September 13, 1966

To the Graduate Council:

I am submitting herewith a dissertation written by Will T. Butts, Jr. entitled "The Effects of Inbreeding on Various Performance Traits of Angus Calves." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

Charles S. Hobbs
Major Professor

We have read this dissertation
and recommend its acceptance:

Harold J. Smith

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J. T. Miles

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Dean of the Graduate School

THE EFFECTS OF INBREEDING ON VARIOUS PERFORMANCE TRAITS OF ANGUS CALVES

A Dissertation

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

---

by

Will T. Butts, Jr.

December 1966

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CHAPTER I

INTRODUCTION

The generally detrimental effects of inbreeding on performance are of considerable interest to the beef cattle industry, since they are a major part of the price a breeder must pay for the use of inbreeding as a tool. The theoretical benefits possible with various mating systems involving inbreeding are widely accepted. However, actual progress through the employment of such systems has been difficult to demonstrate empirically.

A relatively long generation interval and low reproductive rate argue effectively against expecting the same degree of success through hybridization in cattle as that achieved in certain of the plant species. While evidence of heterosis has been found for most performance traits of beef cattle, some doubt remains that this heterosis is a result of non-additive genetic variance. It has been pointed out that evidence of heterosis can be explained on purely additive grounds.

A more general problem in the beef cattle industry is the mild inbreeding resulting from a buildup of relationship in a herd for purposes of increased uniformity, fixation of desired characteristics, or inability to locate satisfactory replacement animals outside of the herd. This increase in relationship fundamentally results from the relatively small numbers typical in large animal operations. From a breed standpoint, the increased use of artificial insemination may

contribute to this problem in the future by decreasing the effective number of sires.

This study was undertaken to estimate the effects of inbreeding on birth weight, average daily gain, type score, and condition score at approximately 120 days of age and at weaning. It was felt that these data offered an excellent opportunity to obtain relatively independent estimates for the effects of inbreeding of calf and inbreeding of dam, since the correlation (0.23) between the two inbreeding coefficients was lower than that usually encountered in closed inbred lines. In addition to the usual fixed environmental effects, an effort was made to consider cow size and the relationship between weaning condition score of the calf and the maternal contribution of the dam. Heritability estimates from these data were also of interest.

CHAPTER II

REVIEW OF LITERATURE

The effects of genetic and environmental forces on variation in weaning gain and type score have been investigated extensively. Estimates for these effects on birth weight and preweaning performance traits are much less numerous. A few studies of variation in condition score at weaning and in weaning index have been reported.

The variation among estimates from different studies emphasizes the extreme difficulty in establishing biological parameters. It is seldom completely clear whether differences among estimates are due to sampling variation within a population, differences among populations, or merely differences among the statistical procedures used to compute the estimates. Hence, the following review is intended to suggest reasonable ranges of response based on studies thought to be comparable to the present investigation.

I. EFFECTS OF CERTAIN FIXED SOURCES OF VARIATION

Sex. Most investigators have found male calves to weigh more at birth and gain faster from birth to weaning than heifer calves. Smith and Warwick (1954) summarized data from 4,113 Hereford calves from ten states and 366 Angus calves from four states. They found that Hereford and Angus males outweighed females at birth by 4.63 and 5.48 pounds, respectively. In other reports (Dawson, Phillips, and Black, 1947;

Burris and Blunn, 1952; Gregory, Blunn, and Baker, 1950; Knapp, Lambert, and Black, 1940; Koch and Clark, 1955a; and McCormick, Southwell, and Warwick, 1956) the average birth weight of males ranged from 3.5 to 7.2 pounds heavier than the average birth weight of females.

Petty and Cartwright (1966), in an extensive summary of genetic and environmental statistics for growth and conformation traits of young beef cattle, found an average birth weight advantage of 4.6 pounds in favor of males. In this same summary, they reported that bull calves gained 0.15 pound per day faster from birth to weaning than heifer calves and 0.06 pound per day faster than steer calves. Sex differentials for average daily gain from birth to weaning reported in this summary ranged from 0.11 to 0.22 pound per day.

Marlowe, Mast, and Schalles (1965) reported estimates of some non-genetic influences on calf performance based on 17,294 Angus records and 11,663 Hereford records. The genetic and environmental bases of these data are believed to be quite similar to those found in Tennessee. Non-creep-fed Angus bull calves gained 0.22 pound per day more from birth to weaning than heifer calves and 0.11 pound per day more than steer calves. Creep-fed Angus bull calves gained 0.26 and 0.14 pound per day more than heifers and steers, respectively. Comparable estimates for Hereford calves were 0.21 and 0.10 pound per day for calves receiving no creep and 0.28 and 0.09 pound for creep-fed calves.

Butts (1951) found steer and heifer calves at two locations in Tennessee to differ in weight at all ages from birth to weaning. This difference when expressed as a percentage of the weight of the steers

and heifers was not found to vary significantly between birth and weaning or between locations within year. A correction factor (1.085) for converting heifer calf weights to a steer basis was reported.

A limited number of studies of the influence of sex on weaning type score have been reported. Koch and Clark (1955a), in a study involving 5,962 Hereford calves, concluded that sex influences on type score at weaning were negligible. Sex differences observed in weaning type score by Marlowe and Gaines (1958), Taylor et al. (1960), Lehman et al. (1961), and Marlowe (1962) were 0.5, 0.3, 0.9, and 0.5 units, respectively, in favor of heifer calves. Loganathan (1962) and Jamison (1966), working with Tennessee data, found male calves to have been scored slightly higher than heifers for weaning type.

Little information concerning sources of variation in weaning condition scores was found in the literature. Pahnish et al. (1964), in a study involving approximately 700 Hereford calves in Arizona, reported average weaning condition scores of 10.9 and 10.5, respectively, for heifer and bull calves. Standard deviations of 1.06 for heifers and 0.82 for bull calves were found. Pahnish reported corroborative results by Synar (1958) in other Arizona work.

Age of dam. Many estimates for the effects of age of dam on birth weight, average daily gain to weaning, and weaning type score have been reported. A summary of recent estimates of these effects, as reported by Petty and Cartwright (1966), are shown (Tables I, II, and III). These estimates of age-of-dam effects are probably larger than the true age

TABLE I

SUMMARY OF ESTIMATED EFFECTS OF AGE OF DAM ON BIRTH WEIGHT EXPRESSED AS DEVIATIONS FROM BASES SELECTED BY THE RESPECTIVE AUTHORS

Author	Breed	Age of dam, years								
		2	3	4	5	6	7	8	9	10
Swiger (1961)	Hereford	0.0	2.3	7.6	9.5	9.5	9.5	9.5	9.5	9.5
Loganathan (1962)	Hereford	-10.3	-2.0	1.6	2.2	1.1	4.4	3.0	-1.3	-1.1
	Hereford	-14.1	-3.4	3.0	0.6	-.5	-2.3	6.5	7.3	3.0
Swiger et al. (1962)	Angus	-4.7	-2.5	0.0	0.3	0.8	1.6	1.6	2.2	0.6[a]
	Hereford	-4.7	-1.9	-.5	1.6	1.9	1.4	3.8	2.2	-1.3[a]
Brinks et al. (1962)	Hereford		-3.7	-1.6	-.7	0.0	-1.1	-1.8	-1.8	-3.4[a]
Ellis (1963)	Mixed	-6.0	-3.2	0.7	0.7	3.0	3.0	3.0	3.0	2.8
Shelby et al. (1963)	Hereford		-1.6	-.3	1.6	1.6	1.6	1.6	1.6	-.3[a]
Petty (1966)	Hereford	-8.4	-4.0	0.3	3.9	3.7	1.9	2.3	2.1	1.1
Average[b]		-9.7	-4.8	-1.0	0.0	0.0	1.5	0.8	-.4	

[a]Includes that age and older.

[b]Averages calculated using constants adjusted to a base of 6 years of age from those reports where cows calved at 2 years of age.

TABLE II

SUMMARY OF ESTIMATED EFFECTS OF AGE OF DAM ON AVERAGE DAILY GAIN FROM BIRTH TO WEANING EXPRESSED AS DEVIATIONS FROM BASES SELECTED BY THE RESPECTIVE AUTHORS

Author	Breed	Age of dam, years								
		2	3	4	5	6	7	8	9	10
Marlowe and Gaines (1958)	Mixed	-.30	-.17	-.11	-.08	-.04	0.00	-.06	-.01	-.07
Lehmann et al. (1961)	Mixed	-.13	0.00	0.10	0.14	0.20	0.13	0.14	0.10	0.10
Loganathan (1962)	Hereford	-.23	-.14	-.08	0.00	0.01	0.06	0.05	0.03	0.09
	Hereford	-.24	-.16	-.05	-.02	0.03	0.07	0.30	0.04	0.02
Swiger et al. (1962)	Angus	-.10	-.08	0.04	0.02	0.04	0.06	0.00	0.04	-.01[a]
	Hereford	-.22	-.12	-.02	0.03	0.07	0.06	0.09	0.07	-.01[a]
Brinks et al. (1962)	Hereford		-.14	-.08	-.02	0.00	0.01	0.03	0.02	-.01[a]
Cunningham and Henderson (1965)	Angus	-.26	-.16	-.07	-.04	-.03	0.00	0.00	0.00	0.00
	Hereford	-.26	-.19	-.08	-.03	-.01	0.00	0.00	0.00	0.00
Marlowe, Mast, and Schalles (1965)	Angus	-.18	-.10	-.06	-.03	-.02	0.00	0.00	-.01	-.01
	Hereford	-.23	-.11	-.07	-.03	0.00	0.00	0.00	-.01	-.01
Petty (1966)	Hereford	-.28	-.16	-.08	0.01	0.05	0.10	0.07	0.04	0.12
Average[b]		-.25	-.16	-.07	-.03	0.00	0.02	0.03	0.00	

[a]Includes that age and older.

[b]Averages calculated using constants adjusted to a base of 6 years of age from those reports where cows calved at 2 years of age.

TABLE III

SUMMARY OF ESTIMATED EFFECTS OF AGE OF DAM ON WEANING TYPE SCORE EXPRESSED AS DEVIATIONS FROM BASES SELECTED BY THE RESPECTIVE AUTHORS

Author	Breed	Age of dam, years								
		2	3	4	5	6	7	8	9	10
Marlowe and Gaines (1958)	Mixed	-.9	-.4	-.3	-.1	0.1	0.0	-.1	-.3	-.3
Lehmann et al. (1961)	Mixed	-.7	0.0	0.2	0.5	0.6	0.3	0.4	0.2	-.3
Loganathan (1962)	Hereford	-.9	0.1	-.1	0.3	0.4	0.4	0.3	0.3	0.5
	Hereford	-.5	-.6	-.1	-.2	0.7	1.5	0.0	-.8	0.0
	Hereford[a]	-1.0	-.5	0.0	0.2	0.3	0.5	0.1	0.1	0.4
	Hereford[a]	-.4	-.6	-.5	-.3	0.0	1.6	0.7	-.4	0.0
Brinks et al. (1962)	Hereford[b]		-2.6	-1.3	-.3	0.0	-.3	1.7	1.3	-.9[c]
Shelby et al. (1963)	Hereford[b]		-2.0	-.2	1.3	1.3	1.3	1.3	1.3	0.5[c]
Cunningham and Henderson (1965)	Angus	-.5	-.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0
	Hereford	-.5	-.3	0.2	0.2	0.1	0.0	0.0	0.0	0.0
Marlowe, Mast, and Schalles (1965)	Hereford	-.2	-.1	-.1	0.0	0.0	0.0	0.0	0.0	0.0
	Angus	-.1	0.0	0.0	0.1	0.0	0.0	-.1	-.2	-.2

TABLE III (continued)

Author	Breed	Age of dam, years								
		2	3	4	5	6	7	8	9	10
Petty (1966)	Hereford[d]	-.3	-.2	-.1	0.2	0.2	0.4	0.1	0.0	0.1
	Hereford[d]	-.2	-.2	0.0	0.1	0.0	0.2	0.1	0.1	0.0
Average[e]		-.8	-.5	-.3	-.1	0.0	0.1	-.2	-.3	

[a]Condition score constants.

[b]5 points = 1 score as comparable to the other reports.

[c]Includes that age and older.

[d]9 possible scores as compared to 15 in other reports.

[e]Averages calculated using constants adjusted to a base of 6 years of age from those reports where cows calved at 2 years of age. Averages exclude constants for condition score.

effects since, as pointed out by Lush and Shrode (1950), culling would tend to make each successive age group a more select one. It is probable that some continuous selection was practiced in the herds from which these estimates were computed. Loganathan (1962) found age-of-dam effects on weaning condition score (Table III, page 8) to be similar to those for type score. Jamison (1966), studying factors affecting intra-cow variation, found that calves from 2-, 3-, and 4-year-old dams gained 0.10, 0.05, and 0.03 pound per day, respectively, less to weaning than did calves from 6-year-old dams. In Jamison's study, calves from dams 2 years old and those from dams 9 years of age and older were scored lower for weaning type than were calves out of dams between the ages of 3 and 8 years. In general, calves from 2-, 3-, and 4-year-old dams weighed less at birth, gained less to weaning, and scored lower for weaning type than did calves from mature cows. Reported estimates for the effects of ages above 9 years are difficult to interpret, due to differences among environments and the accumulative effects of selection.

Weaning age. Variation in weaning age is another of the factors which make difficult the evaluation of differences in genetic worth among animals. Age of calf is usually confounded with month of birth within a given herd, and its effects on performance traits of calves are almost certain to be affected by differences in weaning dates among herds.

Jamison (1966) found weaning age to be a negligible source of variation in average daily gain to weaning. Barker (1964) reported that

calves 120 through 179 days of age at weaning had a higher average daily gain than those from 180 to 300 days of age. Butts (1951) indicated that calves at two locations in Tennessee grew in an approximately linear manner from birth to weaning. However, there was considerable variation among years in the rate of growth of calves during late summer and early fall. Several year-location subgroups exhibited a tendency for older calves to gain more slowly than younger calves. Swiger et al. (1962) reported a linear association between age and gain to 130 days of age, but a significant ($P<.05$) curvilinear effect from 130 to 200 days.

Marlowe, Mast, and Schalles (1965) considered weaning ages from 90 through 299 days as seven discrete 30-day periods. In general, average daily gain to weaning was not significantly different between adjacent age groups among the non-creep-fed calves, but age did have a highly significant effect on average daily gain over the entire age range. In their study, age was a less important influence on average daily gain among creep-fed calves. Non-creep-fed calves from 90 to 119 days of age gained 0.12 pound per day more than calves 270 through 299 days of age. They also found that age of calf had a highly significant influence on type score in favor of older calves. The increase in type from the 90- to 119-day age group to the 240- to 269-day age group was approximately one-half grade point for the non-creep-fed group and one grade point for the creep-fed group.

Koch and Clark (1955a), Barker (1964), and Jamison (1966) found small positive relationships between age at weaning and weaning type score.

Most workers have found older calves to gain less and grade higher for type than younger calves. It is doubtful that these differences are of practical importance unless age differences are large (over 80 days). No references were found concerning the effect of age of calf on condition score.

II. EFFECTS OF INBREEDING

Most workers have found that increased inbreeding is associated with decreases in growth and in live estimates of type at weaning. However, the magnitudes of the effects of inbreeding vary widely with breed, line, location, sex, and level of environment. The numbers of lines and animals within lines involved in studies of inbreeding have been extremely small relative to the total beef cattle population. Therefore, sampling variation associated with the selection of foundation stocks and random drift of small closed lines appear to be important considerations in an evaluation of differences among reported results. The frequent and often substantial confounding among inbreeding of calf, inbreeding of dam, and year further complicate efforts to estimate parameters for the effects of inbreeding.

The present writer has taken the liberty of converting some recent estimates of the effects of inbreeding into a common statistic for comparative purposes. The effects of two levels of inbreeding on birth weight, preweaning weight, weaning weight, weaning type score, and cow weight are shown in Table IV. Rather wide variation among the estimates is evident.

TABLE IV

EFFECTS[a] OF INBREEDING ON BIRTH WEIGHT, PREWEANING GAIN, WEANING GAIN, AND TYPE SCORE EXPRESSED AS DEVIATIONS FROM A BASE OF 5 PER CENT INBREEDING

Author	Birth weight, pounds				Preweaning gain (birth-128 days), pounds				Weaning gain (birth-228 days), pounds				Weaning type score				Cow weight	
	Inbr. of calf		Inbr. of dam		Inbr. of calf		Inbr. of dam		Inbr. of calf		Inbr. of dam		Inbr. of calf		Inbr. of dam		Inbr. of cow	
	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25	0.15	0.25
Present investigation	-.6	-3.9	1.5	1.8	-1.8	-5.9	-6.5	3.8	-2.3	-18.2	6.8	6.8	0.1	-.2	-.2	-.1	-3	-61
Brinks, Clark, and Kieffer (1965)																	-33	-65
Males	-1.3	-2.6	0.1	0.2					-4.6	-9.2	-18.9	-37.8	0.2	0.3	-.5	-1.0		
Females	-4.0	-8.0	0.9	1.8					-17.1	-34.2	-4.3	-8.6	-.6	-1.2	0.0	0.1		
Swiger et al. (1961)																		
Lincoln	-3.8	-7.6	-.3	-.6					-11.9	-22.8	-1.4	-2.8						
Fort Robinson	-.6	-1.2	1.3	2.6					0.0	0.0	-1.1	-2.2						
Swiger et al. (1962)	-1.9	-3.8	-.7	-1.4	-3.6	-7.2	-1.0	-2.0	-5.1	-10.2	-1.5	-3.0						
Burgess, Landblom, and Stonaker (1954)									-17.6	-35.2	-11.5	-23.0						
Bradford, Chapman, and Grummer (1958)									5 mo. pig weight									
									-6.0	-12.0	-1.5	-3.0						

[a]Reported statistics converted to pounds at two levels of inbreeding.

Brinks (1965), in a comprehensive review of inbred lines and their uses, stated that inbreeding of the individual calves had a detrimental effect on all calf traits studied in investigations in Colorado, Montana, Oregon, and Virginia. He referred to a Wyoming study in which inbreeding of calf significantly affected 180-day weaning weight, -1.38 pounds per 1 per cent increase in inbreeding. However, inbreeding of dam was observed to be a negligible source of variation in all traits. Average inbreeding levels in the Wyoming study were 12 per cent for the calves and 8 per cent for the dams. In contrast to this, he reported Colorado work which indicated that inbreeding of dam had a greater effect on weaning weight than did inbreeding of calf. In another study carried out in New Mexico, Brinks concluded that the results suggested that inbreeding of dam had a greater effect than inbreeding of calf on weaning type and condition but a lesser effect on weaning weight. Studies at two locations in Nebraska were reported to indicate that calves with higher than average inbreeding levels were below average in performance. However, the effects of inbreeding of dam were negative for all traits at one location but positive for most traits at the other. Brinks further stated that, in studies of response to selection within inbred lines, there was evidence of selection against increased homozygosity.

Several workers have observed a differential response in males and females for the effects of inbreeding on growth to weaning. Brinks, Clark, and Kieffer (1965) reported that inbreeding of calf had a more

pronounced effect on females than on males. He discussed the hypothesis that male and female calves with the same genotype, except for sex, may respond differently to the same environment because of the difference in growth potential for the two sexes. He suggested that the effects of maternal environment could mask the response to inbreeding, especially in male calves. Stonaker (1963), in discussing the same phenomenon, advanced an hypothesis that genetic differences between the two sexes may exist because of differences in the sex chromosomes. He supported this hypothesis with studies of heterosis in Hereford cattle and poultry which indicated that the homogametic sex exhibited more heterosis than did the heterogametic sex. He further stated, however, that some studies of this subject did not support the conclusions he had reached. Data reported by Stonaker did not rule out the possibility that variation among species in environment for the two sexes could have caused responses similar to those observed.

III. HERITABILITY ESTIMATES

Since 1946, when Knapp and Nordskog reported the first estimates of heritability, many workers have investigated this subject. Summaries of these studies have been reported by Warwick (1958), Temple (1964), and Petty and Cartwright (1966). Heritability estimates from these summaries (Tables V, VI, and VII) for birth weight, average daily gain from birth to weaning, and weaning type are presented. Weighted averages of paternal half-sib estimates for birth weight (0.44), gain to weaning (0.34), and weaning type score (0.36) are noted.

TABLE V

SUMMARY OF HERITABILITY ESTIMATES[a] OF BIRTH WEIGHT

Author	Sex	Number of calves	Number of sires	Heritability estimate
Dawson, Phillips, and Black (1947)	M	227	13	0.11
Gregory, Blunn, and Baker (1950)	M	281	6	0.45
Knapp and Clark (1950)	S		110	0.53
Burris and Blunn (1952)	M	502		0.22
Koch and Clark (1955b)	M	4,553	137	0.35
Shelby, Clark, and Woodward (1955)	S	635	88	0.71
Dawson, Yao, and Cook (1955)	S	58	9	0.51
McCormick, Southwell, and Warwick (1956)	M	372	34	0.26
Shelby et al. (1957)	B	542	116	0.59
Thornton, Gaines, and Kincaid (1960)	H	646		0.16
Swiger (1961)	M	748	23	0.22
Lasley, Day, and Comfort (1961)	M	414	8	0.67
Swiger et al. (1962)	M	2,739	187	0.35
Loganathan (1962)	M	469	34	0.88
	M	160	27	0.89
Shelby et al. (1963)	B	616	87	0.54
Pahnish et al. (1964)	M	720	17	0.20
Hagan et al. (1964)	M	1,428	84	0.28
Brinks et al. (1964)	H	3,548		0.38
Fitzhugh (1965)	M	4,052	360	0.49
Petty (1966)	M	892	36	0.17
Weighted average (21 estimates)				0.44

[a]Paternal half-sib method.

TABLE VI

SUMMARY OF HERITABILITY ESTIMATES[a] OF DAILY GAIN FROM BIRTH TO WEANING

Author	Sex	Number of calves	Number of sires	Heritability estimate
Gregory, Blunn, and Baker (1950)	M	69	4	0.45
	M	270	6	0.00
Koch and Clark (1955b)	M	4,553	137	0.21
Shelby et al. (1957)	B	542	116	0.40
Lasley, Day, and Comfort (1961)	M	414	8	0.03
Lehmann et al. (1961)	M	1,987	115	0.20
Loganathan (1962)	M	469	34	0.39
Swiger et al. (1962)	M	2,739	187	0.09
Meyerhoeffer, Carter, and Priode (1963)	M	1,659		0.23
Mahmud and Cobb (1963)	M	1,306	28	0.26
Pahnish et al. (1964)	M	720	17	0.05
Hagan et al. (1964)	M	1,428	84	0.21
Brinks et al. (1964)	H	3,548		0.40
Marlowe and Vogt (1965)	M	12,145	580	0.38
	M	8,279	409	0.33
Fitzhugh (1965)	M	4,052	360	0.42
Cunningham and Henderson (1965)	M	3,191	121	0.59
	M	1,648	55	0.47
Swiger et al. (1965)	M	480		0.58
Petty (1966)	M	892	36	0.18
Weighted average (20 estimates)				0.34

[a]Paternal half-sib method.

TABLE VII

SUMMARY OF HERITABILITY ESTIMATES[a] OF WEANING TYPE SCORE

Author	Sex	Number of calves	Number of sires	Heritability estimate
Knapp and Clark (1950)	S		86	0.28
Knapp and Clark (1951)	S	613	83	0.31
Koger and Knox (1952)	M	715	15	0.30
	M	1,257	88	0.23
Koch and Clark (1955b)	M	3,831	124	0.18
Rollins and Wagnon (1956)	M	577	45	0.36
Shelby et al. (1957)	B	542	116	0.60
Carter and Kincaid (1959)	M	424	76	0.46
Lehmann et al. (1961)	M	1,987	115	0.33
Blackwell et al. (1962)	M	919	78	0.32
Loganathan (1962)	M	469	34	0.19
	M	160	27	0.75
Meyerhoeffer, Carter, and Priode (1963)	M	1,659		0.24
Swiger et al. (1963)	M	1,671	240	0.53
Shelby et al. (1963)	S	616	87	0.23
Mahmud and Cobb (1963)	M	1,306	28	0.36
Wilson et al. (1963)	S	473	56	0.29
Brinks et al. (1964)	H	1,608		0.28
Pahnish et al. (1964)	M	720	34	0.13
Marlowe and Vogt (1965)	M	12,145	580	0.36
	M	8,279	409	0.33
Cunningham and Henderson (1965)	M	3,191	121	0.53
	M	1,648	55	0.49
Petty (1966)	M	653	27	0.05
Weighted average (24 estimates)				0.36

[a]Paternal half-sib method.

Pahnish et al. (1964) found heritability estimates for weaning condition score to differ for males (0.06) and females (0.32). However, estimates of the heritability of type (0.08 and 0.24, respectively) from the same study agree very closely and raise the question of the practical separation of these two traits in Pahnish's investigation.

Since the body of literature concerning the traits and classes of effects considered in the present investigation is extremely large, this review was confined to those references thought to be pertinent to a meaningful evaluation of the experimental procedures employed and the results reported herein.

CHAPTER III

EXPERIMENTAL PROCEDURE

I. SOURCE OF DATA

The data used in this study were collected over an 8-year period (1957-64) from a purebred Angus herd of the University of Tennessee. The herd was located at the Plateau Experiment Station near Crossville. This area is a high plateau (approximately 2,000 ft. elevation) favored with excellent summer temperature and rainfall patterns. Calf gains recorded there are consistently highest or near the highest among the eight experiment station locations in the state.

The herd was established in 1952 for the general purpose of investigating lines and line crosses. Foundation animals related to two bulls, General 26 of Lonjac and Great Oaks Pridemar, were purchased to establish two lines. A few years later a small number of females from a third source were added. By 1957 it had been decided to discontinue the Pridemar line due to unsatisfactory performance of the more highly inbred (over 0.20) Pridemar calves. The Pridemar cattle were retained in the herd, however, with close matings largely avoided. Moderate inbreeding was continued in the General line, although the line was never closed to outside matings. General cattle were largely categorized, as such, through relationship to General 26 of Lonjac rather than through relationship among contemporaries. Hence, inbreeding coefficients in

this rather loosely defined line ranged from 0.00 to 0.35. Inbreeding of Pridemar cattle was generally lower than that found in the General line and often was the result of matings among the offspring of General X Pridemar crosses. Some degree of inbreeding was allowed in cattle unrelated to both of the foundation sires. Thus, the general picture presented by these data is one of all levels (up to 0.35) of inbreeding in all lines or groups of animals in the herd, but with a much greater incidence of coefficients greater than 0.20 in the General line.

All animals represented in these data trace in all lines of descent to approximately 50 foundation parents. The herd increased in size to approximately 200 animals between 1952 and 1964. During the 8 years covered by this study, all of the replacement females and 17 of the 29 sires used originated within the herd. The 12 sires introduced from outside sources were included in the 50 foundation parents.

Very little selection pressure was exerted on females prior to 1960. During the last 4 years considered, sufficient numbers were available to allow some selection among both replacement heifers and older breeding females. Selection among replacement heifers was on type score and average daily gain, with a preliminary selection made at weaning and a final selection made the following spring. It was estimated that about 80 per cent of the heifer calves weaned were added to the herd during the period under study. Selection among cows was on the basis of both reproductive and progeny performance. Cows which were designated open as of a pregnancy check in the fall following a failure to calve the previous spring were usually culled. The progeny record

considered was the average performance of all calves from a cow. Culling for progeny performance was usually done after the preweaning evaluation in June. The large number of heifers retained for breeding was for the purpose of allowing some cow selection simultaneously with a rapid increase in the size of the herd.

Sire selection was similar to that practiced among heifers. All sires used in the herd were evaluated for gain and type at 120 days of age, weaning, and at the end of a postweaning performance test. Prospective bulls from outside sources were selected on the basis of their weaning records. These bulls were purchased at weaning and placed on postweaning test with the calves selected from the Crossville herd. Within the herd, only those calves chosen as bull prospects were left intact at preweaning and weaning for further testing. Approximately 50 and 25 per cent of the male calves at preweaning and weaning, respectively, were selected. The number of bulls progeny tested as yearlings varied from year to year, depending on the excellence of the young bulls and the need for replacement bulls in the herd. At least one or two inbred bulls were included in the yearling progeny test group each year to ensure the continuation of the inbreeding work. In a very few instances, the standards were relaxed somewhat in order to include these inbred calves.

Selection among breeding bulls was based entirely on progeny performance. Sires were continued in use until younger bulls proved superior on the basis of a progeny test. Breeding groups were intended to be as uniform as possible and were largely assigned to sires at random.

However, consideration was given to maintaining a nucleus of inbred cattle, and a certain amount of assortive mating was practiced to accomplish this.

Cows were bred in single-sire breeding groups and were re-randomized into larger groups following the breeding season. The same general feeding and management program was followed over the 8 years under study. All of the calves used in this study were dropped in the spring, and none were creep fed.

II. DESCRIPTION OF DATA

Observations on the calves included in these data were weights at birth, preweaning (approximately 120 days of age), and weaning; subjective scores for type and condition at preweaning and weaning; coefficients of inbreeding; and genetic covariances between each calf and each of the two foundation sires. Measurements on the dams were age at calving, spring and fall weights, and coefficients of inbreeding. Calves with missing information concerning themselves or their dams were deleted from the study.

The calves were graded by two staff members of the Animal Husbandry-Veterinary Science Department of the University of Tennessee. One of these men graded during the entire 8-year period. While the second grading position rotated among several staff members, the same man usually graded at both preweaning and weaning in a given year. Each grader worked independently. However, since these men worked together in grading a large number of calves each year, the means and variances

of their grades were similar. The coded scores of the two graders were averaged to obtain the type and condition scores for the individual calves. The numerical codes for type score were: fancy plus (17), fancy (16), fancy minus (15), choice plus (14), choice (13), choice minus (12), good plus (11), good (10), good minus (9), medium plus (8), medium (7), and medium minus (6). The effective range of type scores in these data was 10 through 15. Very few animals were given scores outside this range. The numerical codes for condition score were the same as those for type score, with the feeder grade replaced by the appropriate slaughter grade. The effective range of these scores was 7 through 12.

Calves and dams were classified as to inbreeding by dividing them into three discrete groups: coefficients of inbreeding less than 0.1000 (1), from 0.1000 through 0.1999 (2), and over 0.1999 (3). Calves were also classified on the basis of the genetic covariances between them and the two foundation sires. Each calf was coded as belonging to one of four relationship groups. These groups and codes were: calves related more than 15 per cent to General 26 of Lonjac and less than 12 per cent to Great Oaks Pridemar (1), calves related more than 15 per cent to Great Oaks Pridemar and less than 12 per cent to General 26 of Lonjac (2), calves showing a combined relationship greater than 25 per cent to both bulls and a minimum relationship of 12 per cent to each of the bulls (3), and calves related less than 15 per cent to either of the sires and less than 25 per cent for the combined relationship to both bulls (4). In defining the various discrete levels of inbreeding and

relationship groups, consideration was given to the distribution of observations among levels and subcells of the classified data.

Based on unpublished data from the University of Tennessee, age of dam at calving was coded into six discrete levels as follows: cows which calved at 2 years of age (30 months of age or less) (1), 3 years of age (2), 4 years (3), 5 and 6 years of age (4), 7 and 8 years of age (5), and 9 years and older (6).

Five discrete levels of spring and fall cow weights were considered. Cows weighing less than 800 pounds, 800 through 895 pounds, 900 through 995 pounds, 1,000 through 1,095 pounds, and more than 1,095 pounds were coded (1), . . ., (5), respectively. Records were further coded: (1) for cows weighed after calving in the spring and (2) for cows weighed prior to calving.

III. METHOD OF ANALYSIS

Of primary interest was the estimation of the effects of 12 independent variables and selected interactions on 8 dependent variables measuring performance traits of calves from birth to weaning. The eight performance traits were: birth weight, average daily gains at preweaning and weaning, type and condition scores at preweaning and weaning, and weaning index. Weaning index was calculated each year from adjusted average daily gain and type score on an individual calf basis. The adjustments were for sex of calf and age of dam. The independent variables included inbreeding of the calf and the dam, several fixed environmental effects known to contribute to variation among calves, and

a group of variables usually associated with inbreeding but suspected of exerting an independent effect on the dependent variables under study. The fixed environmental effects were year, age of dam, and sex. The effects usually associated with inbreeding were group of calf, spring weight of dam, and fall weight of dam.

Preliminary analyses were carried out to determine the adequacy of the somewhat arbitrary levels of the various classes of discrete effects and to test the importance of the following interactions:

sex of calf X inbreeding of calf

inbreeding of calf X inbreeding of dam

inbreeding of calf X group of calf

age of dam X fall weight of dam.

The method of least squares for analysis of data with disproportionate subclass numbers (Harvey, 1960) was used to fit the three models outlined in Table VIII. These models were fitted on a within-year-and-sire basis.

The amounts of variation explained by the three models were very similar for each of the eight dependent variables. This was interpreted to mean that the four interaction classes and the quadratic and cubic terms of the weaning age polynomial could be ignored in subsequent analyses and that the chosen levels of inbreeding, age, and weight were adequate to describe these variables. The effects of the interaction of sex of calf and age of dam were assumed to be negligible on the basis of earlier analyses of comparable University of Tennessee data.

Inspection of the distribution of calves by sire and year showed that 13 of the 29 sires had been used in the herd more than one year.

TABLE VIII

LEAST SQUARES MODELS FOR PRELIMINARY ANALYSES[a]

Dependent variables	Independent variables	Form of independent variables included		
		I	II	III
Birth weight	Weaning age	$X+X^2+X^3$	$X+X^2+X^3$	Regression
	Sex of calf	Discrete	Discrete	Discrete
Preweaning	Inbreeding of calf	Discrete	$X+X^2+X^3$	Discrete
ADG	Group of calf	Discrete	Discrete	Discrete
Type	Inbreeding of dam	Discrete	$X+X^2+X^3$	Discrete
Cond.	Age of dam	Discrete	$X+X^2+X^3$	Discrete
	Spring weight of dam	Discrete	$X+X^2+X^3$	Discrete
Weaning	Time of spring weight	Discrete	Discrete	Discrete
Type	Fall weight of dam	Discrete	$X+X^2+X^3$	Discrete
Cond.	Sex X Inbr. of calf	Discrete		
Index	Inbr. of calf X inbr. of dam	Discrete		
	Inbr. of calf X group of calf	Discrete		
	Age of dam X fall wt. of dam	Discrete		

[a]Analyzed on a within-year-and-sire basis.

In order to obtain year effects which were free of possible confounding with sire, the 479 calves sired by these 13 sires (Table IX) were analyzed. The model utilized contained sire, year, and the independent variables in Model 3 of Table VIII, page 27. The dependent variables of all calves were then adjusted for year differences and seven degrees of freedom were subtracted from the residual degrees of freedom in subsequent analyses.

Sex-by-year subgroup means and standard deviations (Appendix Tables XVII, XVIII, XIX, and XX) were calculated. Inspection of these standard deviations led to the assumption of a common variance for the two sexes and the 8 years in each of the eight dependent variables. This assumption, in conjunction with the lack of significance ($P>.05$) of the sex of calf by inbreeding of calf interaction, suggested that both sexes be considered in the same analysis.

Based on this preliminary work, an individual observation (Y), adjusted for the effect of year, was assumed to be composed of the following effects:

1. The partial regression of Y on weaning age.
2. Sire.
3. Sex expressed as male or female.
4. Inbreeding of calf expressed as three discrete levels.
5. Group of calf (with respect to relationship to foundation sires).
6. Inbreeding of dam expressed as three discrete levels.
7. Age of dam expressed as six discrete levels.

TABLE IX

DISTRIBUTION OF CALVES BY SIRE AND YEAR

Year	Sire													
	5244	5284	5026	5063	9186	5448	5207	1249	9209	9309	5071	5420	9777	Total
1957	12	13												25
1958	11	10												21
1959	24		14	24	6									68
1960	17		14	8	3	12								54
1961	20			19		3	22							64
1962	14					10	16	16	18	16				90
1963	10							11	29	12	5	14	8	89
1964	1							14	12		6	18	17	68
Total	109	23	24	51	9	25	38	41	59	28	11	32	25	479

8. Spring weight of dam expressed as five discrete levels.

9. Time of spring weight of dam expressed as two discrete levels.

10. Fall weight of dam expressed as five discrete levels.

11. Residual variation composed of among-dams and within-dam variation and random errors.

Cows were considered random in this analysis, and a second analysis was run to partition the residual variation into an among-cows component and a residual component composed of within-dam variation and random errors. This was accomplished by fitting the same model on a within-cow basis. The difference between the residuals from the first and second analyses was considered to be the among-cows variation. The mean square for cows was considered the appropriate error term for the other effects in the model. The theoretical expectation of the mean square for cows (among-cows) contains a component of variance within cows and random errors (s_W^2) and a component of variance among cows (s_D^2). Since effects above cows in the analyses of variance table are fixed effects, their expected mean squares contain only the component of variance appropriate for the respective lines (s_i^2, i = i^{th} effect in the model) and $s_W^2 + s_D^2$. The variation within cows and random errors (s_W^2) was used to test variation among cows ($s_W^2 + s_D^2$).

Heritabilities of the eight performance traits were estimated by the frequently used paternal half-sib method in which components of variance for sires, dams, and within-dams were obtained by equating the observed mean squares to their expectations and solving algebraically

for the components. Weighting factors (k values) used in the expectations of the mean squares were calculated by the following formula (Snedecor, 1956):

$$k = \frac{1}{n - 1} \left(\Sigma k_i - \frac{\Sigma k_i^2}{\Sigma k_i} \right)$$

where:

n = the number of sires or dams, respectively

k_i = the number of offspring for the i^{th} sire or dam.

The assumption of random mating underlying this method of estimating heritabilities was based on a study of similar data by Koch and Clark (1955b). In these data, when the paternal half-sib correlations were corrected for the effects of inbreeding, the heritabilities agreed almost exactly with those found under the assumption of random mating. Presumably, the opposing tendencies in the inbred lines and linecrosses canceled each other.

The relationship between weaning condition score of the calf and the maternal contribution of the dam was investigated by comparing estimates of heritability and maternal ability calculated from the analyses of variance previously described with estimates computed from a second set of analyses in which the partial regression of the dependent variable (Y) on weaning condition score was added to the previous model. Estimates of maternal effects (m^2) were calculated from the following formula:

$$m^2 = \frac{s_D^2 - s_S^2}{s_T^2}$$

where:

s_S^2 = sire component of variance

s_D^2 = dam component of variance

s_W^2 = random errors and within-dam variation

$s_T^2 = s_S^2 + s_D^2 + s_W^2$.

CHAPTER IV

RESULTS AND DISCUSSION

I. THE EFFECTS OF VARIOUS INDEPENDENT VARIABLES ON CERTAIN PERFORMANCE TRAITS OF CALVES AND FALL WEIGHT OF COWS

Mean squares from the analyses of variance for the eight performance traits studied are shown in Table X. The tests of significance in these analyses were considered to be more conservative, and more widely applicable, than those in many similar previous published analyses. The mean squares for cows, used to test mean squares appearing in lines above the mean squares for cows in the analysis of variance tables, are larger than the frequently used residual error term containing all sources of variation except those being tested in a given F-test.

Some general considerations concerning the subjective scores for type and condition should be noted. First, while they are considered to be measurements describing the calf, they are, in reality, variables measuring the grader's impression of the calf's expression of the trait. Hence, it is probable that criteria on which the scores are based differ among graders. If the criteria differ, it would seem reasonable to expect that the effects of genetic and environmental forces acting on the trait would also differ. For example, apparent differences in the response of type score to a given factor in two studies may indicate

TABLE X

ANALYSIS OF VARIANCE OF PERFORMANCE TRAITS STUDIED

Source	d.f.	Birth weight	Preweaning			Weaning			
			ADG	Type score	Condition score	ADG	Type score	Condition score	Index
Weaning age	1	25.4009	0.0139	4.8159	9.8819**	0.1001	0.9281	2.3973	91.5677
Sire	28	139.0821**	0.1327**	2.9093**	1.3048	0.0689**	4.4773**	1.1967	233.9559*
Sex	1	3,615.4566**	2.1924**	29.1909**	38.0505**	5.9330**	0.7224	233.9914**	1,897.9703**
Inbr. of calf	2	204.9088	0.0274	1.7798	1.0460	0.0785	2.7695	1.0596	337.0939
Group of calf	3	296.8072**	0.0947	2.7388	1.3129	0.0414	2.4613	0.9259	310.8243
Inbr. of dam	2	164.3589	0.1364	0.4421	0.4302	0.0392	1.4778	1.0963	5.7399
Age of dam	5	206.9659*	0.2944**	10.2552**	6.8684**	0.1885**	6.9482**	4.7329**	195.4716
Spring weight of dam	4	62.9783	0.0441	1.1460	1.8713	0.0194	0.5476	1.1114	105.6551
Time of spring weight	1	23.1845	0.0342	0.0504	1.3552	0.0002	1.1957	0.0392	9.9982
Fall weight of dam	4	133.6128	0.0179	1.0609	2.0410	0.0377	1.0720	1.5233	74.3895
Cows	207	76.4653**	0.0527**	1.3558**	1.2635**	0.0293**	1.5823**	1.1036**	134.3341**
Residual	367	38.4346	0.0347	0.9634	0.8476	0.0186	1.0689	0.7509	83.7140
R^2		.693	.630	.583	.579	.721	.603	.681	.630

*P<.05.

**P<.01.

only that type score did not measure the same trait in both instances. Secondly, the amount of variation which a grader is able to detect in a given set of animals and the consistency with which he adheres to his particular grading standards, exert a marked effect on the response of the variable to environmental or genetic influences. Low values for estimates of heritability of a subjective trait could mean that the grader was unable to measure the trait accurately rather than that additive genetic variance was unimportant.

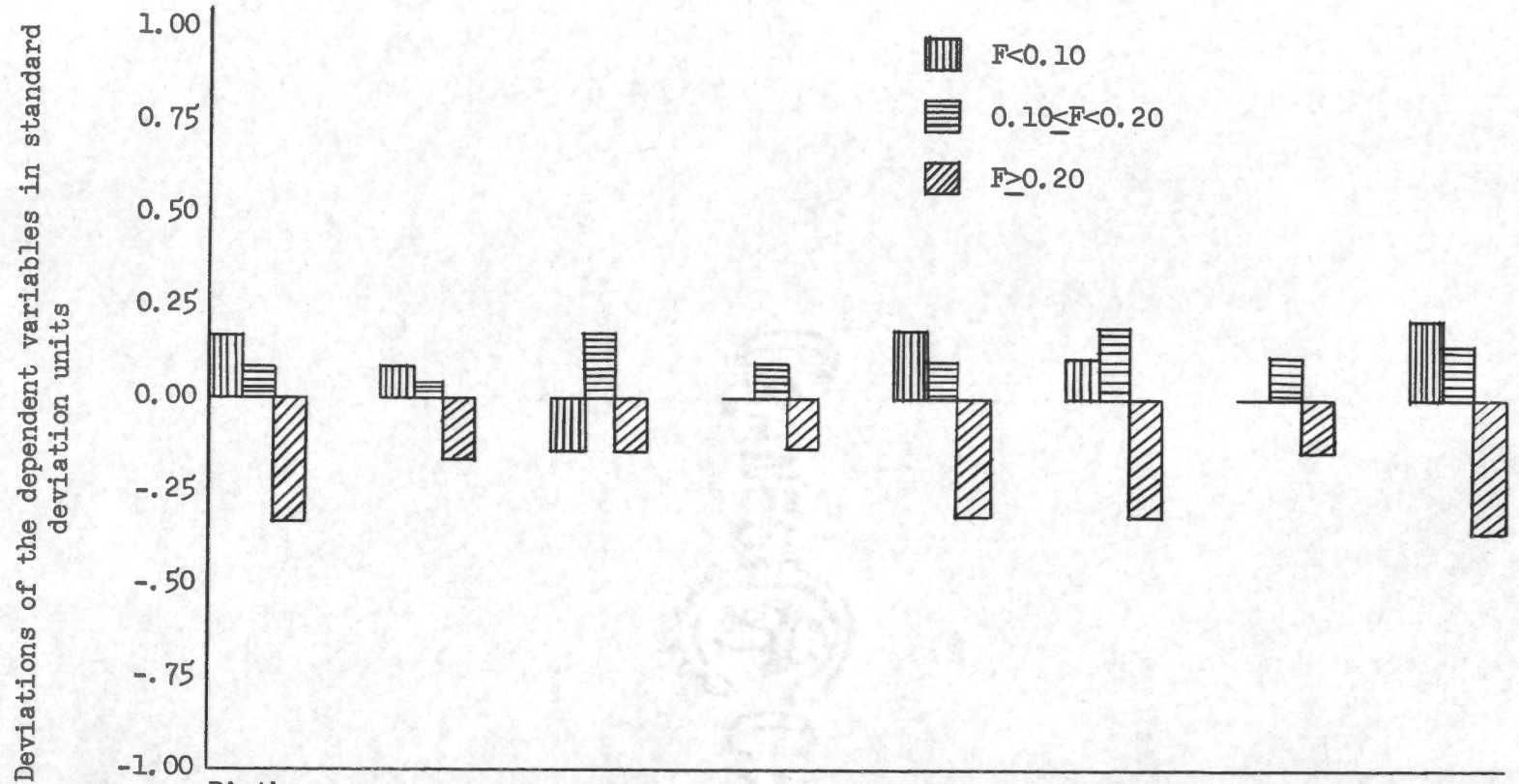
The analyses presented in Table X, page 34, indicate the generally strong influence of sire, dam, sex, and age of dam, in contrast to the relative unimportance of the remaining classes of effects on the eight dependent variables. The significant ($P<.01$) effect of weaning age on preweaning condition score is believed to be a reflection of the interrelationship of birth date and the change from winter feeding to pasture rather than an effect of age as such. Neither of the cow weights significantly ($P>.05$) affected any of the performance traits of the calves.

Age of dam was an important source of variation in all dependent variables except weaning index. This indicates that age-of-dam adjustments of average daily gain for use in calculating the index was effective in removing the age-of-dam variation from the adjusted gain values. The sex correction factor, however, apparently did not adequately reduce variation due to sex differences since the effect of sex on weaning index was significant ($P<.01$). These data suggest a correction factor of 1.12 rather than the 1.07 in current use.

The relatively high proportion of bull calves left intact until weaning probably explains this discrepancy, since the correction factor used was developed from field data where, perhaps, more male calves were castrated at an early age.

Variation among cows was a significant ($P<.01$) source of variation for all traits studied. Sire effects were significant ($P<.01$) with respect to birth weight and both average daily gains and type scores, but did not contribute to variation among calves for either of the two condition scores.

Neither inbreeding of calf, inbreeding of dam, nor group of calf significantly ($P>.05$) affected any of the calf performance traits with the exception of birth weight, which was affected ($P<.01$) by group of calf. However, the pattern of response to these three factors (Figures 1, 2, and 3) is informative. The magnitude of the response to different levels of inbreeding (Appendix Tables XXI and XXII) represented in these data is within the range reported by the other workers. However, the differential between the sexes in response to inbreeding, reported by Brinks, Clark, and Kieffer (1965), was not detected here. The sex-of-calf-inbreeding-of-calf intraction was not significant ($P>.05$) with respect to any of the eight dependent variables in this study. Further, inspection of the standard deviations of the sex-by-year subgroups (Appendix Tables XVII, XVIII, XIX, and XX) shows that there was no appreciable difference between the sexes with respect to variation in the performance traits. These results are interpreted as evidence that sufficient nutrition was available to permit the full expression of



	Birth weight	Birth-128 days Preweaning			Birth-228 days Weaning			
		ADG	Type	Cond.	ADG	Type	Cond.	Index
Mean	62.3	1.66	11.9	9.0	1.75	12.3	9.7	119
Std. dev.	8.5	0.23	1.2	1.1	0.20	1.2	1.2	11

Figure 1. Least squares constants for inbreeding of calf expressed in standard deviation units.

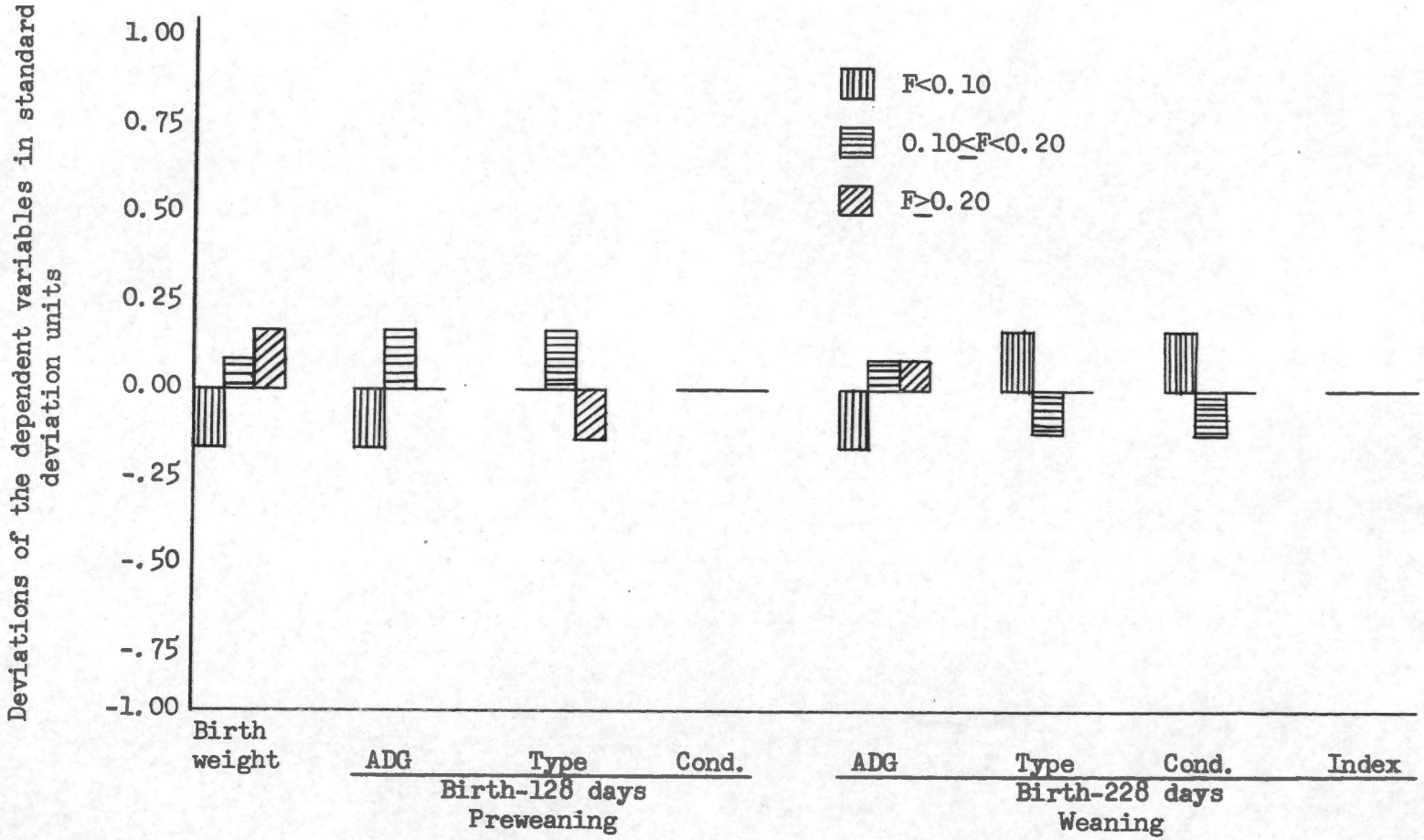


Figure 2. Least squares constants for inbreeding of dam expressed in standard deviation units.

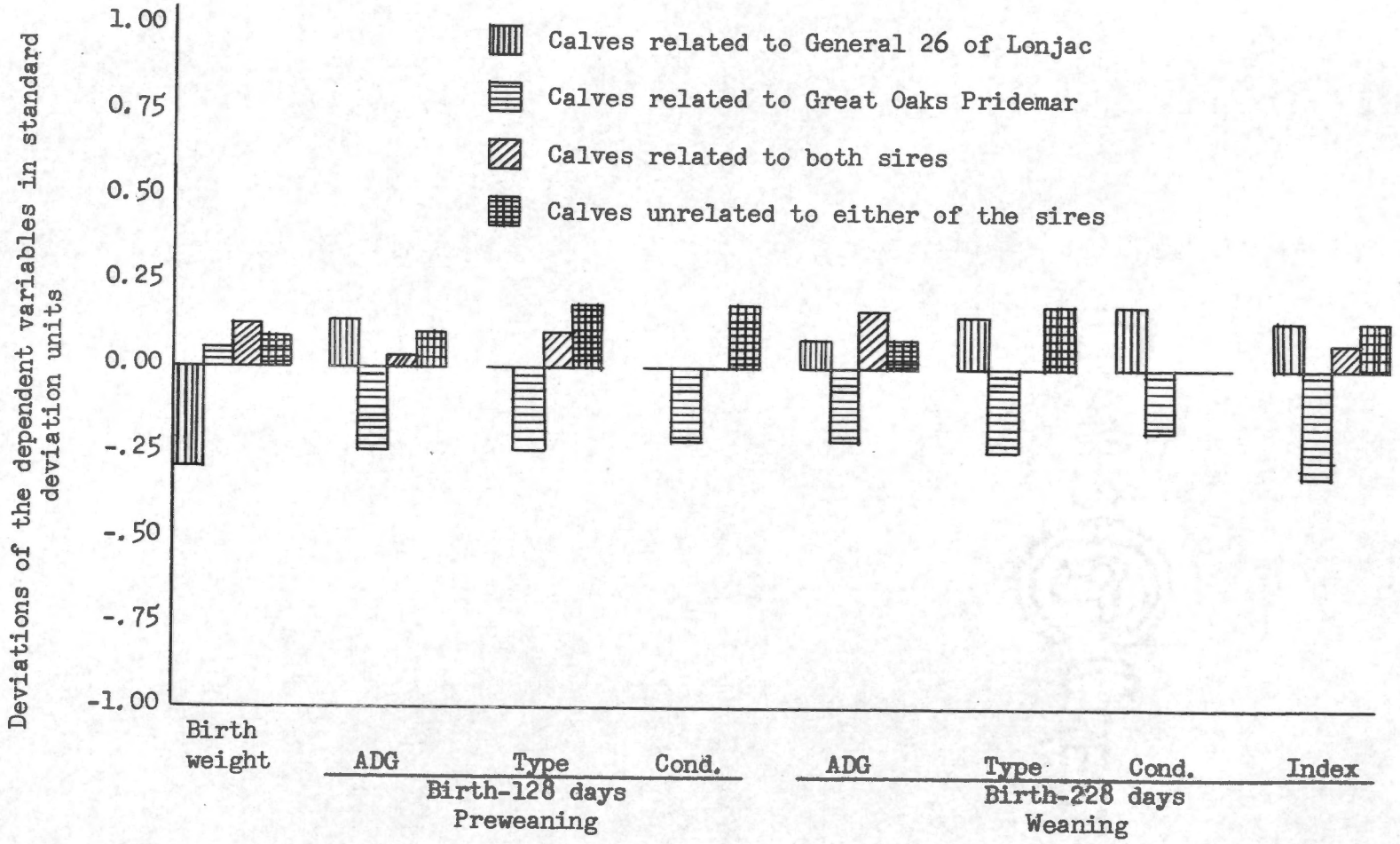


Figure 3. Least squares constants for group of calf expressed in standard deviation units.

genetic differences among male calves in this study. The suspicion that Hereford cows under range conditions, as reported by Brinks, Clark, and Kieffer (1965), would provide a somewhat lower nutritional level for their calves than would Angus cows under the near ideal pasture conditions of this work lends credibility to this hypothesis. The non-linear response to inbreeding (Figure 1, page 37) found in these data could not be interpreted as either contradictory or confirmatory of results reported by other workers since their results were reported as the linear regression of Y on inbreeding. The relatively small effects of inbreeding on preweaning traits (Figure 1, page 37), perhaps, illustrates more the difficulty of measuring performance in young calves than any possible effects of inbreeding on these traits. The effects of inbreeding of dam (Figure 2, page 38) are considered unimportant since none of the performance traits were significantly ($P>.05$) affected by this class of effects and no pattern of response could be detected. While group of calf was not a significant source of variation in these analyses, the pattern of response (Figure 3, page 39) indicated that its inclusion in the model did serve the useful purpose of preventing the possible correlation between geneology of the calves and inbreeding from causing a spurious reflection of the effects of inbreeding.

Analyses of variance of cow weights are shown in Table XI. The relative importance of the effects of inbreeding and age on fall cow weight are shown in Figure 4. The non-linear response of fall cow weight to inbreeding is similar to the pattern of response noted in the calves. Weaning age and condition score of the calf had little effect

TABLE XI

ANALYSIS OF VARIANCE OF SPRING AND FALL COW WEIGHTS

Source	d.f.	Mean squares	
		Spring weight	Fall weight
Year	7	188,257.06**	150,552.54**
Inbreeding	2	108,055.02**	103,147.71**
Age	5	856,878.68**	649,697.09**
Time of spring weight	1	1,537,831.60**	10,736.67
Residual	617	8,932.37	6,558.88
R^2		.584	.547
Weaning age of calf	1		8,399.62
Year	7		138,371.51**
Inbreeding	2		103,734.47**
Age	5		642,157.12**
Weaning condition of calf	1		6,355.73
Residual	616		6,559.91
R^2			.548

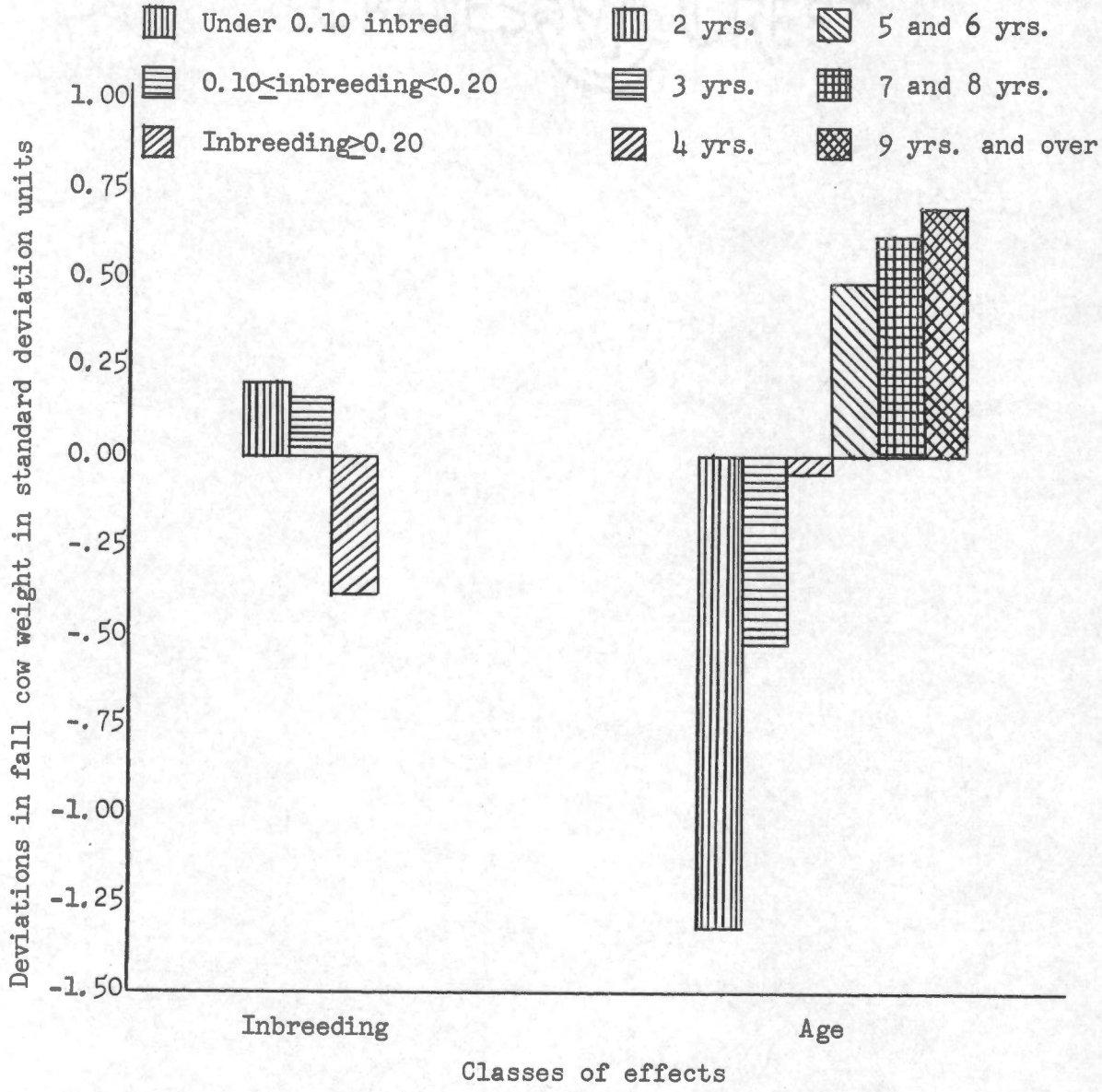


Figure 4. Least squares constants for the effects of inbreeding and age on fall cow weight expressed in standard deviation units.

on fall cow weight. Time of spring weight was a significant ($P<.01$) source of variation in spring cow weight but not in fall cow weight. This classification is actually a measure of age of calf with respect to fall cow weight.

A comparison of the effects of inbreeding found in this investigation and those reported by other workers is shown in Table IV, page 13. The estimates contained in this table should not be considered to be statements by the respective authors but merely rough estimates for comparative purposes. Due to the different statistics reported and the differing ages of animals to which they applied, much interpolation was necessary. Since much of the work cited involved closed inbred lines, confounding probably existed between level of inbreeding and year and between inbreeding of calf and inbreeding of dam. The variation in the effects of inbreeding found by different workers and different investigations effectively illustrates the difficulty of obtaining estimates of these effects free of influence from other sources of variation.

II. CORRELATIONS

Correlations, calculated on a within-year-and-sex basis, are shown in Table XII. Correlations between cow weight and calf gain measurements (0.27 to 0.32) are assumed to be a result of the correlation between cow weight and cow age, since the effect of age differences on variation in these traits was significant ($P<.01$) while the effect of differences in weight was not. Generally small and consistently negative correlations between inbreeding of calf and each of

TABLE XII

CORRELATIONS AMONG CERTAIN VARIABLES DESCRIBING AND/OR AFFECTING PERFORMANCE[a,b]

	2	3	4	5	6	7	8	9	10	11	12	13
1. Age of dam	0.53	-.17	-.03	0.08	0.19	0.24	0.14	0.18	0.28	0.12	0.13	0.06
2. Fall weight of dam		-.16	0.01	0.04	0.31	0.27	0.10	0.11	0.32	0.07	0.07	0.06
3. Inbr. of dam			0.23	-.03	0.00	0.02	-.04	0.03	-.02	-.07	-.06	-.07
4. Inbr. of calf				-.08	-.08	-.01	-.11	-.04	-.12	-.23	-.12	-.23
5. Weaning age					-.06	0.03	0.22	0.18	-.11	0.16	0.17	-.02
6. Birth weight						0.30	0.16	0.09	0.40	0.10	0.04	0.23
Preweaning												
7. ADG							0.38	0.44	0.77	0.28	0.27	0.59
8. Type								0.70	0.29	0.72	0.57	0.55
9. Condition									0.37	0.54	0.56	0.49
Weaning												
10. ADG										0.35	0.36	0.79
11. Type											0.73	0.78
12. Condition												0.61
13. Index												

[a]Correlations calculated on a within-year and sex basis.

[b]Correlation of 0.08 and 0.11 required for significance ($P<.05$) and ($P<.01$), respectively.

the eight dependent variables were noted. Correlations of average daily gain with type score and with condition score were similar at both preweaning and weaning. Type and condition scores were highly correlated (0.70 and 0.73, respectively) at preweaning and weaning. Weaning index appeared to be affected equally by type score and weaning average daily gain. It was interesting to notice that weaning condition score, while not used in calculating the indexes, was highly correlated (0.61) with it, which certainly indicates the existence of correlation of weaning condition with one or both ingredients of the index.

III. HERITABILITY ESTIMATES

The heritability estimates (Table XIII) from these analyses are within the range of estimates reported by other workers. However, estimates for some traits were not found in the literature. Comparison of the h^2 (estimate of heritability) and m^2 (estimate of maternal ability) for birth weight, preweaning condition score, and weaning condition score suggests that these traits are affected to a greater extent by non-additive genetic forces and/or permanent maternal differences than are the remaining traits. Since the non-additive estimates shown (m^2) contain only one-fourth of the dominance deviations and all of the permanent maternal contributions, it is believed that these estimates reflect primarily the permanent maternal effects. Heritability and maternal estimates for preweaning and weaning average daily gain are similar. The increase in heritability of type score from preweaning to weaning probably represents the difficulty in effectively scoring

TABLE XIII

VARIANCE COMPONENTS AND HERITABILITY ESTIMATES CALCULATED FROM THE ANALYSIS OF VARIANCE SHOWN IN TABLE X

	Birth weight	Preweaning			Weaning			
		ADG	Type	Cond.	ADG	Type	Cond.	Index
s_S^2	2.9737	0.0038	0.0738	0.0020	0.0019	0.1375	0.0044	4.7310
s_D^2	12.4978	0.0059	0.1289	0.1367	0.0035	0.1687	0.1159	16.6349
s_W^2	38.4346	0.0347	0.9634	0.8476	0.0186	1.0689	0.7509	83.7140
s_T^2	53.9061	0.0444	1.1661	0.9863	0.0240	1.3751	0.8712	105.0799
h^2	0.22±.42	0.34±.36	0.25±.35	0.01±.36	0.31±.37	0.40±.36	0.02±.36	0.18±.37
m^2	0.18	0.05	0.05	0.14	0.07	0.02	0.13	0.11

$k_S = 21.057$

$k_{DS} = k_{DD} = 3.043$

$$m^2 = \frac{s_D^2 - s_S^2}{s_T}$$

NOTE: s_S^2 = sire component of variance

s_D^2 = dam component of variance

s_W^2 = within dam and random errors

$s_T^2 = s_S^2 + s_D^2 + s_W^2$.

small calves. In general, the pattern of estimates shown in Table XIII, page 46, is probably the expected one if the cow herd, as a whole, milked heavily enough so that muscular and skeletal growth of the calves would not be limited. In this event, the maternal influence on gain would be much less than the additive genetic influence, and the correlation between condition (fat) and gain would be low. The method of selecting breeding females in this herd would, if effective, favor such a situation.

IV. RELATIONSHIP BETWEEN THE WEANING CONDITION SCORE OF THE CALF AND MATERNAL ABILITY OF THE DAM

The effectiveness of selection at weaning for rate of gain would be increased if the breeder had an estimate of the cow's maternal ability which was independent of rate of gain to weaning. Not only does variation among cows for maternal ability often mask true genetic differences in growth, but several workers (Christian, Hauser, and Chapman, 1965; Koch and Clark, 1955c; Touchberry, 1951; and Dickerson and Grimes, 1947) have suspected a negative genetic correlation between maternal ability and growth potential. In addition to being independent of rate of gain, such an estimate should also be unaffected by additive genetic variance, so that it could be considered an environmental effect with respect to the calf. In the present study, an effort was made to determine, insofar as limitations of the data would permit, whether weaning condition score would provide such an estimate. The effect of sire on both preweaning and weaning condition scores was negligible

while variation among dams was a significant ($P<.01$) source of variation for both traits. In spite of high phenotypic correlations between type and condition at both periods, type showed medium heritability (0.40 at weaning) and low maternal estimates while condition score showed essentially no heritability and a greater response to maternal effects. The partial regression of the dependent variable (Y) on weaning condition score $[b(x-\bar{x})]$ was added to the least squares model previously described and the extended model fitted to the data. The analysis of variance for this model (Table XIV) shows weaning condition score to have a significant ($P<.01$) effect on all variables included except birth weight. The level of significance for the effects of cows dropped to the 0.05 level of probability for preweaning type score and weaning index and became non-significant ($P>.05$) for weaning type. Components of variance were computed from the analyses, and heritability and maternal estimates (Table XV) were calculated. Inspection of these estimates indicates that, in these data, there is no relationship between weaning condition and birth weight, but that the remainder of the estimates are affected by holding weaning condition score constant. Variance components for preweaning and weaning average daily gain and weaning index are similar for sire and dam. This is assumed to indicate that variation in weaning condition score stems largely from the maternal fraction of the dam components of variance for the three traits. Heritability estimates were increased and maternal estimates decreased when these traits were, in effect, adjusted for weaning condition score. However, the effect of this adjustment on weaning type score was quite different. Due to the

TABLE XIV

ANALYSIS OF VARIANCE OF CERTAIN PERFORMANCE TRAITS HOLDING WEANING CONDITION SCORE CONSTANT

Source	d.f.	Birth weight	Preweaning		Weaning		
			ADG	Type score	ADG	Type score	Index
Weaning age	1	28.2105	0.000	1.7256	0.1676**	0.1013	369.8928*
Sire	28	139.6494**	0.1443**	1.9035**	0.0735**	2.5802**	169.1345**
Sex	1	2,705.0204**	3.9972**	135.2916**	7.7279**	95.4133**	14,604.3020**
Inbr. of calf	2	200.6462	0.0201	0.6814	0.0546	0.7956	168.1532
Group of calf	3	300.1432**	0.0628	1.7626	0.0290	0.9441	152.7856
Inbr. of dam	2	168.5383	0.1872	0.9388	0.0661	0.1361	53.8156
Age of dam	5	191.2760*	0.1655**	4.0831**	0.0889**	1.0021	102.1447
Spring weight (dam)	4	64.9250	0.0506	0.7490	0.0112	0.1471	24.1314
Time of spring weight	1	22.8344	0.0388	0.1133	0.0007	1.5809	30.5221
Fall weight (dam)	4	135.1373	0.0362	0.7043	0.0458	0.0481	75.1101

TABLE XIV (continued)

Source	d.f.	Birth weight	Preweaning		Weaning		
			ADG	Type score	ADG	Type score	Index
Weaning cond. score	1	16.9627	1.8977**	161.9897**	1.8554**	345.7755**	22,818.9790**
Cows	207	76.4722**	0.0464**	0.9471*	0.0230**	0.7351	80.9181*
Residual	366	38.4895	0.0332	0.7546	0.0172	0.6062	65.2332

*P<.05.

**P<.01.

TABLE XV

VARIANCE COMPONENTS AND HERITABILITY ESTIMATES CALCULATED FROM THE ANALYSIS OF VARIANCE HOLDING WEANING CONDITION SCORE CONSTANT

	Birth weight	Preweaning ADG	Weaning ADG	Weaning Type	Weaning Index
s_S^2	2.7628	0.0046	0.0024	0.0876	4.1894
s_D^2	12.4820	0.0043	0.0019	0.0424	5.1544
s_W^2	38.4895	0.0332	0.0172	0.6062	65.2332
s_T^2	53.7343	0.0421	0.0215	0.7362	74.5770
h^2	0.21	0.44	0.44	0.48	0.22
m^2	0.18	-.007	-.02	-.06	0.01
h^{2a}	0.22	0.34	0.31	0.40	0.18
m^{2a}	0.18	0.05	0.07	0.02	0.11

[a]Estimates reproduced from Table XIII for comparison. Weaning condition score was not held constant in the analysis from which these estimates were calculated.

relationship between condition score and type score, holding condition constant apparently removed part of the additive genetic variance from the dam component of variance.

McDaniel (1965), working with data from the Tennessee Bull Performance Test Program, found a negative association between weaning condition score and postweaning rate of gain. In view of this association and the results of the current investigation, it appears that the effectiveness of weaning selection for growth rate could be improved by considering weaning condition score and, further, that the adjusted average daily gain would be more indicative of postweaning gain.

CHAPTER V

SUMMARY

Records on 633 Angus calves out of 208 cows and by 29 sires were studied to estimate the effects of inbreeding on certain performance traits and to investigate the relationship between weaning condition score of the calf and maternal ability of the dam. Level of inbreeding was treated as a discrete variable, with calves and dams assigned to three levels of inbreeding on the basis of their coefficients of inbreeding. Calves were further classified into four relationship groups on the basis of their genetic covariance with two foundation sires. These data were considered somewhat unique in that there was little or no confounding between year and level of inbreeding of the herd and in that the correlation between inbreeding of calf and inbreeding of dam was low (0.23). These records were collected during an 8-year period at a location considered to provide an excellent environment for cow-calf performance.

Selection in this herd was primarily on the basis of progeny performance and was considered to have been effective in improving milking ability of the herd.

The effects of inbreeding of calf and inbreeding of dam on the eight performance traits studied were not significant ($P<.05$). However, least squares constants for the effects of inbreeding of calf indicated

a consistant depression of performance traits by the upper level of inbreeding studied (coefficients above 0.20). The nonlinearity of response observed in this study was an interesting point not reported by other workers. The magnitude of response to inbreeding found was within the range of estimates reported from other studies. The effects of inbreeding of dam in these data were negligible. Level of inbreeding was a significant ($P<.01$) source of variation in fall cow weight, but cow weight did not affect performance traits of calves to any measureable extent. Group of calf, while not a significant source of variation in the eight dependent variables, indicated that calves related to Great Oaks Pridemar were below the population mean for all traits except birth weight. In the population which this herd represents and under the selection procedures employed, it appears that levels of inbreeding under 20 per cent would not result in any serious inbreeding depression in the traits studied.

Heritability estimates, for those traits for which estimates have been reported, were within the range of those found by other workers. Heritability of weaning type (0.40) was higher than for weaning average daily gain (0.31). While the size of the standard errors associated with these estimates would preclude considering this to be a real difference, the higher heritability of type score might indicate some virtue in the grading technique employed. It was felt that the average of scores by two graders, scoring according to similar standards, would leave more variation intact in the data than would the average of more

than two completely independent scores. Neither of the two condition scores exhibited significant heritability in this study. Maternal effects were a more important source of variation for birth weight, condition score, and weaning index than for average daily gain or type score.

Holding weaning condition score constant removed that fraction of the dam components of variance for preweaning and weaning average daily gain and weaning index attributed, in earlier analyses of these data, to maternal ability. It was concluded that the effectiveness of selection at weaning, for genotypes superior in their ability to grow would be increased by adjusting weaning average daily gain to remove variation associated with variation in weaning condition, which appears to be an expression of the maternal ability of the dam. In contrast, variation in condition, as measured here, explained a larger portion of the dam component of variance for type score than could be explained by variation among cows in maternal ability. Hence, holding weaning condition score constant removed part of the additive fraction of the dam component of variance for weaning type score. This implied association between type and condition was considered to be "in the eye of the grader" rather than the result of an underlying genetic correlation since condition score appeared not to be a heritable trait. However, these data were not sufficient to reliably substantiate this last hypothesis.

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LITERATURE CITED

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APPENDIX

TABLE XVI

MEANS AND STANDARD DEVIATIONS OF CERTAIN DEPENDENT AND INDEPENDENT VARIABLES--8 YEARS, 633 CALVES

Source	Mean	Standard Deviation[a]
Age of dam	5.4	3.0
Fall weight of dam	985	110
Inbr. of dam	0.09	0.09
Inbr. of calf	0.08	0.07
Weaning age	228	25
Birth weight	62.3	8.2
Preweaning		
ADG	1.66	0.22
Type	11.9	1.1
Condition	9.0	1.0
Weaning		
ADG	1.75	0.17
Type	12.3	1.2
Condition	9.7	1.0
Index	119	11

[a]Standard deviations are calculated on a within-year-and-sex basis.

TABLE XVII

MEANS AND STANDARD DEVIATIONS OF CERTAIN DEPENDENT AND INDEPENDENT VARIABLES, 1957-1958

	1957				1958			
	Male		Female		Male		Female	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
No. of calves	21		19		26		17	
Age of dam	5.7	3.2	5.6	3.0	5.2	2.8	6.7	3.9
Fall weight	1,008	100	1,006	138	997	120	1,017	91
Inbr. of dam	0.08	0.08	0.05	0.07	0.09	0.10	0.05	0.06
Inbr. of calf	0.10	0.05	0.13	0.07	0.11	0.07	0.09	0.06
Weaning age	226	19	225	9	213	16	216	19
Birth weight	65.2	8.8	60.4	7.4	65.3	9.7	59.2	8.2
Preweaning								
ADG	1.78	0.21	1.53	0.18	1.74	0.18	1.56	0.17
Type	12.4	1.4	12.1	1.3	12.5	1.0	11.5	1.6
Condition	8.9	1.2	9.4	1.0	8.7	1.1	9.7	2.0
Weaning								
ADG	1.87	0.19	1.59	0.12	1.84	0.15	1.63	0.14
Type	12.2	1.6	12.1	1.2	12.0	1.0	12.2	1.4
Condition	9.7	1.2	9.9	1.1	9.2	0.9	10.4	1.4
Index	122	13	114	8	124	8	121	11

TABLE XVIII

MEANS AND STANDARD DEVIATIONS OF CERTAIN DEPENDENT AND INDEPENDENT VARIABLES, 1959-1960

	1959				1960			
	Male		Female		Male		Female	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
No. of calves	45		27		32		43	
Age of dam	4.8	2.6	4.6	2.8	5.2	3.4	4.8	2.9
Fall weight	909	105	898	104	904	99	897	106
Inbr. of dam	0.10	0.10	0.12	0.11	0.09	0.09	0.10	0.09
Inbr. of calf	0.11	0.08	0.11	0.08	0.09	0.08	0.11	0.09
Weaning age	241	18	235	31	231	30	239	23
Birth weight	62.2	7.0	58.1	7.4	63.0	5.7	56.6	6.9
Preweaning								
ADG	1.74	0.15	1.61	0.12	1.73	0.26	1.59	0.22
Type	12.0	1.0	11.6	1.0	12.0	1.1	11.7	0.9
Condition	8.4	0.8	9.4	1.3	8.9	1.0	9.1	0.9
Weaning								
ADG	1.83	0.18	1.61	0.11	1.85	0.17	1.63	0.15
Type	11.9	1.0	12.0	0.8	12.0	1.4	12.1	1.4
Condition	8.8	0.9	10.8	0.8	9.4	0.7	10.2	0.9
Index	119	10	115	6	112	11	107	10

TABLE XIX

MEANS AND STANDARD DEVIATIONS OF CERTAIN DEPENDENT AND INDEPENDENT VARIABLES, 1961-1962

	1961				1962			
	Male		Female		Male		Female	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
No. of calves	56		41		55		48	
Age of dam	5.5	2.9	5.7	3.0	5.2	3.4	5.9	3.0
Fall weight	1,007	103	1,026	109	972	125	993	115
Inbr. of dam	0.10	0.09	0.10	0.09	0.09	0.09	0.12	0.09
Inbr. of calf	0.06	0.05	0.06	0.06	0.07	0.08	0.08	0.07
Weaning age	224	25	224	26	236	23	237	21
Birth weight	65.2	8.5	59.1	7.7	63.3	7.6	60.5	8.3
Preweaning								
ADG	1.72	0.30	1.65	0.22	1.61	0.21	1.58	0.18
Type	12.1	1.3	11.7	1.3	11.8	1.1	11.8	1.1
Condition	8.7	1.0	9.5	1.4	8.5	0.8	9.3	0.9
Weaning								
ADG	1.84	0.20	1.68	0.16	1.81	0.18	1.61	0.15
Type	12.1	1.1	12.3	1.2	12.4	1.4	12.3	1.5
Condition	9.1	0.9	10.5	0.9	9.1	0.9	10.4	1.3
Index	121	10	121	9	117	11	111	12

TABLE XX

MEANS AND STANDARD DEVIATIONS OF CERTAIN DEPENDENT AND INDEPENDENT VARIABLES, 1963-1964

	1963				1964			
	Male		Female		Male		Female	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
No. of calves	58		43		56		46	
Age of dam	5.6	2.8	5.3	2.6	5.5	3.1	5.2	2.8
Fall weight	1,035	110	1,039	107	1,005	115	1,022	99
Inbr. of dam	0.10	0.09	0.08	0.07	0.09	0.08	0.07	0.08
Inbr. of calf	0.05	0.08	0.05	0.07	0.07	0.08	0.05	0.07
Weaning age	224	26	221	32	224	28	221	26
Birth weight	64.6	8.5	61.7	8.4	65.8	9.0	62.3	8.8
Preweaning								
ADG	1.69	0.27	1.65	0.25	1.77	0.25	1.59	0.19
Type	12.4	1.0	11.8	1.3	12.1	1.0	11.6	1.1
Condition	8.9	0.6	9.1	1.1	8.9	1.0	9.0	1.2
Weaning								
ADG	1.81	0.17	1.70	0.14	1.86	0.20	1.63	0.19
Type	12.6	1.0	12.7	1.3	12.5	1.1	12.8	1.4
Condition	9.0	0.8	10.5	1.1	9.0	0.9	10.4	1.0
Index	125	9	126	10	125	13	121	13

TABLE XXI

LEAST SQUARES CONSTANTS FOR PREWEANING TRAITS EXPRESSED AS DEVIATIONS FROM THE MEAN

	Birth weight	ADG	Type	Cond.
Mean	62.3	1.66	11.9	9.0
Sex				
Males	2.5	0.06	0.2	-.3
Females	-2.5	-.06	-.2	0.3
Inbr. of calf				
1	1.5	0.02	-.1	0.0
2	0.9	0.01	0.2	0.1
3	-2.4	-.03	-.1	-.1
Group of calf				
1	-2.5	0.04	0.0	0.0
2	0.5	-.06	-.3	-.2
3	1.1	0.00	0.1	0.0
4	0.9	0.02	0.2	0.2
Inbr. of dam				
1	-1.1	-.03	0.0	0.0
2	0.4	0.02	0.1	0.0
3	0.7	0.00	-.1	0.0
Age of dam				
1	-3.7	-.12	-.8	-.6
2	-1.2	-.08	-.4	-.3
3	0.4	0.05	0.2	0.1
4	2.3	0.04	0.2	0.2
5	1.4	0.07	0.4	0.3
6	0.8	0.05	0.4	0.3
Spring wt. of dam				
1	-.9	-.03	0.1	0.0
2	0.3	-.03	0.0	-.2
3	-.1	-.01	0.0	0.0
4	1.3	0.02	-.2	0.0
5	-.8	0.06	0.1	0.2

TABLE XXI (continued)

	Birth weight	ADG	Type	Cond.
Fall wt. of dam				
1	-1.7	-.03	0.3	0.1
2	-.5	0.01	0.0	0.1
3	-1.3	0.00	0.0	0.1
4	1.3	0.02	-.2	-.1
5	2.2	-.01	-.1	-.2
Regression of Y on weaning age	-.01	0.00	0.0	0.0

TABLE XXII

LEAST SQUARES CONSTANTS FOR WEANING TRAITS EXPRESSED AS DEVIATIONS FROM THE MEAN

	ADG	Type	Cond.	Index
Mean	1.75	12.3	9.7	119
Sex				
Males	0.10	0.0	-.6	1.8
Females	-.10	0.0	0.6	-1.8
Inbr. of calf				
1	0.03	0.1	0.0	1.8
2	0.02	0.2	0.1	1.5
3	-.05	-.3	-.1	-3.3
Group of calf				
1	0.01	0.1	0.2	1.5
2	-.04	-.3	-.2	-3.5
3	0.02	0.0	0.0	0.6
4	0.01	0.2	0.0	1.4
Inbr. of dam				
1	-.02	0.1	0.1	-.2
2	0.01	-.1	-.1	-.1
3	0.01	0.0	0.0	0.3
Age of dam				
1	-.09	-.7	-.5	-2.0
2	-.07	-.3	-.3	-1.6
3	0.03	0.2	0.1	2.3
4	0.04	0.2	0.2	0.0
5	0.05	0.3	0.2	-.2
6	0.04	0.3	0.3	1.5
Spring wt. of dam				
1	0.01	0.2	0.2	2.0
2	-.02	0.0	0.0	-.9
3	0.00	-.1	0.0	-.1
4	0.00	-.1	-.1	-.5
5	0.01	0.0	-.1	-.5

TABLE XXII (continued)

	ADG	Type	Cond.	Index
Fall wt. of dam				
1	-.06	0.2	0.2	-2.0
2	-.02	-.2	-.2	-1.6
3	0.01	0.1	0.0	0.5
4	0.04	0.0	0.0	1.6
5	0.03	-.1	0.0	1.5
Regression of Y on weaning age	0.00	0.0	0.0	-.03

TABLE XXIII

LEAST SQUARES CONSTANTS FOR COW WEIGHT[a]

	Spring weight	Fall weight
Mean	905	985
Inbreeding		
1	20	22
2	20	17
3	-40	-39
Age		
1	-146	-141
2	-75	-54
3	-17	-8
4	51	53
5	86	71
6	101	79
Time of spring weight		
1	-68	-6
2	68	6

[a]Year differences accounted for in the model.

CRANES CREST

TABLE XXIV

PARTIAL REGRESSIONS OF DEPENDENT VARIABLES (Y)
ON WEANING CONDITION SCORE

Y	b
Birth weight	0.18
Preweaning	
ADG	0.061
Type	0.6
Condition	0.6
Weaning	
ADG	0.061
Type	0.8
Index	6.7