these traits. The estimated genetic response was fairly near but consistently greater than the expected genetic response for all birth and weaning traits. The estimated genetic regressions on years from 1943 through 1959 for gain from birth to weaning and for weaning weight were greater than corresponding regressions over the entire period of 1934 through 1959. This may be due to the fact that the calves produced in the initial years were either outcrosses or calves from outcross dams.

The ratio of the average phenotypic response to the expected genetic response showed more variability and indicates that environ-

TABLE 20.—*Comparison of expected and estimated average genetic and phenotypic responses in birth and weanling traits per generation, 1943–59*

Trait	Expected genetic response	Estimated genetic response	Ratio to expected	Average phenotypic response	Ratio to expected
Birth weight.....pounds..	1.75	1.85	1.06	0.73	0.42
Gain from birth to weaning..........pounds..	7.24	10.04	1.39	10.31	1.42
Weaning weight...do....	8.99	11.72	1.30	10.92	1.21
Weaning score..percent..	.94	1.09	1.16	1.84	1.96

mental factors probably have an important influence on the phenotypic regressions.

No estimates of actual genetic response were obtained for postweaning traits since the repeat mating information in each of the sex subclasses was considered inadequate. Comparison of the expected genetic change and the average phenotypic change over a fairly long period of years should, however, be useful in assessing progress.

The phenotypic regressions on years for the period 1943 through 1959 for bulls were 3.037 pounds and 3.760 pounds for 196-day gain and final weight off test, respectively. The phenotypic regressions on years for traits measured on the females were gain from weaning to 12 months, 2.993 pounds; 12-month weight, 5.255 pounds; gain from 12 to 18 months, 1.120 pounds; 18-month weight, 6.358 pounds; 18-month score, 0.317 percent; mature spring weight, 10.228 pounds; mature fall weight, 7.135 pounds. These regressions are, in general, greater than the phenotypic regressions over the entire period listed in table 17.

The expected genetic change and the average phenotypic change per generation for postweaning traits of bulls and females are listed in table 21. The phenotypic responses per generation again were obtained by multiplying the generation interval of 5.02 years for bulls and 5.00 years for females by the phenotypic regressions on years.

Genetic progress again was expected in all traits for both bulls and females. There was a positive phenotypic change in all traits which generally was substantially greater than the expected genetic change. The ratio of the average phenotypic change to the expected genetic change shows more variability for the gain periods than is the case with the various weights. It is evident from inspection of the annual means (table 17) that the phenotypic response is influenced strongly by environmental fluctuations. The average phenotypic response per year over the entire period of 1934 to 1959 was generally less than the phenotypic change from 1943 through 1959 for postweaning traits of females.

Although the phenotypic regressions may overestimate the actual genetic response in most of the traits, there was apparently a positive response of considerable magnitude. The data do not suggest that

TABLE 21.—*Comparison of expected genetic and average phenotypic responses in postweaning traits per generation*

Trait	Expected genetic response	Average phenotypic response	Ratio to expected
Bulls:			
196-day gain...pounds..	10.14	15.24	1.50
Final weight off test...do....	19.13	18.87	.99
Females:			
Gain from weaning to 12 months...do ...	3.07	14.96	4.87
12-month weight...do....	14.62	26.27	1.80
Gain from 12 to 18 months...do ...	8.67	5.60	.65
18-month weight...do....	23.29	31.79	1.36
18-month score...percent..	.75	1.58	2.11
Mature spring weight...pounds..	25.74	51.14	1.99
Mature fall weight...do....	23.58	35.67	1.51

this response was less than was expected. This is not in agreement with the results reported by Dickerson et al. (1954) in which apparently selection in mildly inbred lines of swine failed to improve measurably the genetic merit for traits associated with growth and litter size even after adjusting for the effects of inbreeding.

There are several reasons why the apparent differences in results could have been obtained. The types of traits and the nature of variation involved appear to be a large factor. Heritability values for traits associated with growth appear to be much larger in cattle than they were for swine. In addition, there was no selection for multiple births in this study. In these cattle data, there appear to be no strong genetic antagonisms among the traits under selection, and the genetic correlations among traits associated with growth are, as a rule, larger than the phenotypic correlations.

Results from limited topcross tests reported in the work of Pahnish et al. (1961, 1962), bottomcross tests reported in the work of Flower (1962), and other unpublished results indicate that the line has high general combining ability for weights and gains. Although it is not known that general combining ability has increased over the years, this information would suggest that genetic progress has been made or at least genetic merit maintained for traits associated with growth.

The foregoing discussion on response to selection involved data that were not adjusted for the effects of inbreeding. Inbreeding effects reported in previous sections were generally fairly large. If the actual responses were adjusted for the effects of inbreeding, the estimates of actual response would have been much greater than the expected genetic response.

Inbreeding depression is usually ascribed to nonadditive variation, with some degree of dominance thought to be the most likely genetic mechanism (Dickerson et al. 1954). There is also information in the literature (Lerner, 1954) that heterozygosity per se may be responsible for heterozygote advantage and that heterozygous individuals are more buffered against environmental stresses than the inbred. The differential response to inbreeding of calf and dam by sex classes suggests that environment may play an important role in determining the magnitude of the inbreeding effect. The estimates of inbreeding decline were obtained on a within-sire-year subclass basis. If a large portion of the decline was due to a degree of homozygosity × environment interaction, adjusting the data for the effects of inbreeding over years may not be justified. This would be especially true if the environmental conditions showed a positive trend over the years, as appears to be the case for several of the traits. Although part of the decline associated with inbreeding is probably due to the accumulation of deleterious recessives, it is apparent that use of the values obtained would lead to an overadjustment for the effects of inbreeding.

SUMMARY AND CONCLUSIONS

The purpose of this analysis was to study the intensity and effectiveness of selection for several economic traits in a closed Hereford line under a breeding system that combined mild inbreeding and selection. The data were collected at the U.S. Range Livestock Experiment Station, Miles City, Mont., under a cooperative project between the U.S. Department of Agriculture and the Montana Agricultural Experiment Station. A total of 2,027 calves by 33 sires were weaned during the period of 1934 through 1959. The traits studied were weights, gains, and body scores from birth through maturity, which were adjusted for several environmental sources of variation before the analyses were made.

Inbreeding was relatively mild and increased from an average of 0.7 to 21.6 percent from 1934 to 1959. It averaged 16.1 percent over the entire period. Facilities and practices such as calving and weaning dates, wintering regimes, feeding methods and rations, and other management factors have remained fairly constant over the entire experimental period.

The following conclusions are drawn from the study:

1. Increased inbreeding had a detrimental effect on all traits studied. The effect of inbreeding on weight reached a peak at 18 months of age in heifers and declined somewhat at mature weights. Final weight off test (12 to 13 months) was affected more by increased inbreeding than were weights taken earlier in life in bulls.

2. Increases in inbreeding of dam had a detrimental effect on growth from birth to weaning and on weaning weight, presumably through decreased milk production. This effect was completely compensated for at 18-month weight in heifers and was greatly reduced in bulls at final weight off test (12 to 13 months).

3. There was a differential response by sex to inbreeding of calf and inbreeding of dam in weanling traits. Inbreeding of calf had a more pronounced effect on females than on males, whereas inbreeding of dam had a greater effect on preweaning gain, weaning weight, and weaning score of bulls than of heifers. It is postulated that bulls, having a greater growth potential, are held back more than heifers by the decreased milk supply of their dams that is associated with increased inbreeding of dam. This maternal environment may mask the response to inbreeding of calf to a greater extent in bull calves than in heifers.

4. The selection differentials for inbreeding of calf were small but consistently negative for both sires and dams. Selected sires and dams that produced offspring averaged −1.13 and −0.84 percent less inbred than the average of the unselected population in which they were born. Selection differentials for inbreeding of dam were also fairly consistently negative and averaged −0.30 and −0.44 percent per generation for sires and dams, respectively. Because there was some selection against homozygosity, the selected individuals may be somewhat less homozygous than the calculated coefficients of inbreeding would indicate.

5. The average generation interval for birth and weanling traits was 4.93 years. The sires and dams averaged 4.31 and 5.55 years of age, respectively, when their progeny were born. The generation interval calculated for postweaning traits averaged about 5 years.

6. Selection pressure for increased weights, gains, and body scores was fairly intense on the sire side. The mean selection differential per generation in standard units for final weight off test was 1.46σ, which is representative of the top 18 percent of the population under truncation selection. Selection practiced among females was less intense but was consistently positive except for gain from weaning to 12 months (first winter period) and for mature weights. The mean selection differential per generation for 18-month weight was 0.21σ, which corresponds to the top 89 percent of the population.

7. The selection indices that were actually practiced were calculated in retrospect using the phenotypic correlations and standardized selection differentials. The selection index in standard measure actually practiced on bulls on the average was:

$I_S = 0.2083$ birth weight $+0.1324$ weaning weight $+0.2629$ weaning score $+1.1994$ final weight off test.

The selection differential for the index was $1.50\sigma_I$.

The selection index for females was:

$I_D = -0.0068$ birth weight $+0.1353$ weaning weight $+0.1054$ weaning score -0.1612 12-month weight $+0.3942$ 18-month weight $+0.0758$ 18-month score -0.2034 mature spring weight -0.1093 mature fall weight $+0.0337$ producing ability.

The selection differential for the index was $0.36\sigma_I$.

8. The calculated values for expected genetic progress in the various traits, derived from the heritability values, genetic correlations, and relative weights in the index, indicate that considerable positive genetic change was expected in all traits studied.

9. The average phenotypic changes during the period 1934 through 1959, calculated as the regressions of the annual mean values of the traits on years, indicate sizable positive change for all traits studied except gain from weaning to 12 months in heifers, which was essentially zero. In general, these changes were somewhat greater than the expected genetic change.

10. Estimates of environmental changes from 1934 through 1959, calculated for birth and weanling traits from repeat mating information, indicate slight negative trends for birth weight and weaning score and substantial positive trends for gain from birth to weaning and for weaning weight. Estimates of environmental trends for postweaning traits were not obtained.

11. Estimates of genetic changes, calculated by subtracting the environmental trend from the phenotypic trend, indicate that substantial genetic progress was obtained for birth weight, gain from birth to weaning, weaning weight, and weaning score. Estimates of total genetic response from 1934 through 1959 were 9.7 pounds in birth weight, 21 pounds in gain from birth to weaning, 30 pounds in weaning weight, and 6.5 percent in weaning score.

12. Comparisons of expected and estimated genetic response from 1943 through 1959 indicate that slightly more response than expected was obtained in birth weight (106 percent) and weaning score (116 percent), and considerably more than expected was obtained in gain from birth to weaning (139 percent) and weaning weight (130 percent). Adjustments for the detrimental effects of inbreeding were not included in these values. If adjustments for the effects of inbreeding had been made, estimates of considerably more progress than expected would have been obtained in these traits.

13. Comparisons of expected genetic response and actual phenotypic response for postweaning traits from 1943 through 1959 indicate that, in general, the actual response was as great as or greater than expected. Although environment is a factor in these trends, there apparently has been some genetic response, and the data do not suggest that this response is less than expected.

The results of this study indicate that a long term breeding program that combines intense selection and mild inbreeding in a fairly large closed line should be beneficial in improving the genetic merit of traits associated with growth. Results on the effectiveness of selection in other inbred lines need to be studied before conclusions can be made on the general application of this breeding system.

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U.S. GOVERNMENT PRINTING OFFICE: 1965

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