


AN ABSTRACT OF THE THESIS OF

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Title SELECTION APPLIED, RESPONSE OF TRAITS AND COM-
BINING ABILITIES OF INBRED LINES OF BEEF CATTLE.

Abstract approved


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The investigations reported are based on two studies; the first is concerned with the selection practiced for performance in one inbred Angus and three inbred Hereford lines of cattle, the realized responses, levels of inbreeding and associated performance, and heritabilities of the performance traits.

Selection differentials for all performance traits were positive when the averages for both parents were considered. Selection differentials computed from the sire side of the matings were all positive and were higher than those on the dam side as a consequence of greater selection intensity through the sires.

Automatic selection against inbreeding occurred on the sire side in conjunction with selection for increased performance. Due to the low selection intensity for females, selection was for increased inbreeding on the dam side of the matings.

Inbreeding increased in all lines over a 12 year period.

Performance increased early in the inbreeding program, then levelled off and subsequently declined. Score improved in all lines. Generally favorable response in the Angus line resulted from a lower initial performance, a broader genetic base and more animals from which to select.

Data from repeat matings showed that more variability in performance existed during the preweaning than in the postweaning period.

Zero and low levels of inbreeding were associated with high preweaning performance and low postweaning performance. At higher stages of inbreeding, the reverse was true.

Heritability estimates differentiated between the highly heritable traits, postweaning rate and economy of gain, and the lowly and moderately heritable traits respectively, preweaning gain and score.

In the second study the performance data on calves resulting from a complete diallel cross between the three Hereford lines involved in the first study were analyzed. In addition, blood samples were analyzed at 450 and 750 pounds for amino acid nitrogen, urea nitrogen and creatinine.

Differences in general combining ability between lines were found for postweaning rate and economy of gain. The Lionheart line was the best general combiner, followed by the David and Prince lines. Specific combining ability differences in rate of gain favored

crosses between the more rapidly gaining Lionheart and David lines. The Prince and David cross was the lowest performing cross among the specific crosses. The analyses of differences in economy of gain were similar to those for postweaning rate of gain, but there was also a significant difference in favor of linecross over inbred calves. This was probably due to the economy of gain contributed by the Prince line to the linecross calves. A highly significant association existed between postweaning rate and economy of gain, with rate of gain accounting for 77 percent of the variation in economy of gain.

Higher scores were given to Lionheart x Prince calves than calves resulting from crosses involving the lower scoring David line. Linecross calves were scored higher than inbred calves, with the Prince and David inbred calves contributing to the low scores of all inbreds. Line of dam differences in score at 800 pounds were due to the less rapidly gaining David calves during the preweaning period scoring lower at 800 pounds.

When all inbred and linecross calves were considered, blood creatinine was higher at 450 pounds in calves from David dams which were inferior milkers, and lower in the calves at 750 pounds sired by the David bulls, due to lower gaining inbred David calves. A significant difference in blood amino acid nitrogen at 750 pounds was due to the low content in calves sired by the Prince bulls, which is possibly a function of economy of gain contributed by this line. Urea

nitrogen at 750 pounds and feed required per 100 pounds of gain were negatively correlated. At 450 pounds, blood creatinine and amino acid nitrogen were highly associated.

SELECTION APPLIED, RESPONSE OF TRAITS AND
COMBINING ABILITIES OF INBRED LINES OF BEEF CATTLE

by

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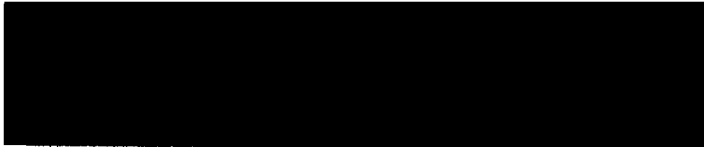
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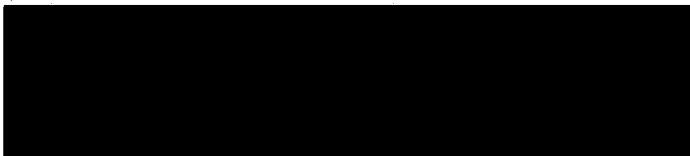
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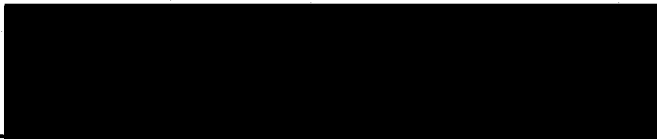
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SELECTION APPLIED, RESPONSE OF TRAITS AND COMBINING ABILITIES OF INBRED LINES OF BEEF CATTLE

INTRODUCTION

Variation in biological material has held the attention of mankind for ages. Attempts to capitalize on variation, therefore, have not been restricted to the formally educated geneticist and breeder, much to the benefit of animal improvement. The intricacies of inheritance and variation, however, have fallen to the geneticist to explain on the basis of cytological, physiological and statistical evidence. When hypotheses are offered, they must undergo testing to assess their validity. The results of such testing may decide the course of further attempts to exploit the naturally occurring variation.

Variation in beef cattle can be exploited for aesthetic or economic ends and the means by which these ends are attained may be entirely divergent, and neither may be compatible with the well being of the animals concerned. Performance, to the animal breeder, means the attainment of the maximum reproductive potential and maximum conversion of feedstuffs to a salable product in the shortest period of time, coupled with normal form and function of the animal body. The development of inbred lines within which selection is applied for desired performance has furnished information on the importance of variation in cattle. That inbreeding without selection causes fixation of gene loci is evident. With selection, the amount of

fixation is dependent on the adaptiveness of the loci in question to the homozygosity attained. If inbreeding, with or without selection, has a detrimental effect on some measure of performance, an organism will display the effect noticeably and one with the monetary value of beef cattle will cause concern to the owner.

Alexander and Bogart (1) showed that inbreeding of calf had a significant depressing effect on suckling gain, but not on postweaning rate of gain and feed efficiency. The work of Brinks, Clark and Kieffer (7) indicated that there was a negative influence on growth of cattle from birth to weaning. The success of King (28; 29) with inbred rats involved rigid selection practiced for performance whereas loss of genetically weaker lines of guinea pigs occurred when Wright and Eaton (54) practiced inbreeding with no conscious selection. These investigations emphasize the effects of inbreeding on the performance of diverse representatives of the animal world. All studies give support to the necessity of a strong selection program whenever inbred lines are maintained.

If, as a result of inbreeding and selection, fixation of loci occurs differentially between lines, then crossing the lines should give results that reflect the differential fixation. This should occur even though selection in itself has maintained several loci in the heterozygous state. This may in itself be essential for the maintenance of performance levels.

Upon the crossing of inbred lines, the differences observed in the performance of the lines when crossed in all possible combinations may be referred to as the differences in general combining ability of the lines. On the other hand, specific crosses that result from the combinations of all lines may appear to be better or worse than one would expect on the basis of the average performance of the lines involved. This would be referred to as the specific combining abilities of the lines. Originally proposed as a method of progeny testing by Johs Schmidt (45; 46), the diallel cross has been used to estimate general and specific combining abilities of lines as it allows for all possible combinations of lines or partial combinations depending on the aims of the investigator (20, p. 463).

The work reported herein is divided into two phases. The first phase represents the analysis of the actual selection practiced for performance in four inbred lines of cattle, the response realized from the selection practiced, the levels of inbreeding and associated performance, and heritabilities of the performance traits. The second phase gives the results of the first complete diallel cross between three Hereford lines, the analysis of general and specific combining abilities of the lines, and the results of analyses of blood constituents as related to growth.

One purpose of carrying out the inbreeding-selection program and the subsequent line-crossing is the attainment of the one trait

which was present initially, variability, but at a different level and in a form that will allow quantitative progress from a stronger genetic base.

I. ASPECTS OF SELECTION, RESPONSE, AND INBREEDING

REVIEW OF LITERATURE

The evaluation of selection intensity in closed lines of cattle was reported by Flower et al. (17). The intensity of selection was defined as the annual selection differentials, or the average performance of the animals used as parents minus the average performance of the group of animals in which they were born. For preweaning performance, selection differentials were computed on both the sire and dam side of the pedigree, with the result that selection intensity was greater on the male side. Selection differentials for postweaning gain were computed on the sire side only due to different management of males and females during the postweaning period and due to the conclusion that nearly all the selection pressure was exerted on the male side. Selection pressure for daily gain was positive in all lines. Phenotypic response was measured by the regression of traits on years. Using repeat matings, environmental changes were estimated and used to correct the phenotypic regressions, giving a genetic response. Phenotypically, all lines showed a decrease in birth weight over the years. During postweaning period inbred heifers showed a decline in size over the years except for one line. Inbred bulls showed slight increases in size. When

environmental effects were considered, there were positive estimates of genetic improvements for birth and weaning weights.

Koch and Clark (31) point out that response to selection is more than the result of direct selection for a particular trait, but is the combined result of the direct selection and indirect selection caused by genetic correlations between traits. Phenotypically, Falconer (16, p. 187) defined response to selection as the difference of mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection.

In order to determine what affects the response to selection and performance in general, numerous workers have studied environmental effects, determined phenotypic and genetic correlations, and examined the role that inbreeding plays on performance at various stages of growth. One of the variables considered when performance data are analyzed is age of dam. Flower et al. (18) found that age of dam had a highly significant effect on birth weight, weaning weight and postweaning daily gain in heifers. Birth weight increased as age of dam increased up to six years of age, whereas weaning weight increased through seven years. Some compensation in postweaning growth rate occurred as a result of effects on preweaning growth due to age of dam. Swiger (49) computed constants for age of dam which showed that in the first postweaning period of 28 days, the calves from younger cows tended to gain faster or compensate for

preweaning environment. Subsequent to this period, this compensation was overcome and was reversed towards the end of the feed test period. The net effect of age of dam on postweaning gains was concluded to be dependent on the length of the feeding period. In another study, Swiger et al. (50) noted that cows reached their peak production at about six years of age, but that age-of-dam effects were biased to the extent that cows were retained in the herd because of their ability to produce heavy calves at weaning. Flower et al. (17) noted the same thing in that there was little culling of cows practiced in the selection for performance because of the need for them in the herd, so that the age of dam constants may be biased in that the constants for older age groups are too high in comparison to an unselected cow population. Marlowe and Gaines (40) found that age of dam was the most important source of variation affecting preweaning growth rate. They obtained maximum production from cows in the six to ten year old age group. Brown (9) also found an increase in calf weight with increases in age of dam up to peak years of production. Koger et al. (32) found that age-of-dam effects varied significantly with pasture, year, lactation and breed and concluded that indiscriminant use of correction factors, especially for age of dam, may introduce more serious error than working with unadjusted data. Burris and Blunn (11) found a definite relationship between age of dam and birth weight of calf. Maximum birth weight was not reached until

cows reached nine to ten years of age.

Association between growth rates at different periods of an animal's life have been studied by several investigators, mainly with the idea of finding how selection at one stage of life, preferably early, corresponds to actual performance at other stages, under given environmental conditions. Black and Knapp (2) found that when weaning at a constant age, weaning weight was negatively correlated with subsequent fatness and that average daily gain from birth to weaning and weaning to slaughter were also negatively correlated. Swiger (49), studying genetic and environmental influences on gain in beef cattle, found that genetic correlations were large, environmental ones low or negative, and phenotypic associations intermediate between preweaning and subsequent postweaning growth periods. Genetic correlations were higher for adjacent periods than more remote periods. Environmental correlations of weaning weight with postweaning gains indicate good preweaning environment is a handicap to early postweaning gains, but enhances later gains, which is similar to the age-of-dam constants reported. Brinks et al. (6) found slightly negative correlations between 180-day preweaning gain and the 196-day feedlot gain. Phenotypic, genetic, and environmental correlations between final weight and the two gains were fairly large because of the part-whole relationship. The correlation also suggested no serious negative relationships that would hamper progress for increased

weights and gains.

Lehman et al. (35) concluded that growth and type are essentially independent on the basis of genetic correlation coefficients. Phenotypic correlation coefficients were large and positive and led to the further conclusion that weight or probably the degree of finish were positively associated in the eyes of the grader. Correlation coefficients were computed after corrections were made for year, sex, breed, age of dam and month of birth. Carter and Kincaid (13) found little relationship between grades and subsequent gains but moderate to high relationships between gains and subsequent grades. No negative correlations were found between gains in subsequent periods that would handicap selection. Kidwell and McCormick (26) concluded that comparisons of rate of gain and economy of gain are valid only when made over comparable segments of the growth curve. At equal initial weights, animals of greater mature size will increase a greater proportion of fat when full fed for a constant period which does not permit both groups to reach mature weights. The result is a greater economy of gain as measured by pounds of feed per pound of gain, which would not be defined as feed efficiency unless it is shown that the composition of the increase is identical among the animals compared. Kidwell et al. (27) also found little relation between feeder grade and subsequent rate or economy of gain. Knapp and Clark (30) stated that lack of gross correlations could in some cases

work to the advantage of the animal breeder, in that low genetic correlations between scores and gains would make it possible to select within any type of animal for greater rates of gain without materially affecting type or conformation.

Swiger et al. (50) computed adjustment factors for preweaning growth of calves and found that the effects of inbreeding of the calf and of the dam were negatively associated with birth weight and with two stages of preweaning growth. When the effects of inbreeding were computed simultaneously with the effect of age of calf, the inbreeding effects were lower than when computed separately, emphasizing the confounding that may exist between season of birth and inbreeding. Brinks, Clark and Kieffer (7) found that inbreeding of the calf had a larger depressing effect on females than on males, and that inbreeding of the dam had a greater depressing effect on male calves than on females as determined by partial regressions of birth weight, 180-day preweaning gain, weaning weight and weaning score on inbreeding of calf and inbreeding of the dam by sex of calf. Alexander and Bogart (1) studied the effect of inbreeding and selection on performance and noted that year and inbreeding were confounded as well as inbreeding with selection. When effects of year and inbreeding were separated, there appeared in every case to be a significant effect of years, whereas inbreeding effects were either non-significant in excess of the positive effects of selection, or there was an effect significant at

the one percent level of probability. Birth weight, rate of gain and feed consumed per unit of gain did not appear to be affected by inbreeding in excess of the selection effect, whereas suckling gain and ages at 500 pounds and at 800 pounds were significantly affected. Inbreeding increased age at 500 and at 800 pounds primarily because of the depressing effect on suckling gain. Inbreeding of the dam affected only postweaning performance of the calves, with more highly inbred dams producing calves with more rapid gains at this stage of growth. Decreased suckling gains of calves were not attributed to decreased milk supply of highly inbred dams, because there was no significant depression of suckling gain associated with inbreeding of the dam.

Heritability estimates have been computed by numerous investigators in various ways depending on the amount of data available and the corrections needed to account for non-genetic effects. Swiger et al. (50), using variance components, found at two stations that heritability of birth weight was about .33. Average daily gain to 130 days at one station was estimated to have a heritability of -.16 and at another station +.15. From birth to weaning, these heritability estimates changed to -.02 and +.14, respectively. From 130 days to weaning, the estimates were +.44 and +.28. The changing estimates indicated to the authors that the genetic potential for growth is masked by differences in mothering ability of the dams to a greater extent during early periods. Repeatability estimates by Taylor et al. (51),

after adjustments using least squares estimates of effects of sex, breed of sire, and gain level of sire (high or low selected sire), were computed by intra-class correlations, regressions, and product-moment correlations. The intra-class correlation coefficients were obtained from data gathered from cows placed in groups born in the same year and calving in the same subsequent years, which separated variance due to age, year and fecundity from variance due to "permanent" differences among cows. Regressions were run as records of second calves on first calf records, all subsequent calf records on the record of the first, and regression of second records on first after division of the herd into high and low halves on the basis of first records. Repeatability of birth weight at one station ranged from .06 using the regression of second records on the first, to .29 using the correlation of first with the average of subsequent records. From birth to weaning the two estimates ranged from .26 to .38. At another station, the average repeatabilities were .30 for birth weight, .41 for gain from birth to midsummer, .32 for midsummer, .42 for birth to weaning gain, and .23 for grade at weaning. Blackwell et al. (3) found that individual differences in gaining abilities of young cattle were relatively highly heritable when the cattle received uniform treatment. Grades at different times were moderately to highly heritable. Genetic correlations were relatively high among traits involving size, growth rate and grades. Grades and gains or weight at

different times tended to exhibit low to negative genetic correlations.

Shelby et al. (47) computed heritability estimates by paternal half sib correlations and found postweaning rate of gain, final weight at 13 months, and feed efficiency to yield estimates of .46, .77, and .32, respectively.

The determination of effects, correlations, and heritabilities, coupled with the desirability of traits economically, have determined to a large extent the emphasis placed on traits considered in selection from which response is sought.

MATERIALS AND METHODS

Performance records were analyzed from three closed Hereford lines of cattle and one closed Angus line from 1951 through 1962. Of the three Hereford lines, the Lionheart line has been closed to outside breeding since 1950. An interchange of breeding females occurred between the Prince and David lines prior to 1950. No outside bulls have been used in any of the three Hereford lines since 1948. The Angus line has been closed since 1950 with the exception of one bull introduced and used in 1953, 1954, and 1955. Management of the lines has been similar from year to year, with calves weaned at 425 pounds or the first part of November, allowed an adjustment period in the barn until they reached 500 pounds, then individually fed with a high roughage ration up to 800 pounds body weight. Suckling gains, postweaning rates of gain, feed efficiency, and conformation and condition score at 500 and at 800 pounds were recorded for each calf. Bull calves remained intact throughout the testing period. Selection was on the basis of pre- and post-weaning performance plus the score for conformation given the animals at 800 pounds, all on an index basis. Abnormalities and inherited defects were considered on a minimum culling basis.

Selection differentials within each of the closed lines were computed by the method shown by Brinks (5), using the performance

records of the sires and dams compared to the performance records of their contemporaries. This basically gives a selection differential based on the mean of the selected parents compared to the mean of the entire population from which they were selected. Computations were as follows:

On the sire side,

$$\Delta S = \frac{n_1^s s_1 + n_2^s s_2 + \dots + n_i^s s_i}{N\bar{A}}$$

On the dam side,

$$\Delta D = \frac{n_1^d d_1 + n_2^d d_2 + \dots + n_i^d d_i}{N\bar{A}}$$

For sire and dam combined,

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

where ΔS , ΔD , or ΔP are the selection differentials, n_i^s and n_i^d are the number of progeny by a particular sire or dam in a given year and s_i and d_i are the superiority or inferiority of a particular sire or dam. N is the number of progeny in a given year, and \bar{A} is the average age of the parents when the offspring are born, or

$$\bar{A} = \frac{\sum \frac{n_i^s A_i^s + n_i^d A_i^d}{2N}}$$

\bar{A} is the generation interval and puts the selection differential on a yearly basis when divided into the selection intensity.

Differentials were computed for the following traits: suckling

gain, postweaning rate of gain, economy of gain, and score. A selection differential for inbreeding was also computed for each line.

Phenotypic responses of performance traits and inbreeding were obtained by the regression of traits on years for each line by sex of calf. The following numbers of calves were involved in the analysis of response:

	<u>Lionheart Line</u>	<u>Prince Line</u>	<u>David Line</u>	<u>Angus Line</u>
male calves	59	64	61	78
female calves	64	66	49	111

Environmental variations in performance traits were estimated by data on repeat matings. These matings were not planned, but occurred randomly. Data occur across lines yearly, therefore, instead of each line having repeat matings yearly. The numbers of repeat matings which contributed to estimates yearly are as follows:

1951	> 7	1957	> 5
1952	> 5	1958	> 1
1953	> 3	1959	> 1
1954	> 10	1960	> 2
1955	> 0	1961	> 1
1956	> 0	1962	
1957			

For the two years in which repeat matings did not occur, the average of the entire calf crop were computed for those years and for the years bracketing them, to arrive at the estimates.

Means by line and sex for all performance traits and

inbreeding of calf and dam were obtained for the 12-year period.

The performance trait means were plotted graphically to show trends and yearly variations. For suckling gain, rate of gain, and economy of gain, means were obtained by inbreeding percentage groups of 0, 1 - 6, 7 - 12, 13 - 18, 19 - 24, and 25 percent and above. The means of suckling gain were likewise computed at like increments of inbreeding of dam and also by age of dam. Age of dam was computed by years from 1951 to 1962. Simple linear regressions were computed by regressing performance traits on inbreeding of calf. Variation of suckling gain with inbreeding of dam was also computed in a similar manner.

Heritability estimates of performance traits in the lines were computed by intra-sire regression of offspring on dam, correcting only by adjusting female performance to male performance by the difference between the means of the two sexes.

RESULTS

Selection differentials for each trait considered in the breeding program are shown on a yearly basis in Table 1 for each line. The differentials shown are those computed for the sire side and for the dam side of the mating, plus the average of the two. The generation interval and number of animals in each line are indicated. The differentials, covering the period of years 1951 through 1962 show that selection has been in a positive direction when both sire and dam are considered for all performance traits. The selection differential of +.0172 pounds for suckling gain in the Lionheart line indicates that this many pounds per day increase in suckling gain were selected for when matings were planned each year. The -3.21 selection differential for feed per unit of gain indicates that less feed per 100 pounds of gain were selected for at the same time that an increase of .0169 pounds per day was selected for in rate of gain. A higher score, on the basis of the scores of sires and dams, was selected for, amounting to .0482 units on a scale of 5 to 15, where the lowest score is 5 and the highest is 15. In all cases, the selection differential was larger on the sire side than on the dam side. In order to find the accumulated selection differential over the 12 year period, each figure would be multiplied by 12. As an example, in the Prince line each differential multiplied by 12 shows that selection was for a total

Table 1. Yearly selection differentials for performance traits and inbreeding computed from the sires, dams, and the parents combined.

	Lionheart			Prince			David			Angus		
	Sire	Dam	P ¹	Sire	Dam	P	Sire	Dam	P	Sire	Dam	P
Suckling gain (pounds per day)	+0.0233	+0.0111	+0.0172	+0.0647	+0.0001	+0.0324	+0.0453	+0.0052	+0.0252	+0.0408	+0.0012	+0.0210
Rate of gain (pounds per day)	+0.0194	+0.0144	+0.0169	+0.0617	+0.0009	+0.0313	+0.0480	+0.0058	+0.0269	-0.0388	+0.0198	+0.0293
Economy of gain (pounds per 100 pound gain)	-3.46	-2.95	-3.21	-11.02	+0.02	-5.42	-12.89	-2.04	-7.46	-12.15	-10.79	-11.47
Score (units)	+0.0598	+0.0367	+0.0482	+0.2019	-0.0041	+0.0989	+0.0562	+0.0186	+0.0374	+0.0662	+0.0266	+0.0464
Inbreeding (percent)	-0.0003	+0.0008	+0.0002	-0.0054	+0.0007	-0.0023	-0.0009	+0.0014	+0.0002	-0.0031	-0.0014	-0.0022
Generation interval (years)	4.17			3.93			4.17			4.24		
Number of animals 1951-62	123			130			110			189		

¹Both parents

increase in preweaning rate of gain of 0.39 pounds per day. Selection was also for a total increase in postweaning rate of gain of 0.38 pounds per day on 65 pounds less feed per 100 pounds of gain. At the same time a total increase of 1.17 units in score for conformation was selected for.

Selection was practiced against inbreeding in the Prince and Angus lines, but not in the Lionheart and David lines. In the latter lines, the selection for inbreeding was due to that contributed by the dams. In all cases, the selection differential was against inbreeding on the sire side of the matings.

The generation interval, given in Table 1, averaged approximately four years, being longest in the Angus line and shortest in the Prince line.

Differences in performance of the lines by sexes are shown in Table 2 and Table 3. The performance prior to the time that selection differentials were computed is presented in Table 2. Average figures for all years from 1951 through 1962 are given in Table 3. Upon examination of the means of the traits in Tables 2 and 3 and the graphs of the means by years in Figures 1 through 16, it is evident that positive responses for the postweaning performance traits were obtained subsequent to the first three years. Preweaning performance, on the other hand, was generally higher during these three years except in the case of Angus females. Average inbreeding of

calves and of dams is also indicated in Table 3. Referring to this table, it is seen that suckling gain was superior in the Angus line, but that this line averaged lowest in postweaning rate of gain and was highest in feed required per unit of gain. Inbreeding averaged lowest for both the Angus calves and their dams. The David calves were lowest in suckling gain. Rates of gain during the feed test for the three Hereford lines were similar among the males, but the David females gained more rapidly than Prince females, which in turn gained at a faster rate than Lionheart females. Prince calves were the most economical in converting feed into gains. Lionheart males and females scored highest for conformation and were followed by the Prince and David calves in that order. Inbreeding of calves and of dams was highest in the David line of Herefords.

Phenotypically, each performance trait and inbreeding responded to selection from 1951 to 1962 as indicated in Table 4. Each value shows the yearly response which, when multiplied by 12, would give the accumulated response for the 12-year period. Graphically, the phenotypic trends in performance traits are shown in Figures 1 through 16 by lines. The first three years not covered by this study are included in the graphs for comparative purposes. In all lines, from 1951 to 1962, response was positive for score. Response to selection in the other traits varied between lines and sexes. Suckling gain declined in all lines except the Angus, whereas rate of gain

declined in all cases except for males in the David line and females in the Angus line. Feed economy improved in the case of Lionheart males, David males, and Angus females, and declined in all other cases. Inbreeding increased in all lines. Among the Herefords, whenever negative responses occurred in rate of gain and feed economy, greater declines were made by females than males. Results for suckling gain were variable.

More year-to-year variation occurred in suckling gain due to environmental causes than in postweaning rate of gain as indicated by plots of differences in repeat matings shown in Figure 17. Conditions generally indicated improvement for suckling gain through 1958, after which there was a decline. Rate of gain during the feed test showed a trend opposite to that shown in suckling gains. Points were plotted from the repeat matings in Figure 18 for economy of gain and score. Economy of gain improved in every case in which there was an improvement in rate of gain, whereas score improved generally through 1958, after which it declined. The curvilinear aspect of all plots is evident from the graphs.

Histograms showing levels of performance of traits by lines and sexes according to inbreeding of the calves are presented in Figures 19, 20 and 21. The numbers of calves by sex are indicated with the initial M for male and F for female. For suckling gain, the lower percentages of inbreeding were associated with higher suckling

gain for both males and females as shown in Figure 19. Inbred calves gained more rapidly during the postweaning period than non-inbred calves, but there was an indication of decreasing performance as inbreeding increased (Figure 20). Economy of gain tended to decrease with increased inbreeding, but there were differences among the lines. Means of suckling gain by sexes according to the inbreeding of the dams are shown in Figure 22. Non-inbred dams in the Hereford lines had calves with a higher suckling gain than inbred dams. Male calves in the Angus line did not show the decline upon inbreeding of dam that females of the Angus line did.

Suckling gain means by age-of-dam groups are shown in Table 5. Two and three year old cows constitute one age bracket while four year old and older cows make up the other bracket. In all cases, with the exception of the Lionheart line, suckling gain was lower for calves produced by cows in the two and three year old age bracket of dams. The young Lionheart females in this study had excellent gaining calves during the suckling period. The ages of the dams used in the breeding program yearly are presented in Table 6. The ages of the Lionheart cows that were kept for breeding steadily increased from 1951 to 1962, with those in 1962 being 2.5 years older than those in 1951. The same trend was present for ages of the Prince cows. In the David line, there were older cows at the beginning of the study, the average age decreased in the middle

years of the study, and then the ages of the cows increased until the cows were the oldest of all the lines in later years. In the Angus line, the cows were older at the beginning of the study, the average age increased till 1954 and then declined until 1959. Subsequent to this date the average age has increased.

Responses of traits with inbreeding of calf are shown in Table 7, as a supplement to the histograms previously noted. In most cases, except for score, a decline in the traits is noted with each percent increase in inbreeding. Suckling gains showed a negative response to increased inbreeding of dams for both sexes and for all the lines, with the magnitude of the responses presented in Table 8.

Heritability estimates for each trait, given in Table 9, show a similarity between estimates for rate of gain and economy of gain within each of the lines. Estimates of heritability for suckling gain were all negative and were entered as zero. There was a wide variation in heritability estimates for score among the lines.

Table 2. Means of performance traits by line and sex prior to 1951.

		Lionheart		Prince		David		Angus	
		Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain (pounds per day)	1948	2.27	1.75	2.00	1.65	--	--	2.04	1.72
	1949	--	--	1.82	1.52	--	--	2.05	1.69
	1950	1.85	1.70	1.87	1.77	1.66	1.56	2.02	1.66
Rate of gain (pounds per day)	1948	2.22	1.62	2.39	1.62	--	--	2.23	1.51
	1949	--	--	2.25	2.10	--	--	2.41	1.77
	1950	2.04	1.72	2.29	1.97	2.17	2.00	2.05	1.81
Feed economy (pounds feed per 100 pounds gain)	1948	846	1048	858	1007	--	--	766	1265
	1949	--	--	623	781	--	--	674	936
	1950	716	890	637	766	724	825	745	849
Score (units)	1948	--	--	--	--	--	--	--	--
	1949	--	--	9.7	9.9	--	--	7.9	9.9
	1950	9.3	9.9	9.6	10.2	8.3	9.6	8.9	9.6
Numbers	1948	6	7	3	5	0	0	6	3
	1949	0	0	7	5	0	0	8	4
	1950	2	9	2	4	2	6	7	2

Table 3. Means of performance traits by line and sex from 1951-1962.

	Lionheart		Prince		David		Angus	
	Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain	1.77	1.61	1.77	1.57	1.60	1.51	1.97	1.73
Rate of gain	2.70	1.96	2.64	2.06	2.69	2.16	2.46	1.84
Feed economy	706	971	664	854	714	889	788	1030
Score	12.17	11.96	11.22	11.22	10.70	11.10	11.10	11.10
Inbreeding ¹	13.9	11.3	12.1	12.8	19.1	17.5	6.94	7.9
Number of animals	59	64	64	66	61	49	78	111
Inbreeding ¹ of dam	5.5	6.1	4.9	6.2	9.7	7.1	3.6	3.0

¹ Expressed in percent.

Table 4. Phenotypic responses of traits yearly from 1951-1962, determined by regression of traits on years.

	<u>Lionheart</u>		<u>Prince</u>		<u>David</u>		<u>Angus</u>	
	Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain	-0.020	-0.026	-0.035	-0.007	-0.013	-0.012	+0.008	+0.001
Rate of gain	-0.019	-0.028	-0.012	-0.040	+0.003	-0.010	-0.024	+0.019
Feed economy	-7.46	+15.25	+1.30	+12.01	-0.35	+12.84	+11.00	-3.34
Score	+0.16	+0.10	+0.25	+0.15	+0.08	+0.13	+0.34	+0.38
Inbreeding	+.70		+.98		+.42		+.62	

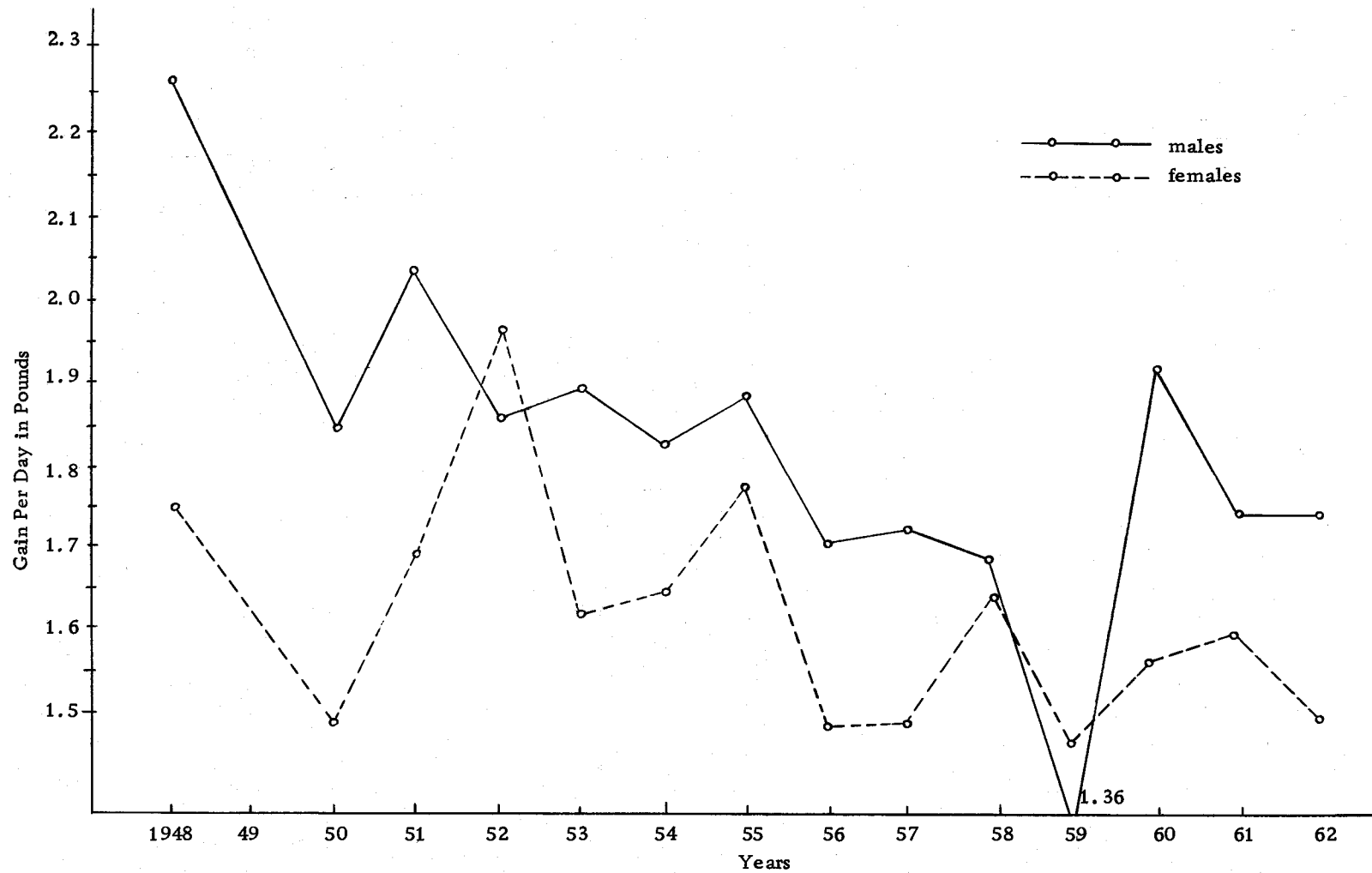


Figure 1. Yearly means by sex of calf for preweaning gain of Lionheart calves.

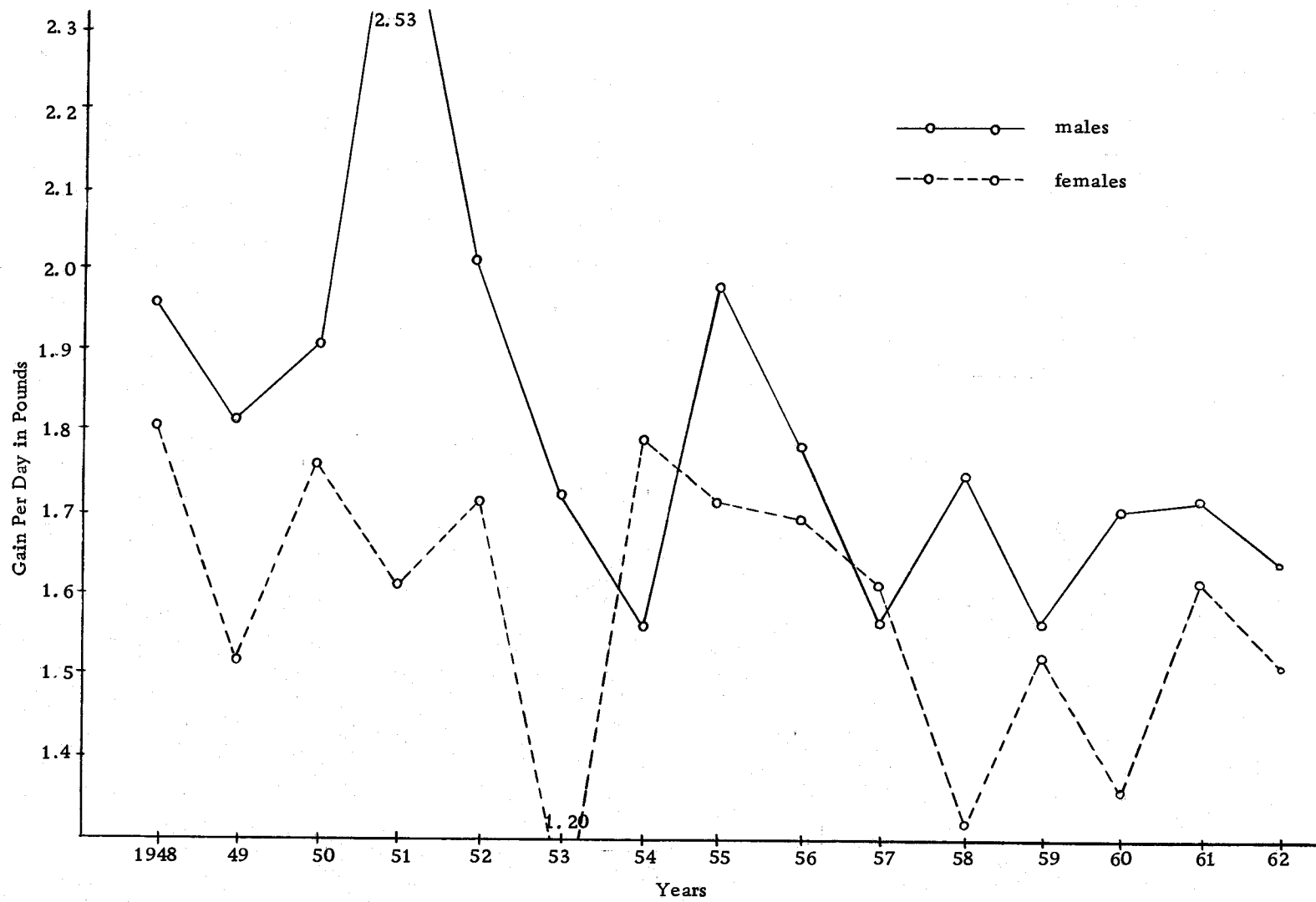


Figure 2. Yearly means by sex of calf for preweaning gain of Prince calves.

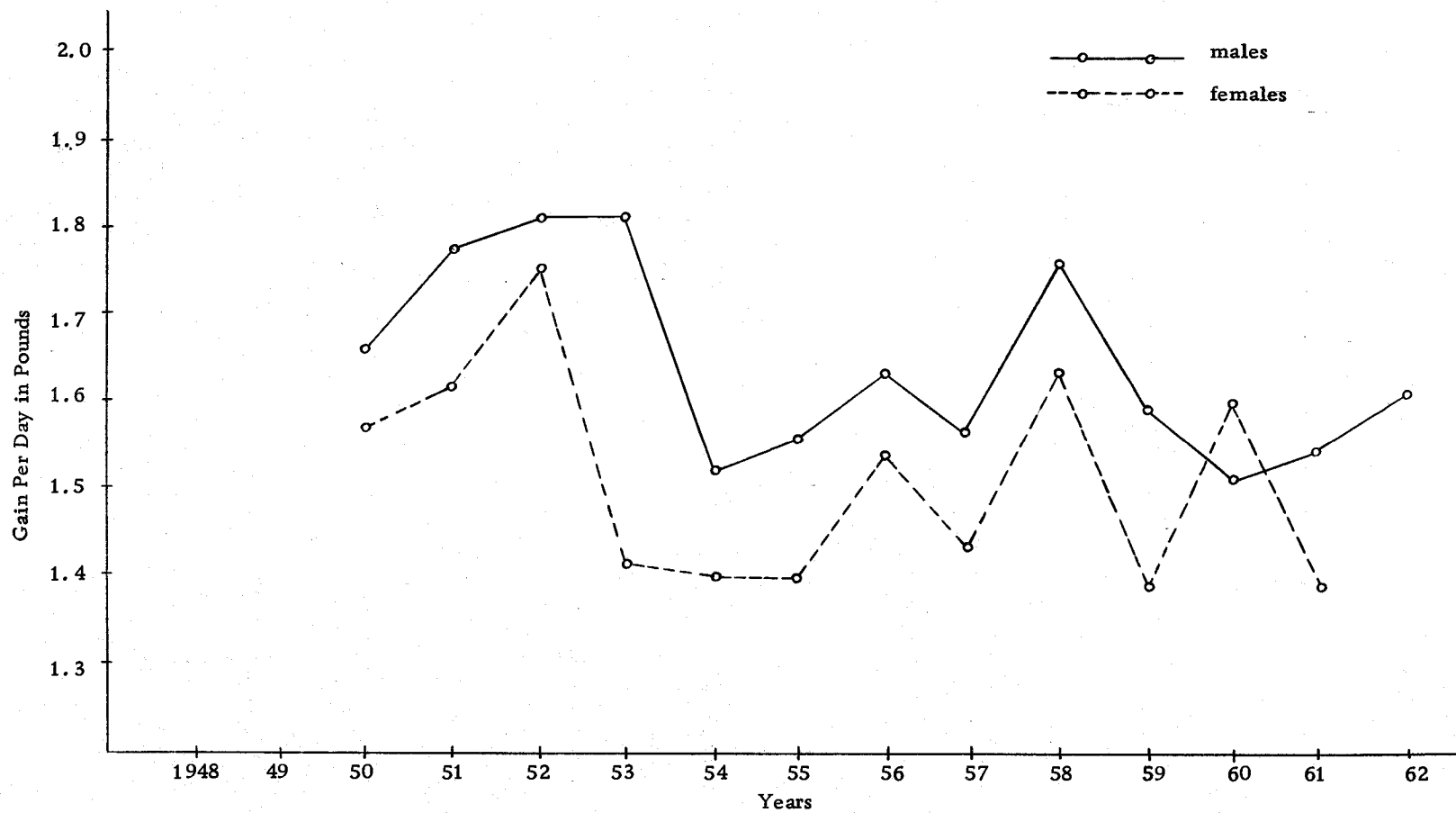


Figure 3. Yearly means by sex of calf for preweaning gain of David calves.

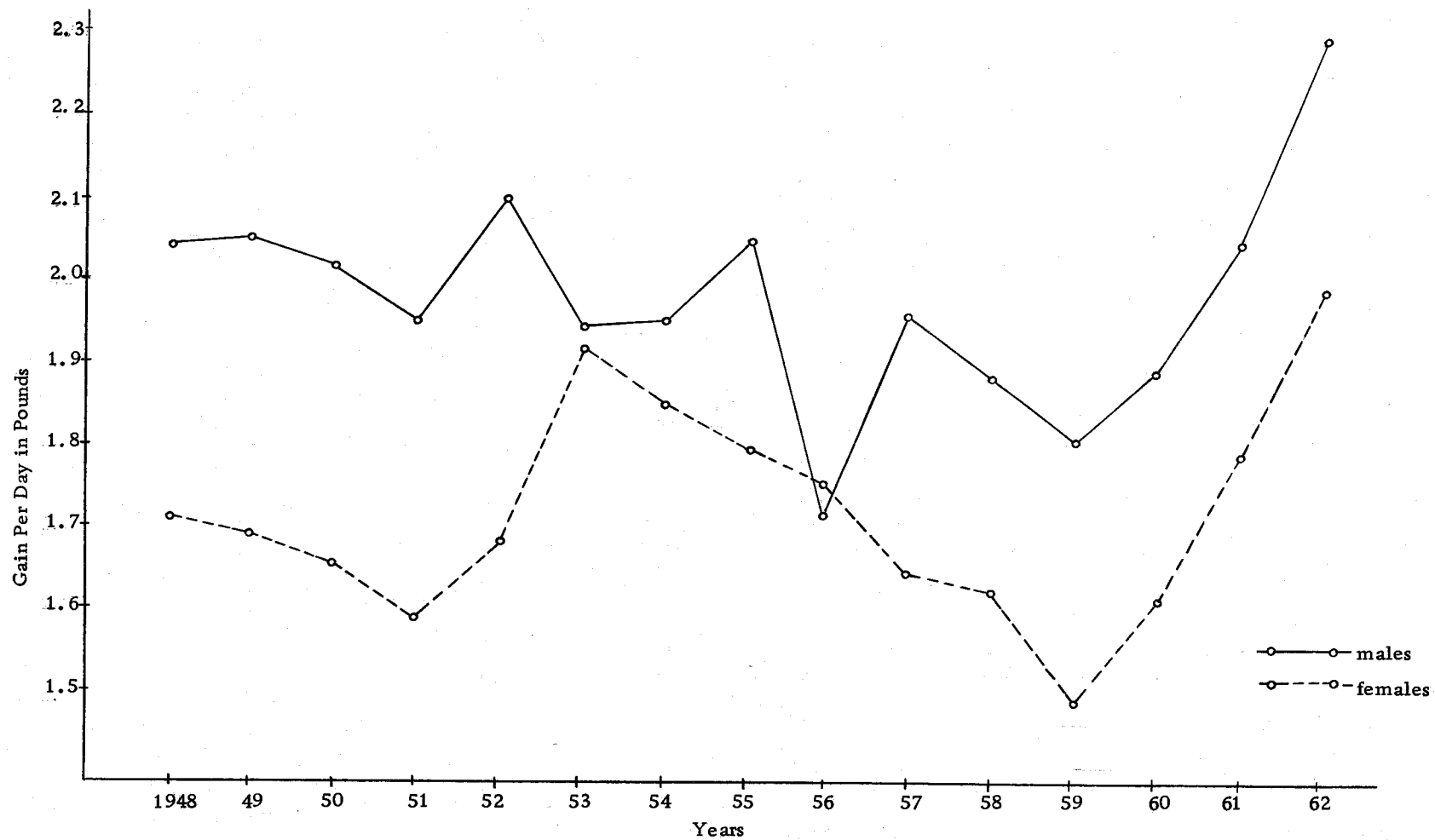


Figure 4. Yearly means by sex of calf for preweaning gain of Angus calves.

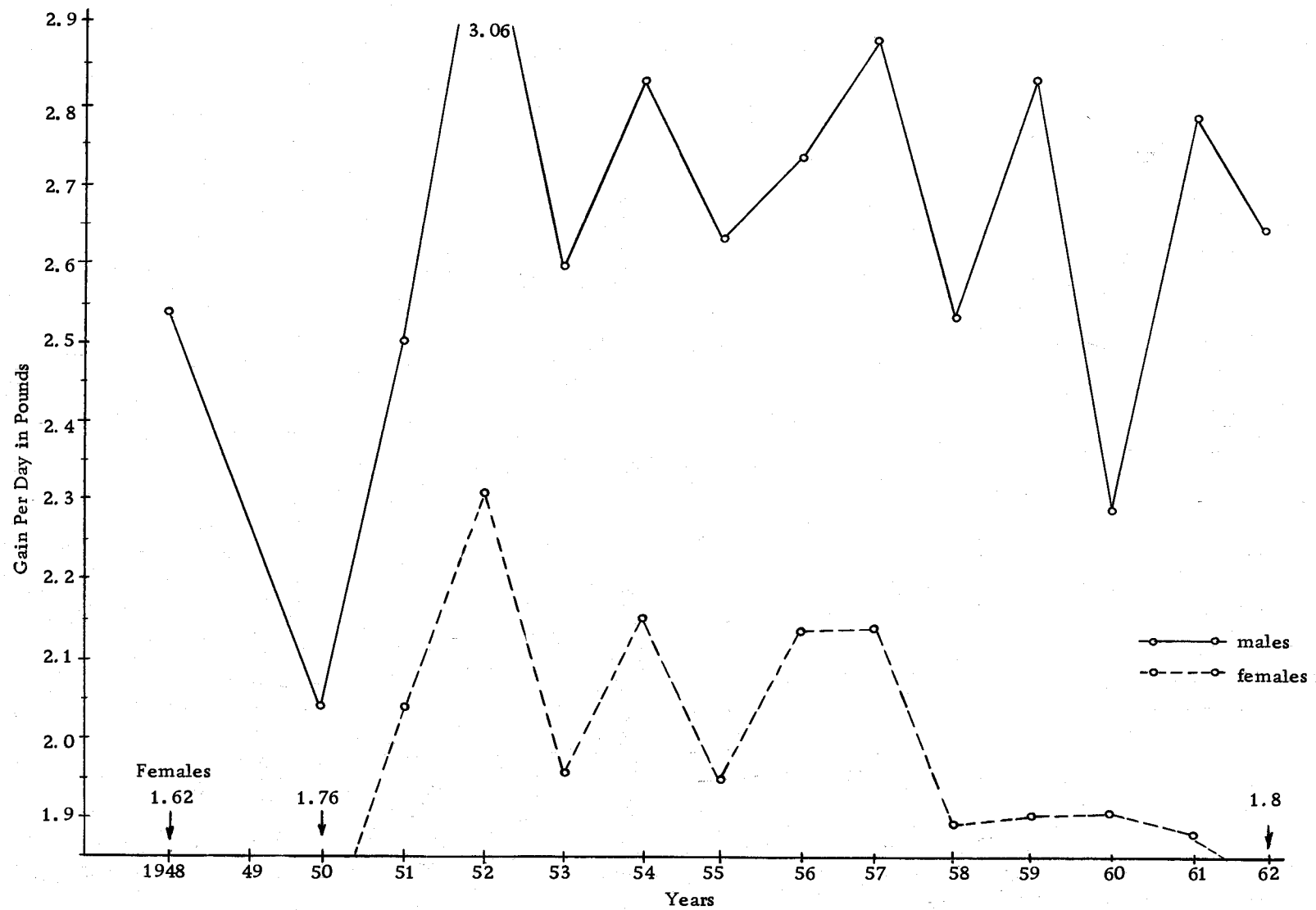


Figure 5. Yearly means by sex of calf for postweaning gain of Lionheart calves.

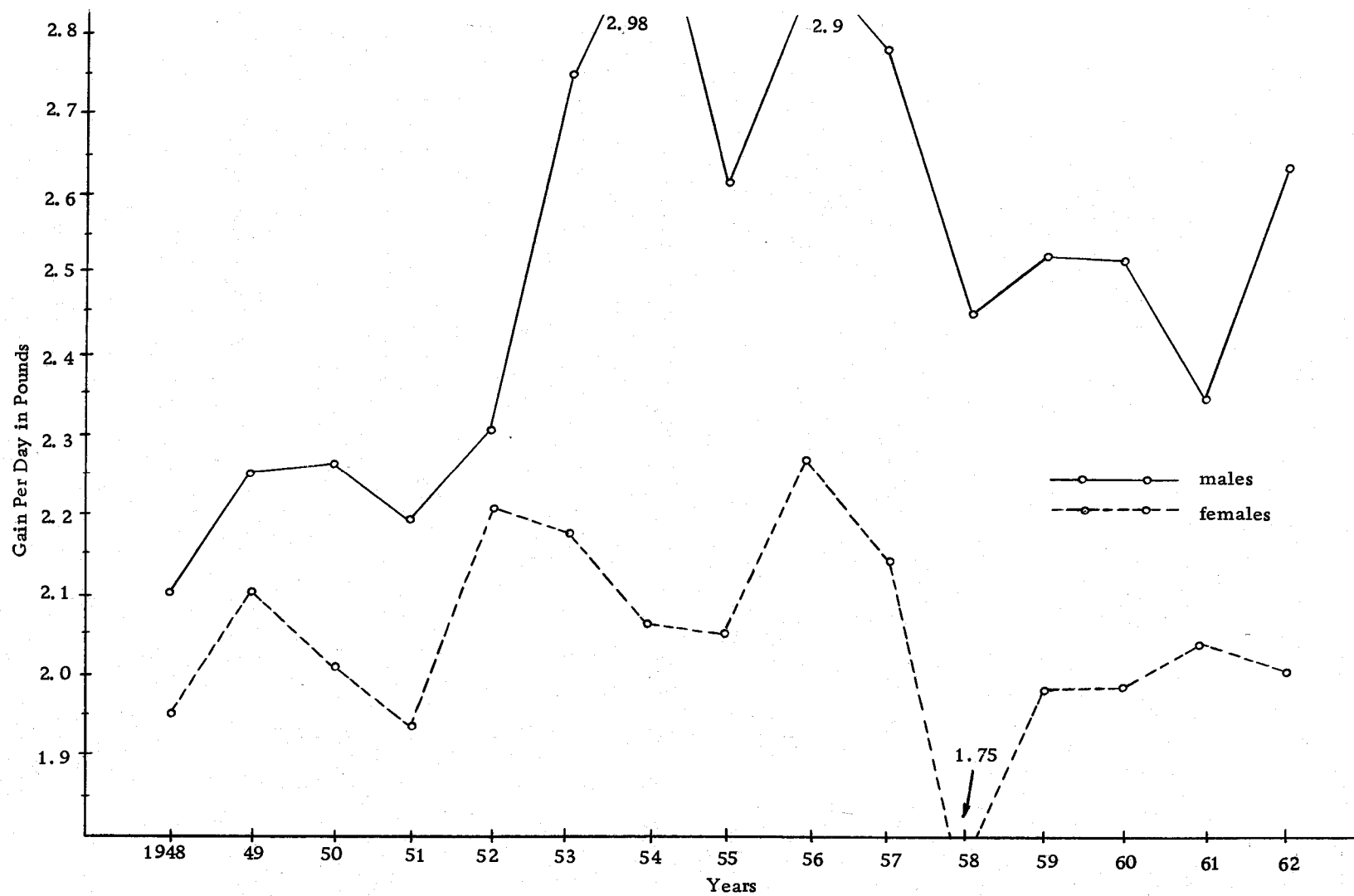


Figure 6. Yearly means by sex of calf for postweaning gain of Prince calves.

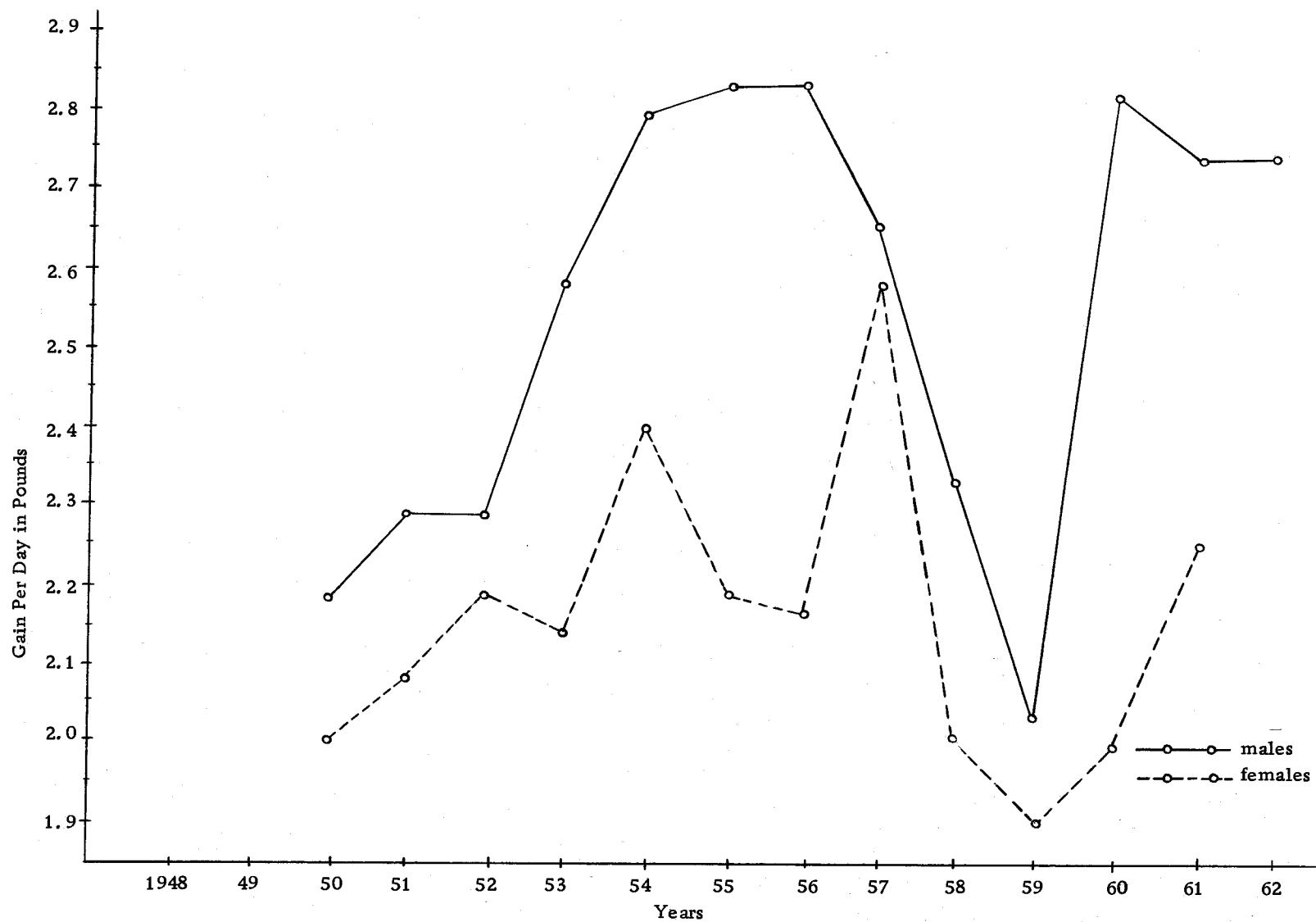


Figure 7. Yearly means by sex of calf for postweaning gain of David calves.

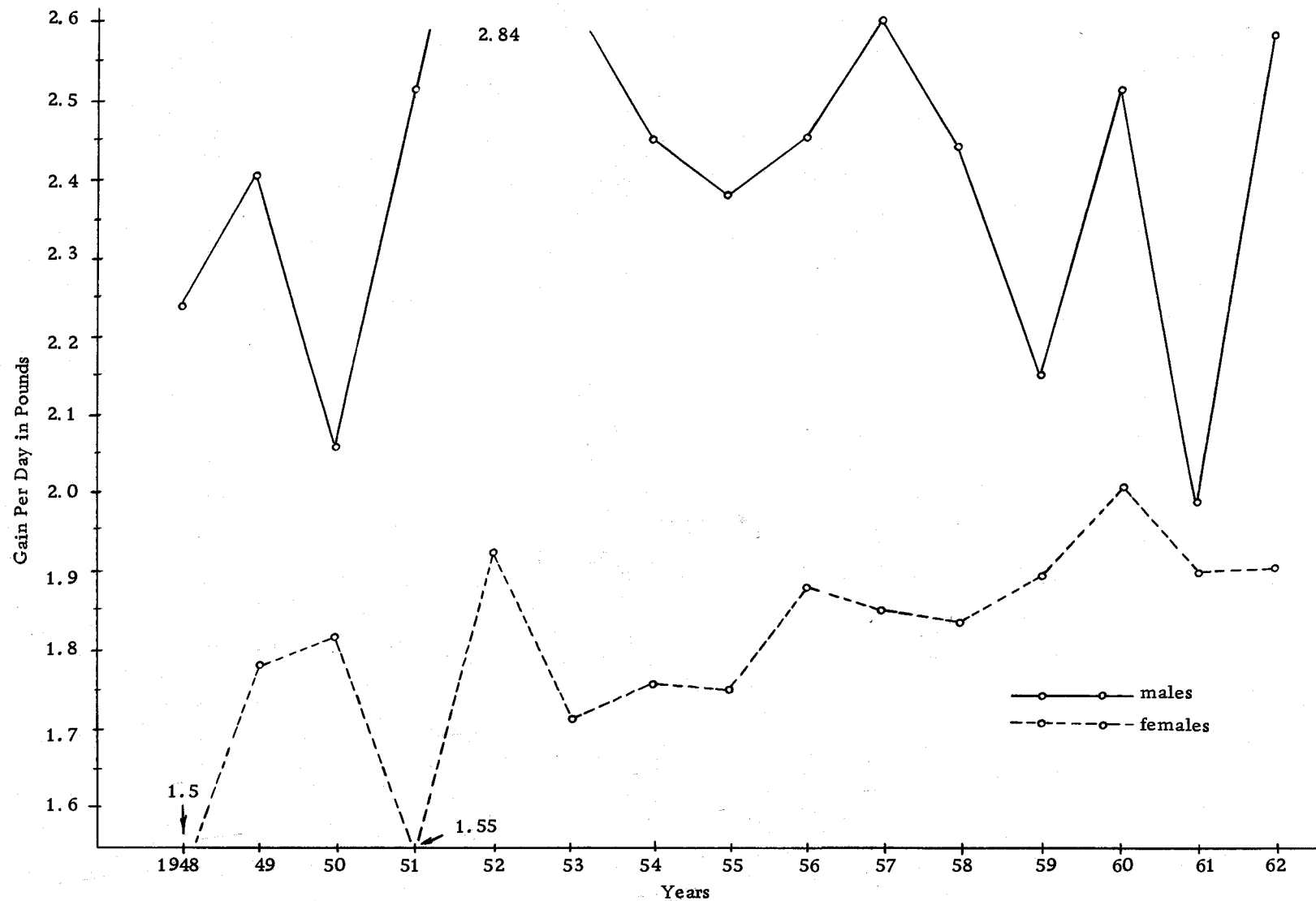


Figure 8. Yearly means by sex of calf for postweaning gain of Angus calves.

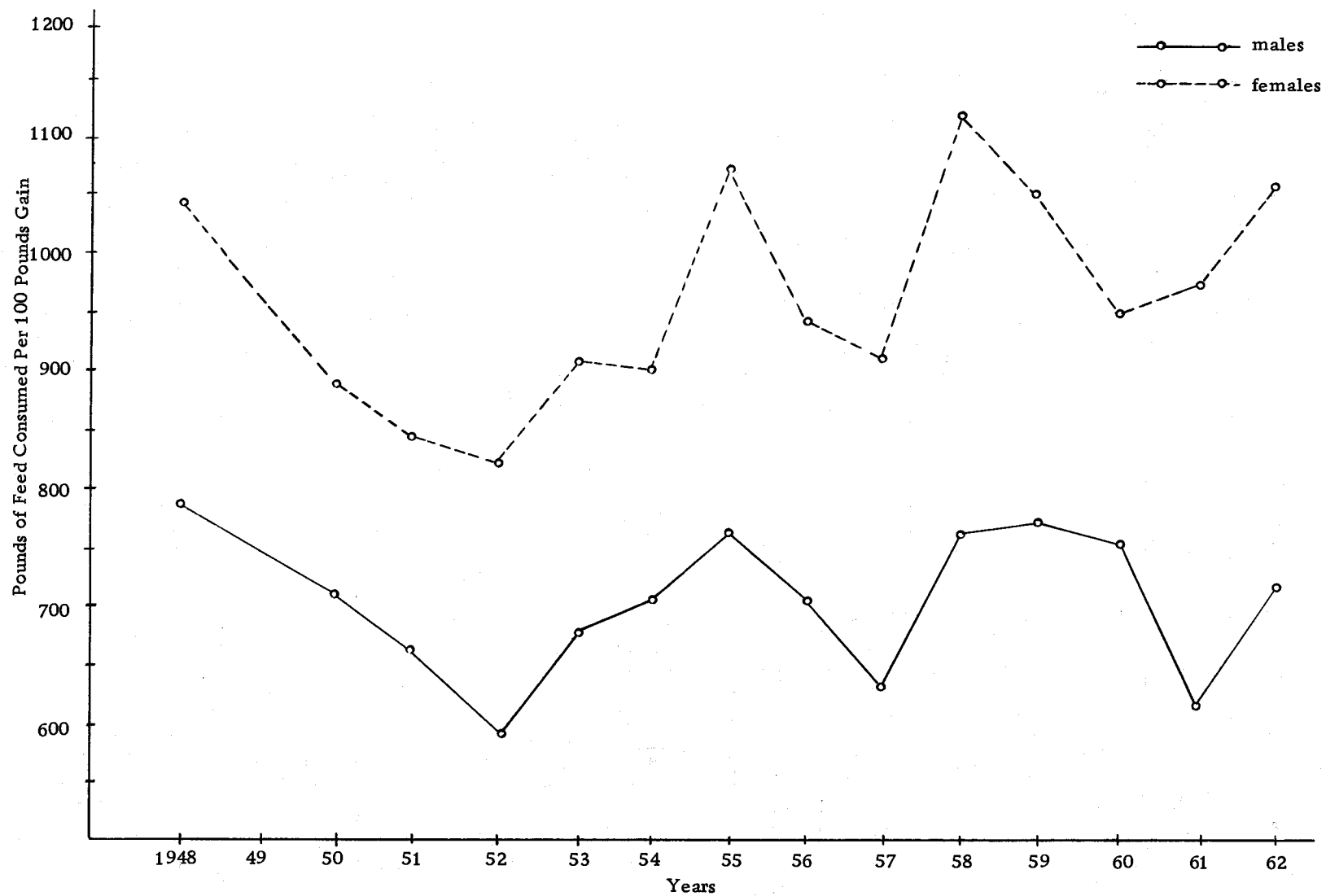


Figure 9. Yearly means by sex of calf for economy of gain of Lionheart calves.

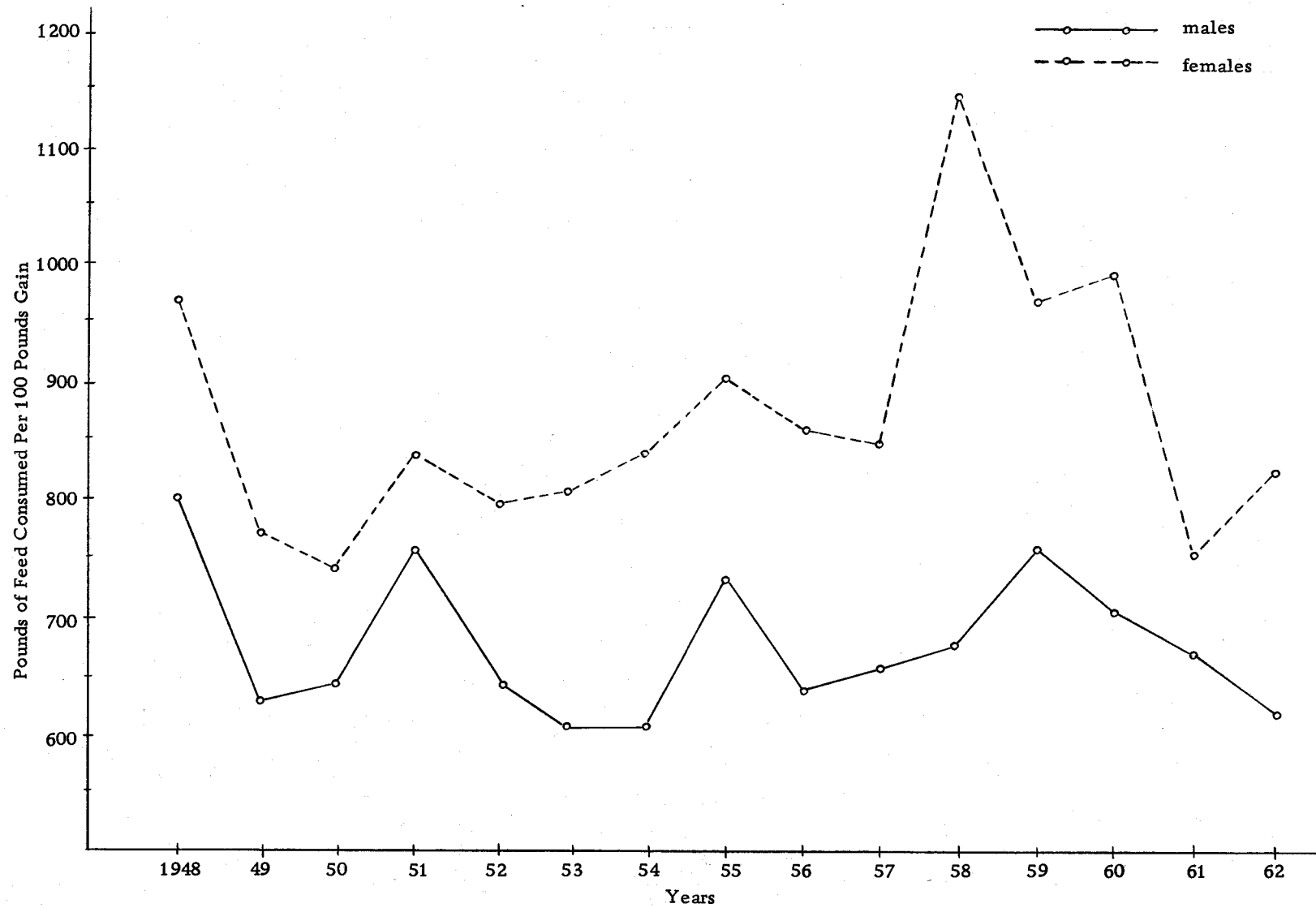


Figure 10. Yearly means by sex of calf for economy of gain of Prince calves.

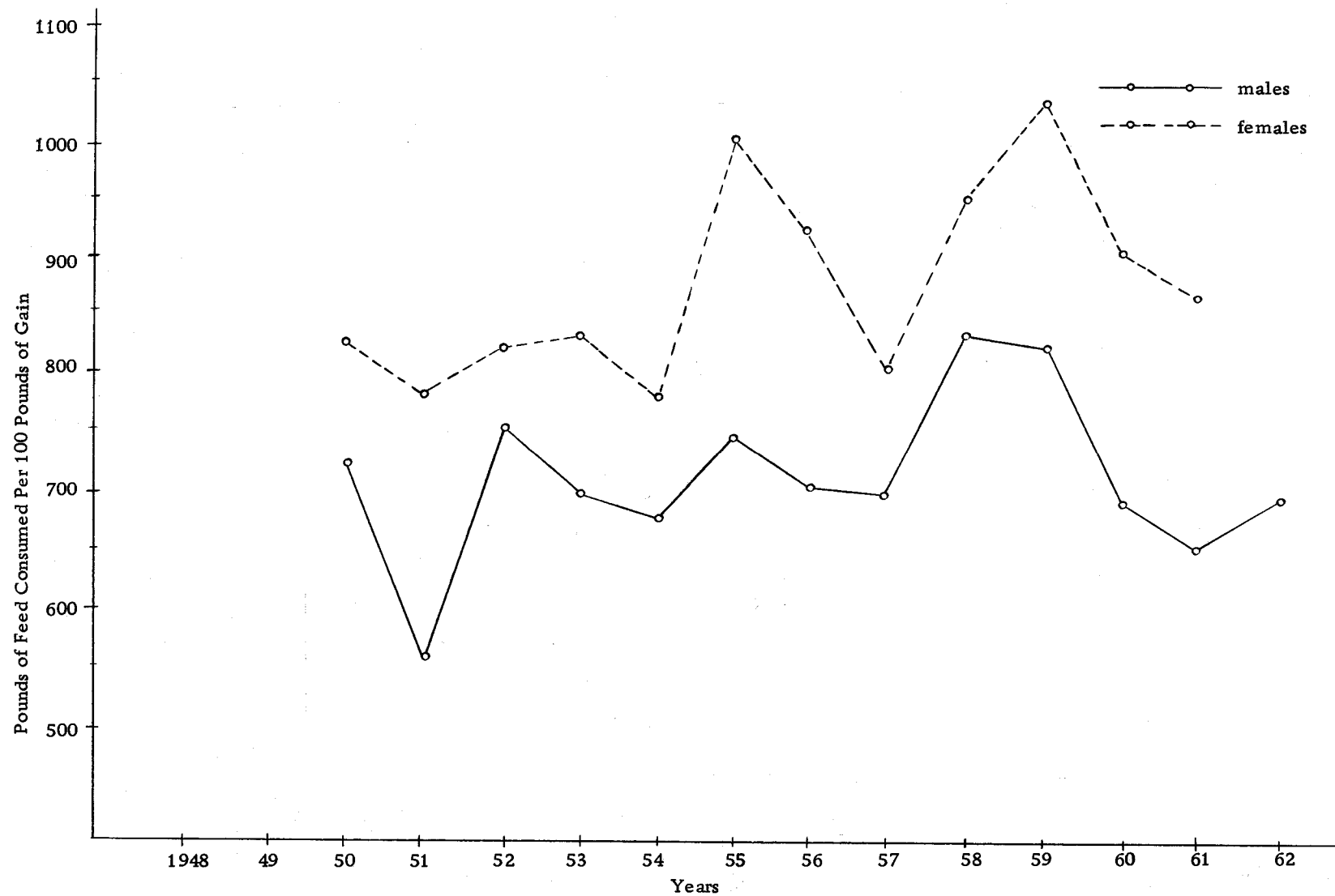


Figure 11. Yearly means by sex of calf for economy of gain of David calves.

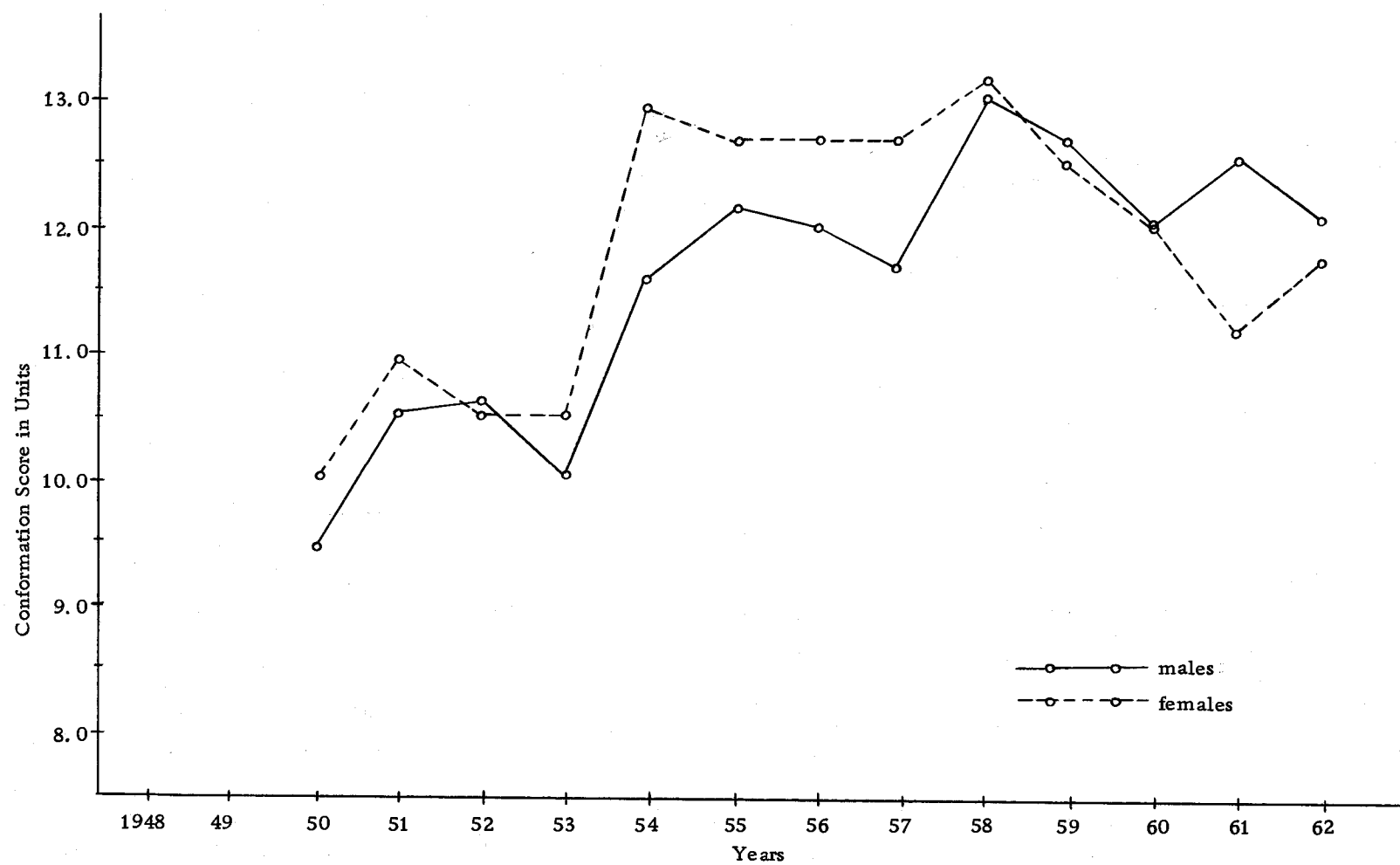


Figure 13. Yearly means by sex of calf for conformation score of Lionheart calves.

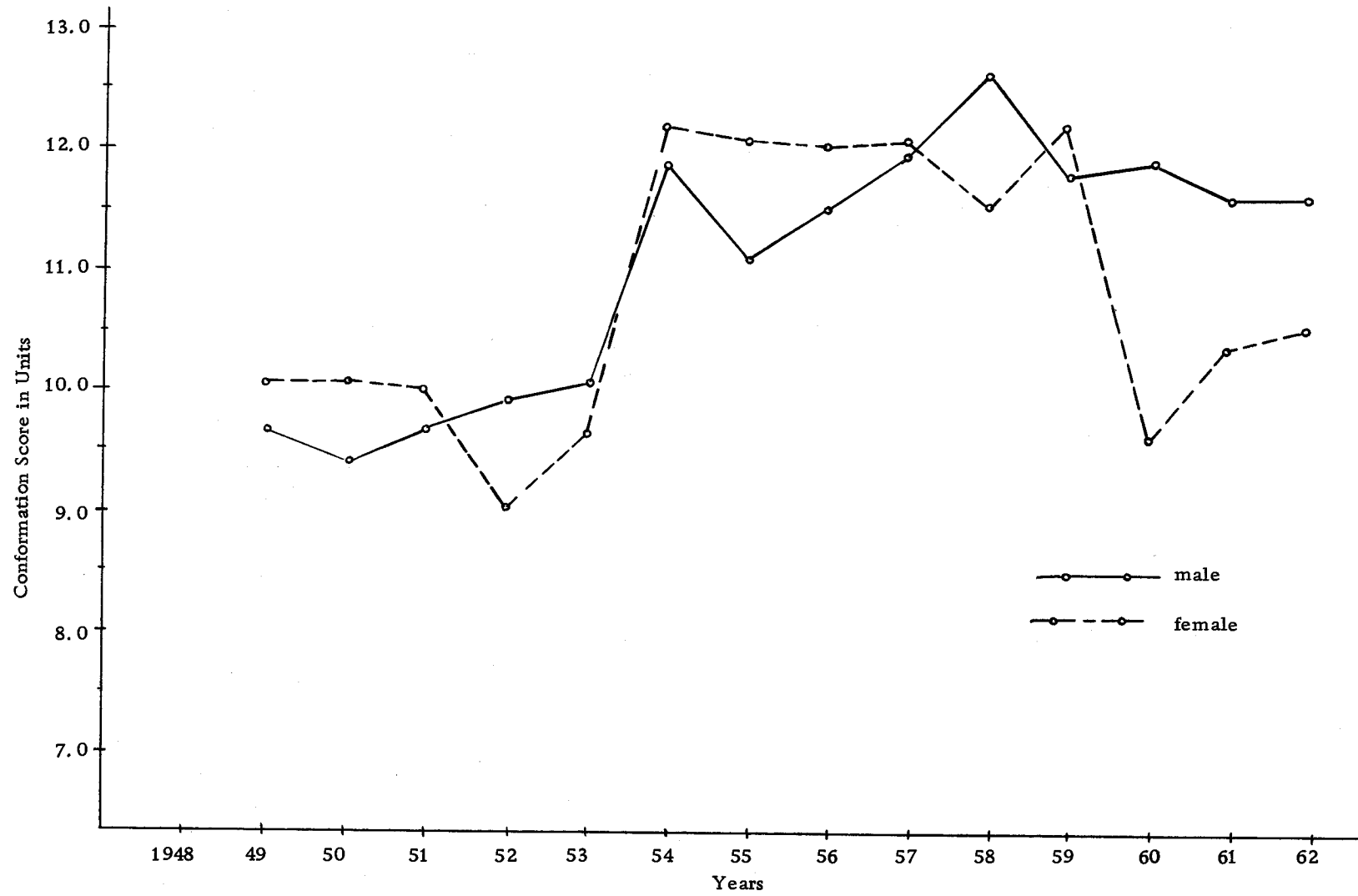


Figure 14. Yearly means by sex of calf for conformation score of Prince calves.

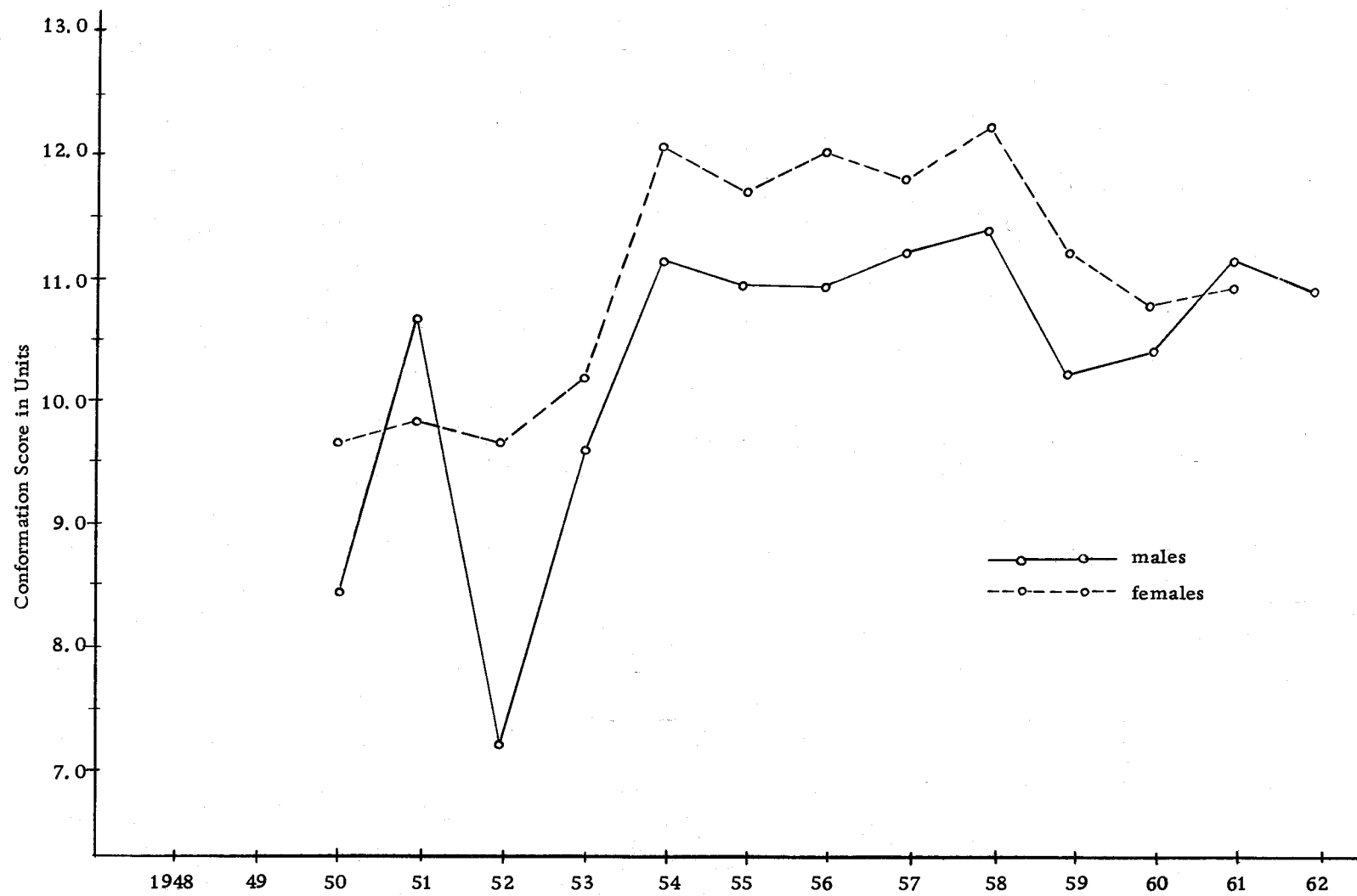


Figure 15. Yearly means by sex of calf for conformation score of David calves.

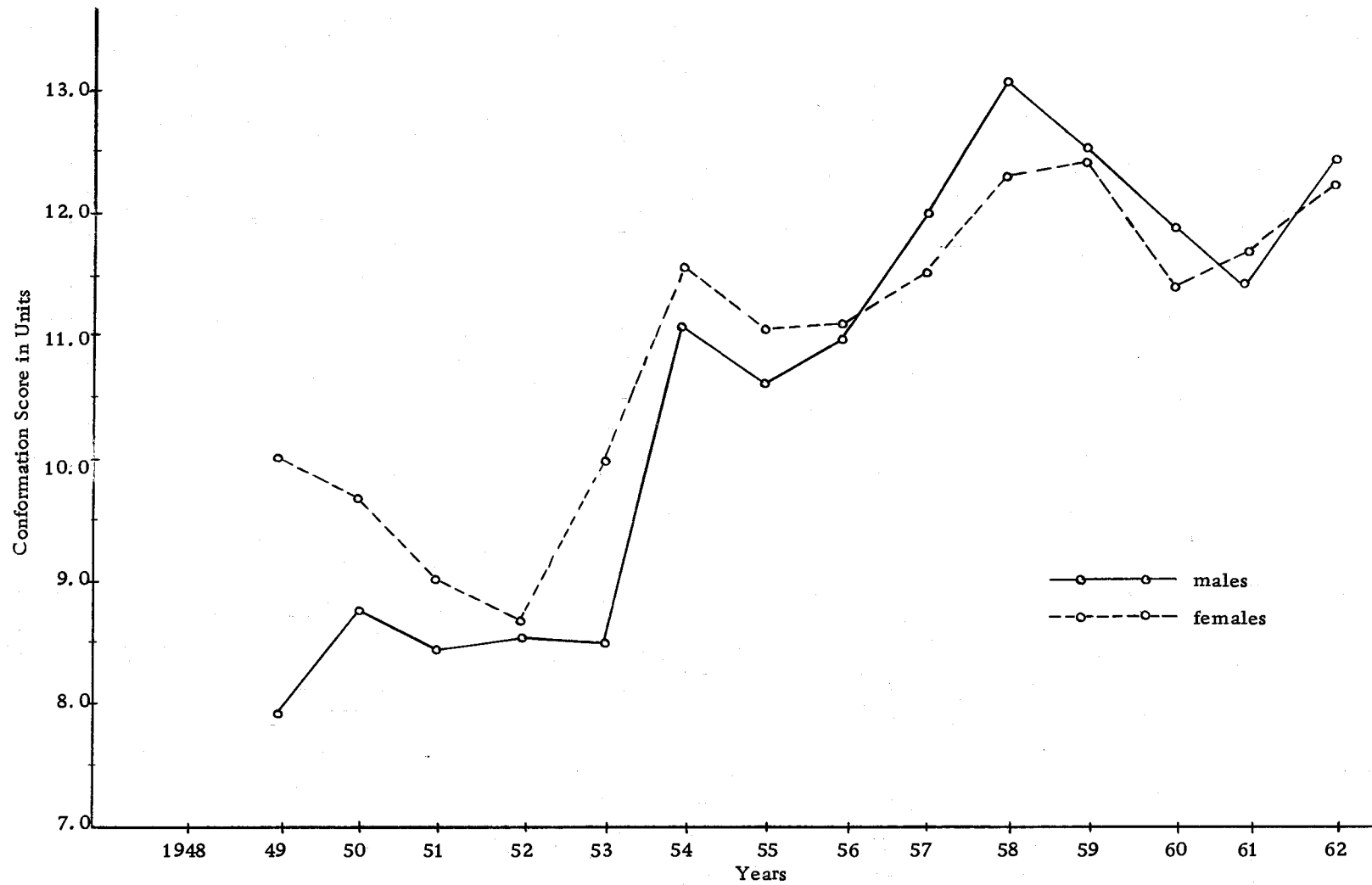


Figure 16. Yearly means by sex of calf for conformation score of Angus calves.

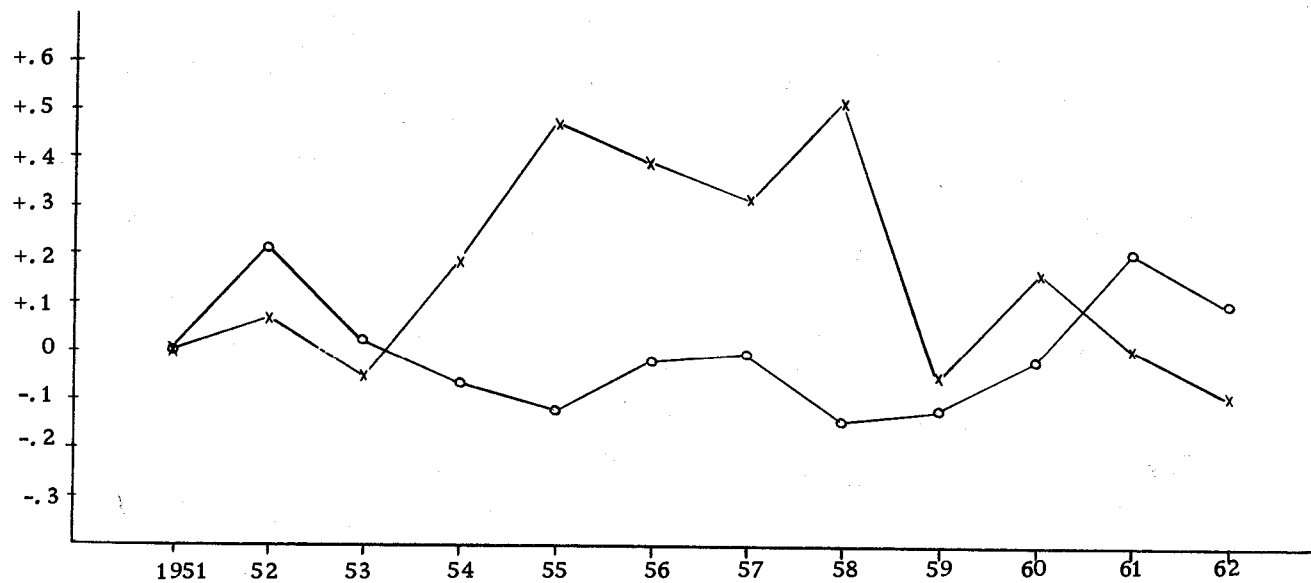


Figure 17. Environmental variations as estimated by repeat matings.

x = Suckling gain, expressed as pounds per day gain deviations.

o = Postweaning rate of gain.

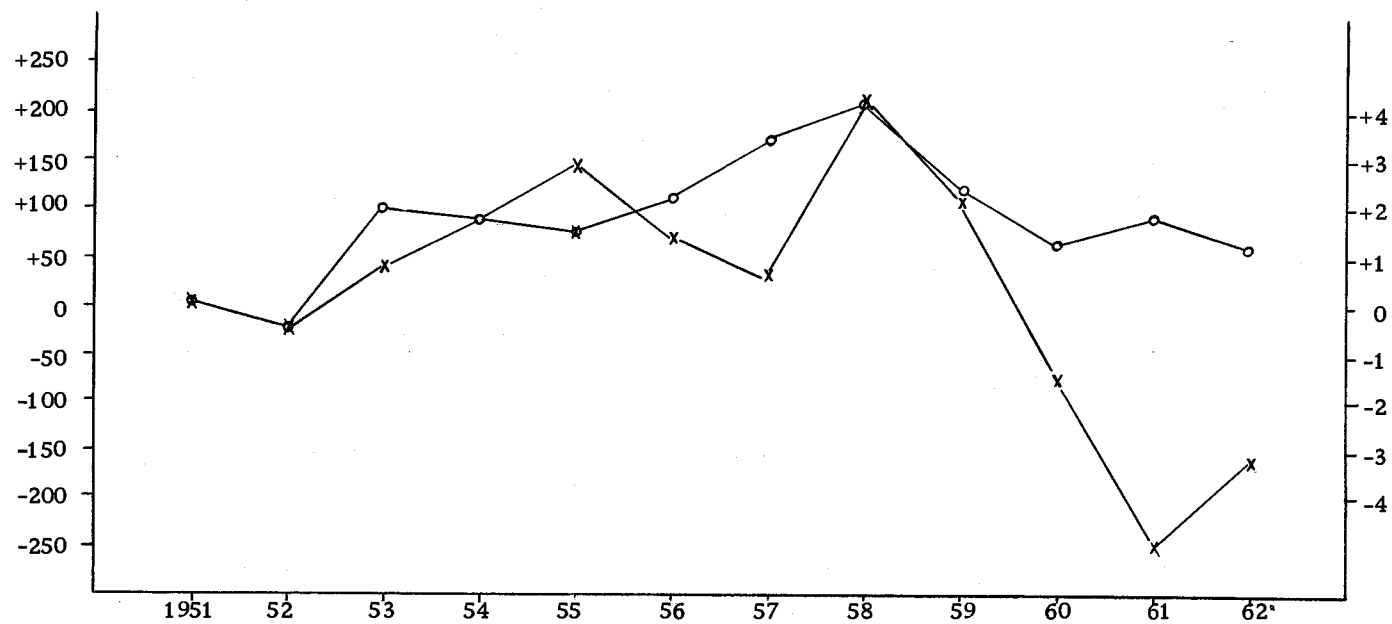


Figure 18. Environmental variations as estimated by repeat matings.

x = Economy of gain. Left hand scale in pounds feed per 100 pounds gain deviations.
 o = Score. Right hand scale in unit deviations.

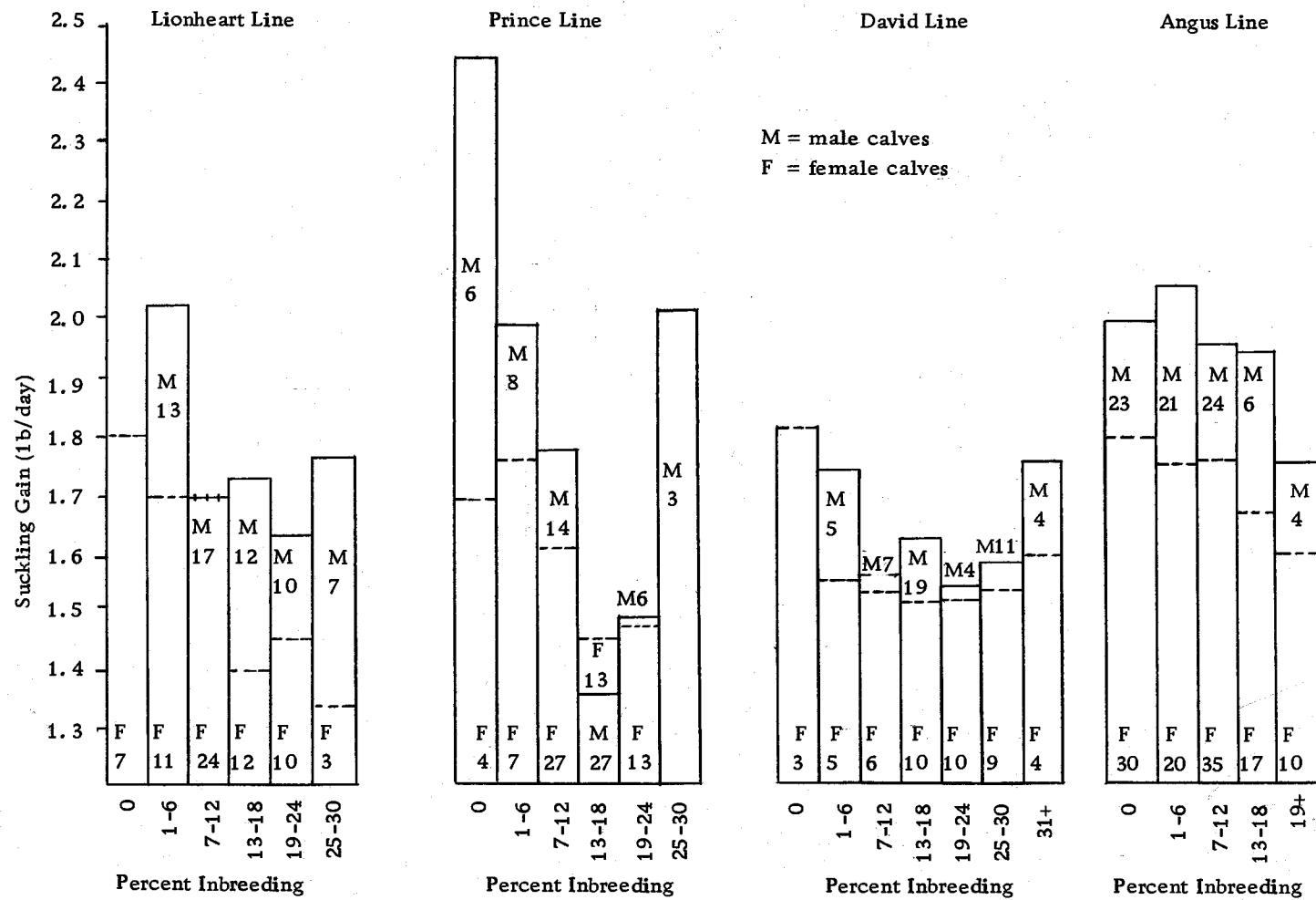


Figure 19. Suckling gain means by sexes and lines at different levels of inbreeding of calf.

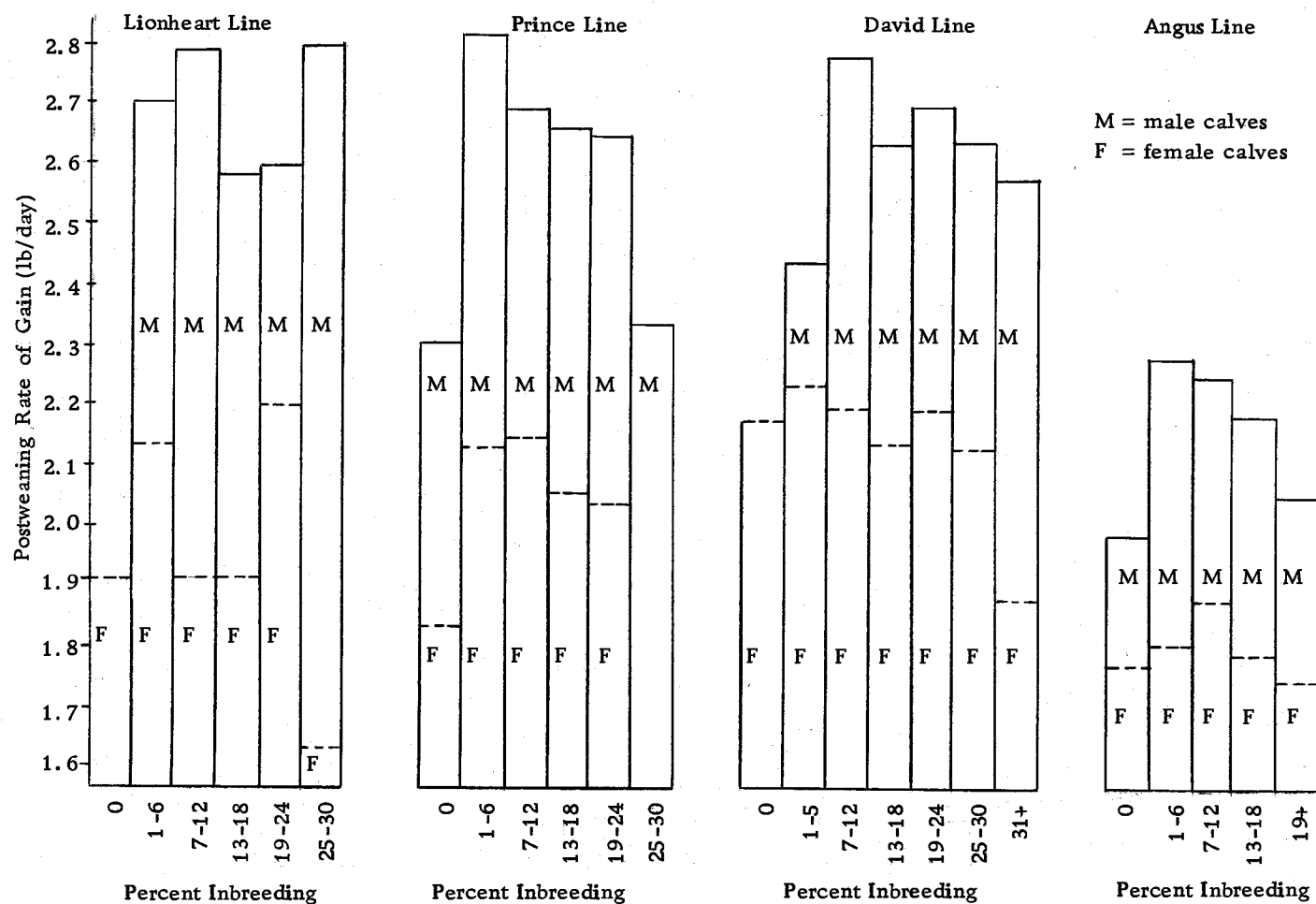


Figure 20. Postweaning rate of gain means by sexes and lines at different levels of inbreeding of calf.

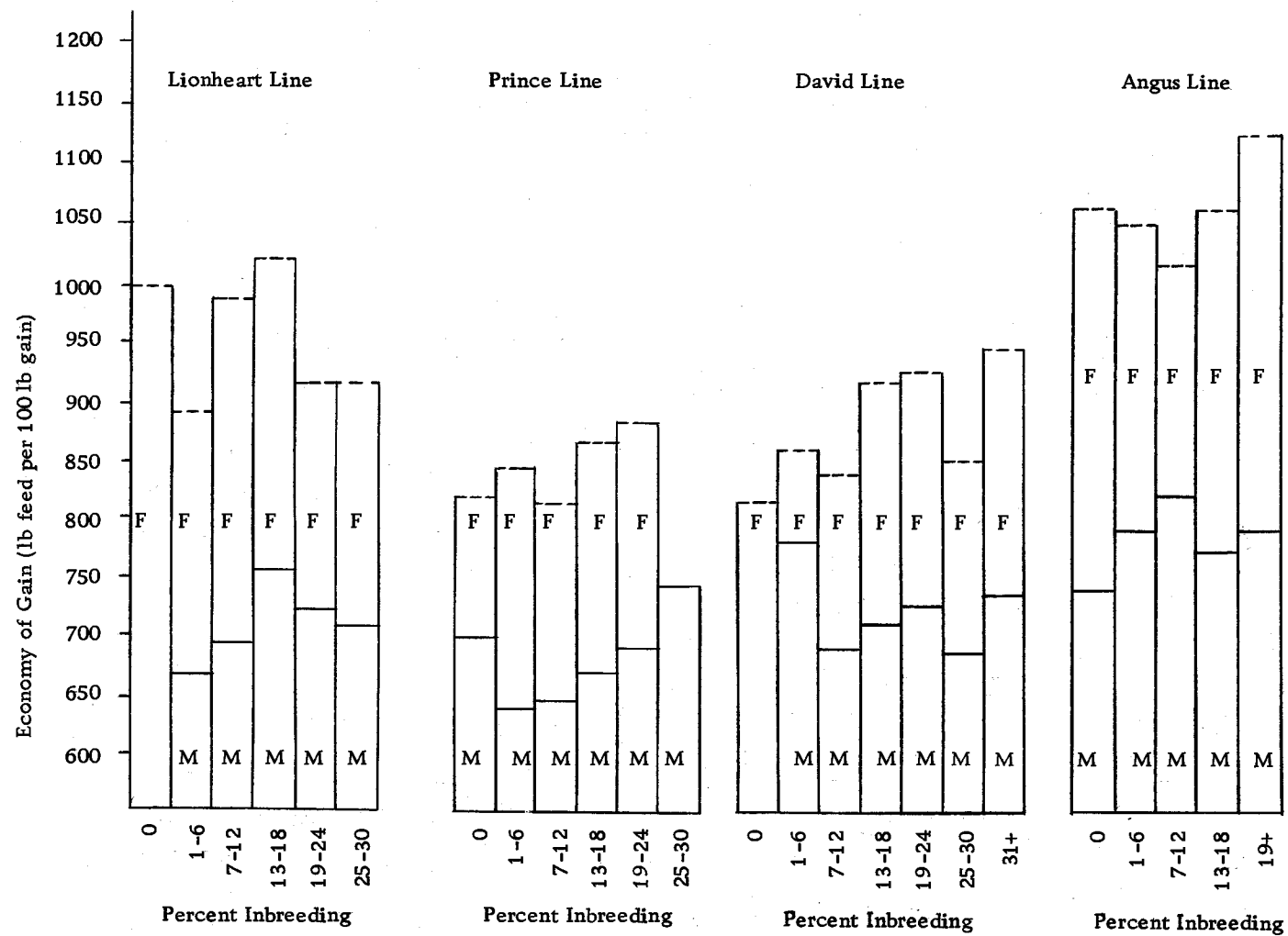


Figure 21. Economy of gain means by sexes and lines at different levels of inbreeding of calf.

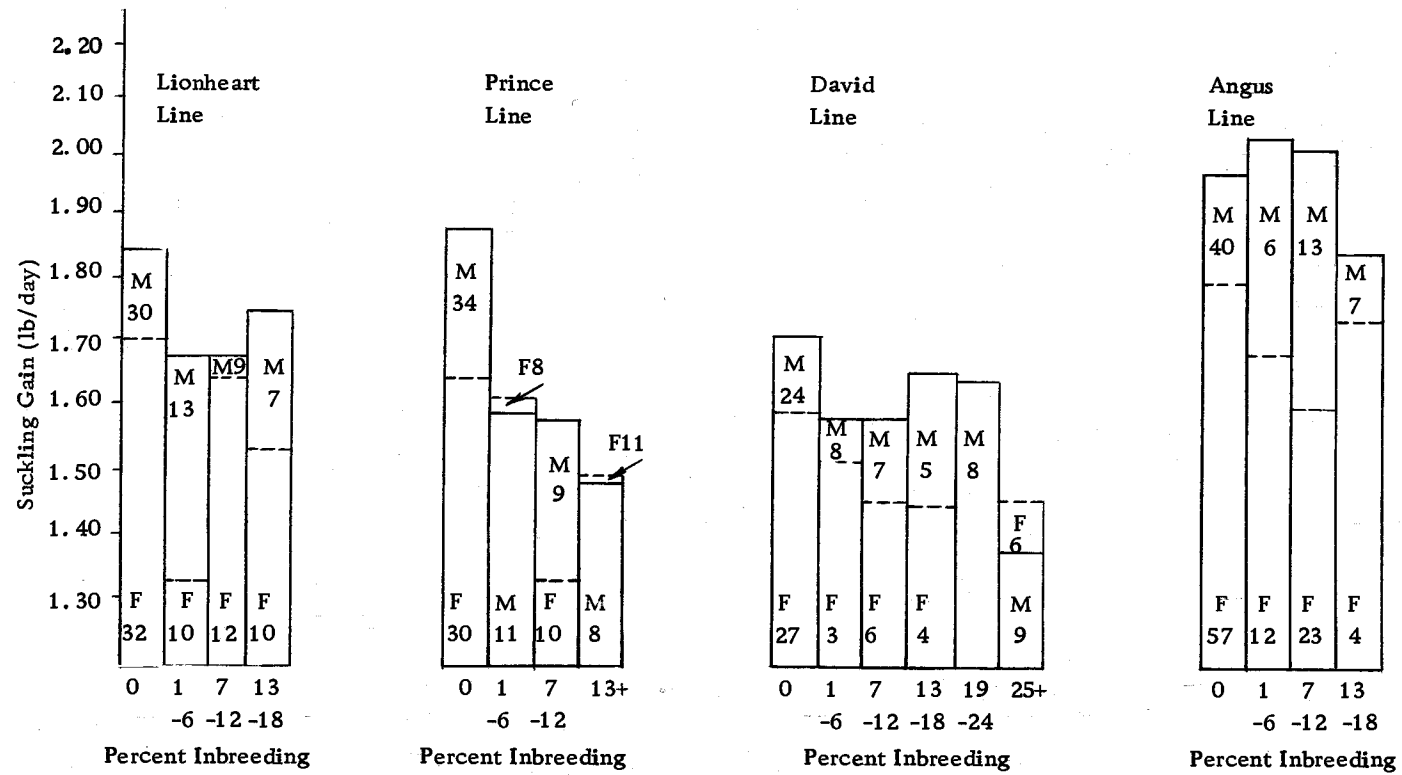


Figure 22. Suckling gain means by sexes and lines at different levels of inbreeding of dam.

Table 5. Suckling gain by lines for age of dam groups.

Age of Dam	Lionheart				Prince			
	Male	No.	Female	No.	Male	No.	Female	No.
2-3	1.76	21	1.46	19	1.59	22	1.39	15
4+	1.77	38	1.67	45	1.86	42	1.62	51

Age of Dam	David				Angus			
	Male	No.	Female	No.	Male	No.	Female	No.
2-3	1.56	16	1.41	10	1.87	16	1.62	39
4+	1.62	45	1.58	37	2.00	62	1.79	72

Table 6. Ages of dam by years and lines.

Year	Lionheart	Prince	David	Angus
1951	3.0	4.5	6.0	6.4
1952	3.4	4.6	6.6	6.3
1953	3.7	3.6	5.4	7.2
1954	4.8	4.9	4.1	7.2
1955	5.4	5.2	4.3	5.8
1956	4.5	5.3	4.5	6.2
1957	5.8	5.9	4.9	4.2
1958	5.5	6.0	5.2	4.6
1959	6.1	5.9	6.1	4.3
1960	5.8	6.0	6.4	5.0
1961	5.4	6.3	7.4	4.8
1962	5.5	6.0	7.6	6.5

Table 7. Responses of traits with inbreeding as determined by regression of traits on inbreeding of calf.

	Suckling Gain (pounds per day per percent)	Rate of Gain (pounds per day per percent)	Economy of Gain (pounds per 100 pound gain per percent)	Score ¹ units per percent
Lionheart				
Male	-0.010	-0.004	+2.69	+0.30
Female	-0.014	-0.001	+1.82	-0.15
Prince				
Male	-0.027	-0.001	+2.20	+0.03
Female	-0.009	-0.004	+5.65	-0.01
David				
Male	+0.001	+0.001	+0.17	+0.01
Female	-0.001	-0.005	+2.10	+0.01
Angus				
Male	-0.007	-0.009	+2.44	-0.05
Female	-0.006	+0.006	-0.14	-0.04

¹ Last eight years of study only, subsequent to change in scoring system.

Table 8. Responses of suckling gain with inbreeding of dam.

		Suckling Gain (pounds per day per percent increase of inbreeding of dam)
<hr/>		
Lionheart		
Male		-0.008
Female		-0.007
Prince		
Male		-0.014
Female		-0.011
David		
Male		-0.012
Female		-0.010
Angus		
Male		-0.007
Female		-0.015
<hr/>		

Table 9. Heritability estimates by intra-sire regression of offspring on dam, corrected for sex to male basis.

	Lionheart	Prince	David	Angus ¹
Suckling gain	.00	.00	.00	.00
Rate of gain	.29	.37	.42	.22
Economy of gain	.21	.46	.42	.24
Score	.16	.00	.31	.10

¹Calculated from 1954, after which the line was closed.

DISCUSSION

The lines in this study have been maintained for a longer period than the selection study has covered, but data were lacking on parents for calculations of selection differentials during the early years. Responses of traits over the years do not, therefore, show the initial improvement in traits that occurred when the breeding program was started. In effect, a segment of a curvilinear response has been examined in this study. Performance both before the selection study and subsequent to it has been shown in Figures 1 through 16. Upon examination of performance prior to and following 1951, subsequent improvement in postweaning rate of gain is most noticeable.

Yearly selection differentials, shown in Table 1, indicate that in most cases the index method of selection, placing equal emphasis on performance traits, resulted in selection for increased performance. Except for the Angus line, selection was more rigorous on the sire side, a consequence of the low number of males needed as compared to the high numbers of females for replacement purposes. This agrees with the results obtained by Flower et al. (18), but includes additional postweaning evidence. Flower calculated differentials on the dam side only for preweaning growth. In the present study, the two cases of negative selection pressure occurred on the dam side

of the matings, those cases in the Prince line.

The selection for an increase or a decrease in inbreeding was done automatically as a consequence of selection for the other traits. In each line, selection on the sire side was against inbreeding. The selection for less inbreeding of sires was not sufficient to counteract selection for increased inbreeding on the dam side in the Lionheart and David lines, but it was in the Prince line. Selection against inbreeding has occurred for both sires and dams in the Angus line. Evidence indicates that there has been low selection intensity for inbreeding of dams. Had greater intensity been possible, differentials would possibly have been against an increase in inbreeding in all cases. The cases where selection against inbreeding was noted indicates that on an index basis of selection, homozygosity has detracted from the most favorable overall performance. This is the first indication that inbreeding has an effect in some part of the growth cycle of the animals and, although it does not give an indication of the magnitude of the effect or at what stage of growth the effect occurs, it is possibly the most accurate and least confounded indication obtainable.

Selection pressure was not effective enough in most cases to prevent a decline in performance from 1951-1962. The responses shown in Table 4 indicate that general improvement in all traits has occurred only in the Angus line. Score has improved in all lines and

inbreeding has increased. The question arises as to the reality in the improvement of conformation as indicated by improvement in score. A change in scoring systems from an original 100 point system to the present 5 to 15 point system necessitated putting the former system on the latter basis for comparative purposes. It is assumed that this has been done accurately, but another factor deserves attention, that being the change of personnel doing the scoring over the years. Regardless, it is felt that selection for improvement in conformation has been effective.

Means of traits shown in Table 3 include the average inbreeding coefficients for the calves. Increased performance in the Angus line coincided with a low average inbreeding coefficient. In 1953, 54 and 55 an outside bull was brought into the Angus line and the line subsequently closed again. This accounts for the lower average inbreeding coefficients in the Angus line at the present time. In the three Hereford lines (Table 4), a greater negative response in post-weaning rate of gain for female calves than for male calves was obtained which may indicate an effect of sex linked genes becoming homozygous in the female calves as inbreeding increased, resulting in decreased performance. The opposite, however, was true in the Angus line, where the females showed a positive response compared to a negative response in the males. The Angus females were extremely low in rate of gain at the start of the breeding program,

as compared to females in the other lines. Steady improvement from the low initial base has been noted. The same relationship between the sexes was obtained for economy of gain. No clear-cut sex differences in response to selection for increased suckling gain occurred, which may indicate more environmental variation causing the differences in responses that did occur.

Environmental variations affecting performance in cattle are probably never adequately accounted for in any statistical model. Repeat matings, that is, the same bull mated to the same cow in succeeding years to obtain estimates of environmental variations between years, are only partly an estimate of environmental variations. This is due to the fact that segregation and independent assortment, which may make for sizeable differences from year to year, cannot be taken into account. This would appear to make a "year" effect determined in any other way to be even less valid for corrections in a genetic study. A large number of repeat matings yearly would result in a better estimate of environmental variations, but in the present study there were sometimes only one or two. These matings were not planned, but occurred randomly. The results presented in Figures 17 and 18 are, therefore, subject to the qualifications of gametogenesis and few numbers, but are indicative of yearly variations that occurred. The results in Figure 17 show that fluctuations from year to year were much greater in suckling gain than in

postweaning gain. The character of the curves themselves may indicate that most of the environmental variation in postweaning rate of gain was accounted for by variations occurring in suckling gain, at least for the animals involved in the repeat matings herein reported. A more adequate control of environment can be practiced under conditions of the feed test, conducted between constant weights of 500 and 800 pounds and with a similar ration yearly. The curvilinear aspect of the environmental variations as indicated in Figure 17 would make a linear correction for year effects impractical in making an estimate of genetic response to selection.

Histograms drawn in Figures 19, 20 and 21 show the means by sex of calf for suckling gain, postweaning rate of gain, and economy of gain by percentage inbreeding of the calves. These histograms can be read in conjunction with the average responses with inbreeding as shown in Table 7. Suckling gain declined with inbreeding in all cases except for David bull calves. This may be due to there being no noninbred male calves represented in the David line for comparative purposes. There was less decline in suckling gain with inbreeding in David females than in females of other lines. The means shown in Table 3 for suckling gain and inbreeding of calf should be noted, along with the responses in Table 4. Both sexes in the David line averaged lowest in suckling gain, and had the highest inbreeding coefficients, as compared with calves in the other lines.

Less increase in inbreeding occurred in the David line than in the other lines (Table 4), but the inbreeding level in the early years of the selection study was higher in this line than in the other lines. The magnitude of the responses shown in Table 5 are not meant to show that inbreeding of the calves had this much effect on performance. It has been determined by Alexander and Bogart (1) that inbreeding of calf has an effect on preweaning performance, but not on postweaning performance. This would generally coincide with the magnitude of the regression coefficients in Table 7 between suckling gain and postweaning rate of gain except for David females and Angus males, where postweaning rate of gain declined more with increased inbreeding than preweaning rate of gain. Angus male calves actually showed a positive response in preweaning performance over the 12 year period, which would account for the difference in response with inbreeding in this line.

The histograms drawn for rate of gain show that in all cases the noninbred calves, regardless of sex, performed at a lower level than inbred calves, with the tendency downward in performance subsequent to the earlier stages of inbreeding. The accumulation of desirable genes for growth rate during the initial phases of inbreeding may account for the initial increased performance, and the creation of homozygosity in some undesirable genes may account for the

subsequent decline. It might also be postulated that the heterozygous state at certain loci was the object of selection during the postweaning growing period. If this was the case, then higher levels of inbreeding would have fixed some of these loci in the homozygous state and resulted in decreased performance. Fixed epistatic genes which affect performance adversely can have the same effect.

Inbreeding of dam is considered in the case of suckling gain and the data in Figure 22 and Table 8 show that as the dams became more inbred, suckling gains of their calves declined. Brinks (5) showed that inbreeding of dam was associated with decreased suckling gain of calves, with male calves being more affected than female calves due to their greater potential growth being held back more by the decreased milk supply of inbred dams. Alexander and Bogart (1), on the other hand, found no significant decrease in suckling gain with increased inbreeding of dam, but did find a positive effect on inbreeding of dam on postweaning rate of gain. Their analysis pooled all lines and used a least squares model to arrive at effects of line, sex, year and inbreeding. An age of dam effect was not included in the model.

The data in Table 5 show that in most cases mature cows, having satisfied their own growth requirements, are able to provide a greater supply of nourishment for their calves. The ages of dams used in the lines are shown in Table 6 by years. Progressively older

cows were used in the breeding program from 1951-1962 in the Lionheart line, but male calves from this line had equally good gains from the younger cows as from the older ones. Female calves from younger dams however, gained less rapidly. Either the bull calves from the young group of cows were inherently better gainers or these cows performed exceptionally well in milk production due to their own inherent ability or the presence of a good feed supply affecting both their production and the gaining ability of the calves. Probably each factor contributed, especially since the dams used were younger and the pasture conditions were better in the early years of the selection program. Older cows were used in the Prince line in later years. The ages of the cows used in the David line were greater initially, then lower in the middle years, after which there was an increase in the age of the cows. Angus cows generally showed the same trend as that shown in the David line. Upon examination of Figures 1 through 4, it can be seen that despite an increase in age of cows used in the Lionheart line, suckling gains declined over the years. Prince cows, although increasing in age yearly, were older initially. A change in suckling gain associated with change in age of dam can best be seen from Table 5. During the years that David cows averaged older, suckling gains generally were higher as seen by comparing Figure 3 and Table 6. The same holds true for Angus calf performance, except that average performance was higher in this

line than any of the others. In the Lionheart line, the female calves have shown the most marked decline in suckling gain of calves in any of the lines, as seen in Table 4 and Figure 1, despite a general increase in age of dam. Regardless of the age factor, therefore, low selection differentials have had a strong influence on performance of the Lionheart female calves. Environmental influences should not have differentially affected these calves and the percent inbreeding of the female calves was lower than in the other Hereford lines (Table 3).

The heritability estimates given in Table 7 are based on data without corrections except for adjusting females to a male basis. There was some confounding of sires with years. Corrections were not made due to the limited number of animals involved. The figures show the difference in magnitude of estimates for highly heritable traits such as postweaning rate of gain and economy of gain and the lowly heritable traits, such as suckling gain and score. These differences in heritability estimates are substantiated in the literature by Swiger et al. (50), Taylor et al. (51), Blackwell et al. (3), and Shelby et al. (47). That environmental effects were more prominent during the preweaning period is evident from the figures on repeat matings (Figures 17 and 18).

An over-all analysis of performance in the four lines of cattle reflects the genetic background of the lines. They differed in

possibilities for heterozygosity both at the time of starting the study and as the study progressed. The Angus line was based originally on combining Missouri Barbara and Prince Sunbeam breeding after which a bull of Eileenmere breeding was introduced. They were also maintained as a two-sire line with 20 breeding females. There should be greater possibilities for genetic segregation and recombination in this line than in the three Hereford lines. The Lionheart Hereford line was established by combining English bred cattle with the cow herd at the Earls court Ranch, Lytton, British Columbia. This line was maintained largely as a one-sire herd with 15 breeding females.

There were times when two sires were used in the line. The original basis for this line was 14 heifers and a bull chosen from seven bulls on the basis of performance and progeny test. The David and Prince lines were based on a bull in each from good herds combined with a heterogeneous cow herd belonging to Oregon State. The bull used in the David line was from Fulcher breeding and the bull in the Prince line was from the John Crowe Ranch. These lines were maintained generally as one-sire lines with 15 breeding females.

There were occasions when two sires were used. In the Prince line certain genetic abnormalities occurred, and these, along with the selection program employed to eliminate the abnormalities resulted in a decline in the performance of this line during the latter part of the study. No abnormalities occurred in the Lionheart and David

lines.

The basis on which the lines were established, the numbers of males and females used in each line, and the genetic merit of the foundation material going into the lines could influence the response of the lines to inbreeding and to selection. In general the Angus line has shown a greater and a more continued improvement in all traits than the three Hereford lines. This would be expected because of a wider base and the use of a greater number of males and females in the line. The Lionheart line has performed generally at a higher level than the other two Hereford lines. The Prince line has shown a rather marked decline in performance during the latter part of the study. The decline in performance of the Prince line may be attributable to the difficulties with genetic abnormalities in this line. The general pattern for the performance levels of the traits was a marked improvement at first followed by a plateau after which there was a decline. This pattern was evident if one plotted the performance levels of the traits against time or against levels of inbreeding. One might interpret the results on the basis that selection was highly effective initially because inbreeding actually resulted in greater genetic variability. With continued inbreeding and selection a certain amount of homozygosity occurred particularly in the genetic material having an additive genetic effect. This would lead to a plateau in level of performance. Finally, in spite of selection, homozygosity

developed in genetic material showing overdominance effects and in undesirable genes having epistatic effects which resulted in a general decline in performance level of the traits.

The genetic value of the lines for combining with other material to increase production likely would be great even though there had been some decline in performance levels of traits within the lines. However, there would likely be little opportunity for marked improvement within the lines by selection. The only way to create a high state of genetic variability is to combine the lines and re-establish lines.

SUMMARY AND CONCLUSIONS

1. Selection differentials have been calculated for one Angus and three Hereford lines of cattle from 1951 to 1962. Selection was positive for performance on the sire side and usually so on the dam side, resulting in an average positive combined differential. The differentials were higher on the sire side of the matings due to the small number of sires needed; therefore, a greater selection intensity through the sires was made.

2. Selection against inbreeding on the sire side of the matings was automatically done in conjunction with selection for increased performance. Again due to low selection intensity for females, selection was for increased inbreeding on the dam side of the matings, resulting in an average small selection differential for increased inbreeding in two lines and against inbreeding in the other two.

3. Performance since the inception of the lines generally improved prior to and during initial phases of the period covered by the selection-response study. A levelling off and decline then made response to selection generally negative except for score in the three Hereford lines from 1951 to 1962. Score responded to selection positively in all lines. Inbreeding increased in all lines despite only slight selection for or against it, due to the selection placed on

the animals making up the matings having little to do with the contribution of ancestry to the inbreeding of the subsequent offspring.

Selection in the Angus line was generally reflected favorably in the response obtained, due to poorer initial performance, a broader genetic base and more animals from which to select.

4. Repeat matings gave an indication of the variability which years imposed on the selection program. More variation occurred during preweaning than postweaning growth. The trend in yearly influences was curvilinear.

5. Zero and low levels of inbreeding were associated with higher preweaning performance and low postweaning performance, with the opposite being true for higher levels of inbreeding. As the highest levels of inbreeding were approached, postweaning performance also declined as more fixation occurred.

6. Older cows produced more rapidly gaining calves during the preweaning period in all lines except the Lionheart, in which young cows had male calves gaining as well as those from older cows. The average age of dam increased yearly in the Lionheart and Prince lines. Cows used in the David line were older initially, then younger replacements were used, with older cows again making up the breeding herd in later years. Angus cows followed the same pattern. Preweaning performance of the calves showed the same trend as would be expected from the ages of the dams except in the

Lionheart line, where performance has declined, especially in female calves, despite an increase in age of dam. This is possibly due to the selection differential for suckling gain being so small in the Lionheart line.

7. Heritability estimates differentiated between the highly heritable traits, postweaning rate and economy of gain, and the lowly heritable preweaning gain and moderately heritable score. The proximity between estimates of heritability of rate of gain and economy of gain point out the close association between the two traits at the stage of the life cycle in which they were measured.

II. COMBINING ABILITIES OF LINES AND RELATIONSHIPS OF BLOOD CONSTITUENTS TO GROWTH OF INBRED AND LINECROSS CATTLE

REVIEW OF LITERATURE

Combining Abilities

Analyses of the combining abilities of inbred lines of cattle have awaited adequate knowledge of the performance of the lines themselves which involves the collection of data for several years due to the low reproductive rate and long generation interval.

Comparisons of inbred lines and crosses between them have been made by some workers and results have been interpreted on the basis of what might be expected from lines that perform at a certain level. Flower et al. (17) found no significant difference among bulls of three inbred lines as far as postweaning rate of gain was concerned. Rankings of the lines for birth weight and final weight were the same as for linecrosses, using the same inbred tester line for measurements of performance. The conclusion that line cross performance for these traits can be predicted by line performance did not hold true for weaning weight and postweaning daily gain due to inbred line differences in maternal ability and compensation for this effect. Estimates of hybrid advantage as measured by comparisons between linecrosses and the means of the parental lines included

general combining ability and specific combining ability as well as effects due to maternal differences of the inbred lines, since the effects couldn't be separated. Since an outbred control herd was not maintained, it was difficult to tell whether hybrid advantage or heterosis was greater than would be expected simply from recovery of inbreeding depression.

Damon et al. (15) used data from crossbreeding Hereford, Brahman, Angus and Brangus cattle to arrive at general and specific combining ability effects, maternal effects and sex linkage. Differences in general combining abilities showed that the effects were more important in measurements of growth rate than in grades. The more widely divergent genetic crosses yielded higher estimates than crosses of more similar genetic material. Sex linked effects did not play a major role in differences of growth rate and grade. Highly significant differences were found in maternal effects for 180-day weight and postweaning rate of gain, with opposite breeds being responsible for the differences at each growth period. Constants for weight per day of age also showed highly significant differences.

Heterotic effects on age and weight at puberty were found by Kaltenbach and Wiltbank (25) for crossbred beef heifers. Increased growth rate accounted for 66 percent of the difference in age at puberty. Koger et al. (33) found that Brahman-Shorthorn crossbreds

achieved more rapid gain than straightbreds principally by having eaten more feed than the Brahman and storing less fat than the Shorthorns.

Henderson (23, p. 352), in defining general and specific combining ability effects points out that apparent specific effects or nicking can occur because of Mendelian sampling, inaccurate estimates of the additive genetic values of the parents, and of environments affecting progeny which are different from the average environments in which the general combining abilities and maternal abilities were estimated.

Carmon (12) used four lines of mice for testing the degree of heterosis, general and specific combining abilities, and maternal effects. One line was outbred, two were slightly inbred (15 percent) and one line was highly inbred. When all possible crosses were made, the poorest performing line performed the best in crosses and the better performing line performed the worst in crosses, based on 21- and 45-day weights at both ages, but the specific combining ability effect was non-significant. Maternal effects were highly significant. The line with the poorest maternal ability for weights at both ages had the highest inbreeding coefficient of the four lines; the slightly inbred lines had the best maternal ability. Comparison of maternal effects as measured in linebreds with those in crossbreds did not indicate non-additive effects operating within

the lines. Sex linked or reciprocal effects were highly significant for weights at 21 and 45 days.

Jinks and Broadhurst (24) found in rats that males from reciprocal F_1 families did not differ more in body weight than females from reciprocal crosses or more than males from duplicate families, so that there was no evidence of sex-linked genes responsible for any part of the difference in body weight between sexes. Differences in weights from cross to cross were concluded to be due to differences in the action of the same genes in the two sexes; to sex limitation of gene action. Unlike Damon (15), who found no evidence of sex linkage in reciprocal cattle crosses after differences in maternal effects were taken into account, Stonaker (48) found genetic differences between the two sexes. This could be accounted for by the effect of the sex chromosomes either in that an active Y chromosome was coupled with selection for combining ability between the X and Y chromosomes, extra selection pressure for favored dominant and additive genes on the X as compared to the autosomes, or sex linked overdominance. Brinks, Clark and Kieffer (7) note that if increased homozygosis in females due to the two X chromosomes is responsible for inbreeding depression and heterosis, the effect might be expected to hold true throughout life. This does not happen, however, as the differential sex response occurs mainly during the weaning period in beef cattle. The differential responses

of sexes during the preweaning period could be due to the effects of both the maternal and the non-maternal environment acting differently on the two sexes.

Diallel crossing techniques vary depending on whether or not the parental inbreds or the reciprocal F_1 's, or both, are included so that four possible experimental methods are available, according to Griffing (20, p. 463). Each method necessitates a different form of analysis. When a combining ability analysis is used to determine suitable lines to combine into a new variety or line, parents are included in the analysis. Griffing (19) also notes that in terms of general combining ability of gametes, the value of a genotype in a particular cross can be measured by the deviation from the population mean. The specific combining ability effect for the genotype is the deviation from the population mean minus the general combining ability effects of the contributing genotypes. The effects can be extended to the use of lines as there is a 1:1 correspondence between inbreds and gametes. Hayman (22) states that the only circumstance in which a small diallel cross (less than ten parents) is of practical value is when the parents and crosses comprise the whole population under investigation so that parameters to be estimated are those of the restricted group of parents and crosses, their accuracy being determined by replication and control of the environment and not by the sampling theory practiced where many parents are involved.

Blood Constituents

Marshall (41, p. 282), in discussing the function of the liver in deaminating amino acids, stated that excess amino acids which are not required for tissue repair in the animal are deaminized and the nitrogenous portion converted to urea. The non-nitrogenous portion is then utilized for energy or any other function it might fulfill in metabolism. Association with growth has been the aim of investigators studying blood constituents in animals and man, with Colby et al. (14) finding that after feeding bull and heifer calves for 196 days following weaning, blood levels of urea and creatine were negatively, but not significantly associated with rate of gain. Bogart et al. (4) presented data on growing cattle that showed blood amino acid nitrogen increased between body weights of 500 and 800 pounds from 6.72 to 6.80 mg per 100 ml of blood in male calves and from 7.38 to 7.64 mg per 100 ml in female calves. The levels of amino acid nitrogen in female calves were significantly higher than in male calves as were levels of urea nitrogen. Urea also increased with body weight of the animals, ranging from 11.80 mg per 100 ml at 500 pounds to 15.46 mg per 100 ml at 800 pounds in male calves. The range in blood urea nitrogen between these same weights was 14.57 to 19.18 mg per 100 ml in female calves. Negative associations were found with growth rate for both blood amino acid nitrogen and blood urea

nitrogen. These relationships indicate that faster gaining animals resemble younger animals, withdrawing amino acids from the blood for growth, leaving less for deaminization by the liver into urea. Slower gaining animals do not withdraw amino acids as efficiently with the result that urea is formed from the excess. No significant differences were found in blood creatinine for sex, line, or breed. MacDonald, Krueger and Bogart (39) found that normal calves exhibited wide ranges in the concentration of the blood constituents, with blood urea nitrogen decreasing with an increase in weight from 500 to 800 pounds in Hereford and Angus males and females. Amino acid nitrogen increased in Hereford females and Angus males, but was unchanged in Hereford males and Angus females. Females had a higher concentration of amino acid and urea than males at both weights. Creatinine decreased with increases in weight in Angus males and females and increased in Hereford females. No change was observed in Hereford males. Price et al. (44) found an inverse association between amino acid nitrogen in the blood at 800 pounds with rate of gain and feed consumption. Urea at 500 pounds was inversely related to subsequent rate of gain. There was no association between blood creatinine levels at either 500 or 800 pounds and rate of gain. Variation in preweaning conditions were presumed to cause different associations at 500 and 800 pounds. At 800 pounds, lack of a significant association of urea nitrogen with performance

was thought to be due to an increased urinary clearance of urea at this weight or a greater rate of urea formation in the more efficient calves as this weight was approached.

In the ruminant, deaminization occurs in the rumen as well as in the liver, with ammonia formed from the reduction of nitrates and nitrites, as indicated by McDonald (38). The ammonia can be utilized for the growth of rumen microorganisms, but can also be absorbed from the rumen and may in part return to the rumen after passage through the liver by secretion as urea in the saliva, or in part be excreted in the urine as urea. Warner (52, p. 749) states that the concentration of free amino acids in the rumen is at all times low, but the breakdown products of the amino acids, ammonia and volatile fatty acids are found in high concentration when adequate protein is fed. Pearson and Smith (43, p. 153-154) states that sufficient urease activity in the rumen exists to convert all the urea likely to be found there, and that it must be generated by some of the microorganisms of the paunch because of little urease activity in the diet and no secretion into the rumen other than saliva. Lewis (36) also believes that part of the urea produced by the ammonia absorbed from the rumen returns to it via the saliva. Ammonia is not found in peripheral blood so it must go from the ruminal veins via the portal vein to the liver for conversion to urea. Urea levels in sheep seemed to depend largely on the diet.

Looper, Stallcup and Reed (37) stated that the conversion of nitrogen compounds in ruminants is influenced by the conversion of dietary protein to microbial protein, the release of ammonia from dietary protein and nonprotein nitrogen sources and the subsequent absorption of part of the ammonia through the rumen wall, and the synthesis of microbial protein from non-protein nitrogen sources.

Kugelmass (34, p. 30-61) states that amino acids are utilized by the liver for formation of most plasma proteins or are transported to tissues for temporary storage or synthesis of tissue proteins. The rate of amino acid depletion depends on the degree of depletion of plasma and tissue proteins, the pattern of amino acid mixtures for protein formation (human) and the adequacy of hormonal control of protein metabolism. All blood amino acids, originating from absorption from the small intestine or from disintegrated tissue proteins contribute to the common metabolic pool. Protein anabolism is stimulated by growth hormone, insulin, testosterone, and moderate amounts of thyroid stimulating hormone. Protein catabolism is stimulated by adrenocortical and excessive thyroid hormones.

Blood creatinine in the human is the most constant nitrogenous constituent of the blood, according to Kugelmass (34, p. 75), and is formed as the waste product of creatine with loss of phosphoric acid. Buchanan and Hastings (10) state that the rate of creatine formation from dietary and tissue sources occurs at the same rate as

its conversion to creatinine. Brody (8, p. 353) concludes that urea and creatinine represent extremes in the extent to which they are influenced by dietary protein, with creatinine the least affected. He also stated that urinary creatinine reflects the mass of supporting muscle in the body. Since the quantity of blood varies with body weight linearly, the level of creatinine in the blood should reflect the amount being produced, as none is reabsorbed in the kidney.

Marshall (41, p. 282) indicated that creatinine in the urine is a measure of tissue breakdown as it remains approximately the same on low or high protein diets. Miller and Blyth (42) used creatinine excretion levels of human subjects as a measure of lean body mass, finding a correlation coefficient of .826 (no numbers quoted). A possible error inherent in using creatinine levels in predicting lean body mass is that there is no general agreement as to the size of the body component that is responsible for the excretion of creatinine, according to this author. Wurthier and Stratton (55) calculated the association between creatinine levels of the blood and lean composition of the carcass as measured in the boned 9, 10, and 11th rib cut. Within age groups, only 31 percent of the variation of lean in the cuts could be accounted for by differences in serum creatinine levels. The correlation coefficient ($r = .55$) was highly significant. Williams (53) found that creatinine was negatively associated with rate of gain in calves at 500 and 700 pounds and concluded that if creatinine is

considered a measure of muscle activity, the less activity the greater the rate of gain. Age had an effect on creatinine, as animals became muscularly more active with age.

MATERIALS AND METHODS

In 1962, the first of four planned diallel crosses was made between the Lionheart, Prince and David Hereford lines, allowing for inbred and reciprocal matings as follows:

		Line of Dams		
		1	2	3
Line of Sires	1	1x1	1x2	1x3
	2	2x1	2x2	2x3
	3	3x1	3x2	3x3

where 1, 2 and 3 stand for the Lionheart, Prince and David lines, respectively.

The numbers of animals available for the present study are shown in Table 10 by sex and breeding according to the diallel crossing scheme.

Table 10. Numbers of animals by sex and cross.

		Dams			Total	
		1	2	3	MM	FF
Sires	M 1	4	6	3	13	
	F	2	3	4		9
	M 2	1	1	3	5	
	F	3	2	1		6
	M 3	6	4	1	11	
	F	0	3	2		5
Total MM		11	11	7	29	
Total FF		5	8	7		20

Performance Records

Data were obtained on the first diallel cross starting with the birth weights of the calves in the spring of 1963. Bull calves were left intact. Weights during the preweaning period were obtained at two-week intervals and calves were weaned when they reached 425 pounds (bulls) or 375 pounds (heifers). All calves not reaching these weights by the second week in November were weaned regardless of weight. Calves were allowed an adjustment period in the barn before going on feed test, with the heifer calves starting the test at 400 pounds and the bulls starting at 450 pounds. The feed consisted mainly of a pelleted high roughage ration, two thirds of which was composed of equal parts of coarsely chopped alfalfa and grass hay, and one third of concentrate feeds. This was fed individually to the animals twice daily and the weights recorded of the amounts given and weighed back. Some animals received varying quantities of loose hay which was not accounted for during the test period. During the feed test all calves were weighed weekly. Heifer calves completed the test at 750 pounds and bull calves at 800 pounds. The calves were scored by a committee of three at these weights. Postweaning rate of gain and economy of gain were computed on each animal.

Blood Analyses

Blood samples were obtained from all calves at 450 and 750 pounds prior to the morning feeding from the right jugular vein by means of stainless steel bleeding needles. Blood was collected in pyrex tubes using dried neutral potassium oxalate at the rate of one mg per ml of blood (21, p. 541). Filtrates were obtained subsequent to collection (21, p. 543-544) and then stored in the refrigerator with toluene preservative until the evening.

Blood creatinine was determined by the Jaffé reaction following the method of Folin and Wu (21, p. 555-556) using the alkaline-free filtrate with alkaline picrate to form a red color. The color was compared to a standard in a Bausch and Lomb Spectronic 20 colorimeter using a square cuvette.

Urea nitrogen was determined colorimetrically by the method of Karr (21, p. 554) using urease to convert the urea to ammonium carbonate and gum ghatti as a stabilizing agent to maintain a clear solution of the nesslerized ammonium carbonate (ammonium-mercuric iodide compound).

Amino acid nitrogen was determined colorimetrically by the method of Danielson (21, p. 565-566). Color was developed by the action between amino acids and β -naphthoquinone-4-sulfonic acid in alkaline solution provided by sodium tetraborate.

All blood constituents were calculated on the basis of mg per 100 ml blood.

Statistical Analyses

Means by sexes were obtained for all performance and blood constituent data. These data were then adjusted to a male basis multiplicatively using the ratio of male:female means. Means were then plotted by age of dam groups and adjusted to a six-year age of dam basis arithmetically because of the curvilinearity with age.

The data were grouped according to the linecross or inbred group they represented, corresponding to the diallel crossing scheme. The nine cells in the diallel contained unequal numbers of animals, as seen in Table 10, so group totals were adjusted on the basis of the cell containing the most animals, nine, the Lionheart x Prince cross. All degrees of freedom in the statistical analyses of means were based on actual numbers.

A factorial analysis was carried out for each performance trait and blood constituent at 450 and 750 pounds to determine whether a difference existed due to line of sire, line of dam, sire x dam interaction, or genotype. The error mean square was used to test all differences as these crosses represented the population about which inferences were to be drawn. If a difference did not exist, further analysis was not carried out on the data. In terms of

combining ability, if a difference in genotypes (represented by a particular linecross or inbred) did not exist, there was no basis for a combining ability analysis (20, p. 468). If a difference existed due to genotypes, interactions, line of sire or line of dam, appropriate analyses were made as follows:

1. General combining ability analyses were made if genotypic or interaction differences existed. Data were analyzed on the basis of how a certain line performed regardless of whether used on the sire or the dam side of the mating, excluding inbreds, so that for line 1 (Lionheart) for example, data included $(1 \times 2) + (1 \times 3) + (2 \times 1) + (3 \times 1)$ crosses.

2. Specific combining ability analyses were made if any differences existed due to genotype or interaction. The three specific crosses analyzed were (1×2) plus its reciprocal (2×1) , $(2 \times 3) + (3 \times 2)$, and $(3 \times 1) + (1 \times 3)$.

3. If differences due to line of dam were found in the factorial analysis, maternal differences including all linecrosses and inbreds, linecrosses only, and reciprocal crosses, were analyzed.

4. When differences due to the above causes were found in the factorial analyses, an analysis was made of differences between linecrosses and inbreds.

5. Whenever differences were found in the combining ability and maternal analysis, single degrees of freedom were computed for specific line, linecross or maternal differences.

6. Total and within subclass correlation coefficients were computed for each trait.

RESULTS

Unadjusted means by sexes are shown in Table 11 for all traits analyzed in this study. Factors used to adjust all traits to a male basis are also shown in Table 11. Figures 23-25 contain graphs of the performance traits and blood constituents by ages of dam. In Table 12, factors are shown which were used to adjust all the data to a six-year-age-of-dam basis. Performance, as measured by weights, gains and scores, was higher in bull calves than in heifer calves. Bull calves had a higher blood creatinine content than heifer calves at both 450 and 750 pounds, but there was less creatinine in the blood of both sexes at 750 than at 450 pounds. Blood urea nitrogen was higher in heifer calves than in the bull calves at both weights, and there was more urea in the blood of both sexes at 750 pounds than at 450 pounds. Amino acid nitrogen was also higher in the blood of heifer calves than in that of bull calves. The amount of amino acid nitrogen at 750 pounds was less than that at 450 pounds in both sexes.

Adjusted means for all performance traits and blood constituents are shown in Table 13 according to the particular linecross or inbred group they represent.

Sources of variation, degrees of freedom and mean squares are shown in Table 14 and 15 for the factorial analyses of each of the traits whose means are shown in Table 13. Among the performance

traits, no significant differences were found in birth weights and suckling gains due to any of the sources of variation. Highly significant differences were found in postweaning rate of gain, economy of gain and score due to different genotypes and sire x dam interactions. In addition, a highly significant difference existed between scores due to variation between lines of dam. Analyses of the blood constituents revealed significant differences in creatinine content of the blood at 450 pounds due to variation between lines of dam. Differences in blood urea and amino acid nitrogen at 450 pounds were not significant. At 750 pounds, a significant difference in blood creatinine due to genotypes and lines of sire was noted. No difference in blood urea nitrogen was found at this weight, but the amino acid nitrogen content of the blood was significantly different among calves due to variation between lines of sire.

The results of the combining-ability analyses and analyses of differences between inbreds and linecrosses for postweaning rate of gain, economy of gain, score, and creatinine at 750 pounds are shown in Table 20. Significant differences in general and specific combining abilities were found between lines for postweaning rate of gain and economy of gain. Differences in score at 800 pounds were significant due to differences in specific combining abilities of the lines. Economy of gain, score at 800 pounds and blood creatinine were all significantly different due to variation between inbred and

linecross calves.

Results of the analyses of maternal differences are shown in Table 21. Only when all linecross and inbred calves were included in the analysis was there a significant difference due to line of dam for both blood creatinine at 450 pounds and score at 800 pounds.

Differences in general and specific combining ability and maternal or sire differences were further analyzed by individual degrees of freedom. Tables 16-19 should be consulted for the magnitude of the differences. A highly significant difference in general combining ability was found between the Lionheart and Prince lines for postweaning rate of gain. The Lionheart line was the best general combining line, followed by the David and Prince lines, in that order. In the analysis of specific combining ability, highly significant differences were found between the most rapid gainers, calves of the Lionheart x David cross, and calves of the Lionheart x Prince and Prince x David crosses, which followed in that order in performance. No significant difference was found between calves of the Lionheart x Prince and Prince x David crosses. The David and Lionheart lines were the best general combiners for economy of gain, both having calves significantly higher in performance than calves resulting from matings involving the Prince line. Significant differences in the specific combining ability analysis for feed economy were identical to that for rate of gain. Differences were

significant for score at 800 pounds in the specific combining ability analysis. Lionheart x Prince calves scored highest, followed by the Lionheart x David and Prince x David calves, which had comparable scores. The single degree of freedom analysis showed that the maternal difference of the Lionheart vs. the David and Prince lines was highly significant, with the Lionheart dams having both inbred and linecross calves which scored highest. Calves from the David and Prince cows were approximately equal in score. Highly significant maternal differences existed for blood creatinine at 450 pounds due to the low creatinine content in the blood of calves born to Lionheart dams vs. that of calves born to David dams. Sire differences were highly significant at 750 pounds for blood creatinine between calves sired by the Lionheart line, which were highest in blood creatinine, and calves sired by the David line, which were lowest in blood creatinine. Although not significant, the maternal difference at this weight corresponds to the sire difference, reversing the significant maternal difference at 450 pounds. The analysis of sire differences in blood amino acid nitrogen of calves at 750 pounds by single degrees of freedom showed that when all inbred and linecross calves were included, calves sired by the Lionheart and David bulls were significantly higher in blood amino acid nitrogen than Prince sired calves. Although not significant, the opposite was true for maternal differences at this weight.

The coefficients of correlation computed on a total and within subclass basis are presented in Table 22. None of the correlation coefficients involving birth weight were significant. A highly significant positive association existed between suckling gain and the amino acid content of the blood at 450 pounds. Score at 800 pounds was also highly associated with suckling gain. Postweaning rate of gain was negatively, but not significantly associated with suckling gain. Postweaning rate of gain and economy of gain were highly associated, the negative association meaning that fewer pounds of feed were required per 100 pounds gain by the faster gaining animals. The coefficient of determination (r^2) of rate of gain and feed per unit of gain was 0.77. No other correlation coefficients between rate of gain and performance traits or blood constituents were found to be significant. A highly significant correlation coefficient resulted from the positive association between amino acid nitrogen and creatinine in the blood at 450 pounds.

Table 11. Unadjusted means of performance traits and blood constituents by sex of calf, with adjustment factors for sex.

	Bull Calves	Heifer Calves	Sex Adjustment
Birth weight (pounds)	79	72	♀ x 1.09
Suckling gain (pounds/day)	1.71	1.69	♀ x 1.01
Postweaning rate of gain (pounds/day)	2.88	2.18	♀ x 1.32
Economy of gain (pounds feed/100 pounds gain)	584	730	♀ x .80
Score at 800 pounds ¹ (units)	12.10	11.97	♀ x 1.01
Blood creatinine (mg/100 ml blood)			
450 pounds	1.43	1.41	♀ x 1.01
750 pounds	1.41	1.40	♀ x 1.01
Blood urea nitrogen (mg/100 ml blood)			
450 pounds	15.76	16.91	♀ x .93
750 pounds	15.88	17.16	♀ x .92
Blood amino acid nitrogen (mg/100 ml blood)			
450 pounds	6.72	6.90	♀ x .97
750 pounds	6.39	6.88	♀ x .93

¹Based on a scale of 5-15, with 5 being low.

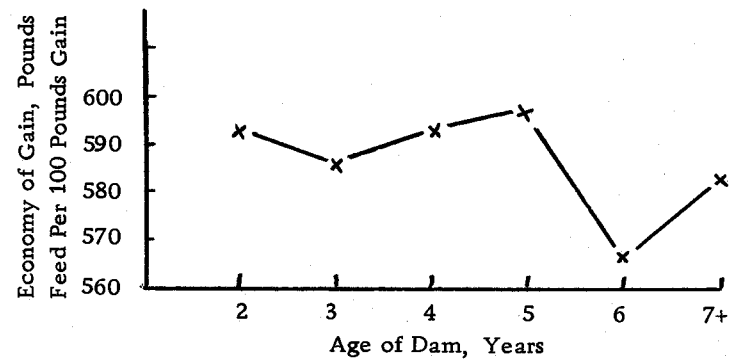
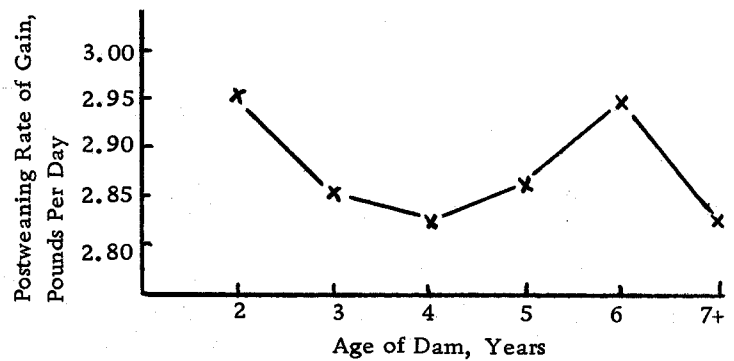
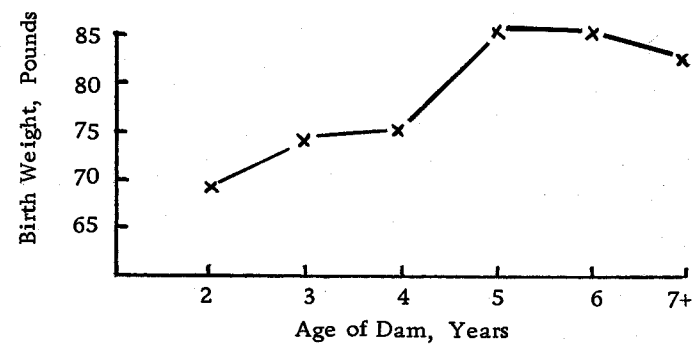
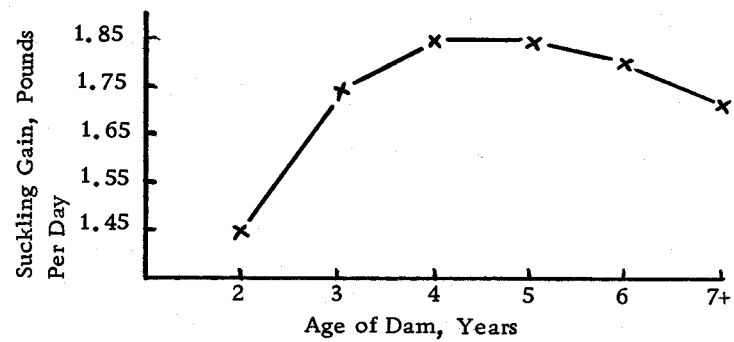


Figure 23. Performance traits by different ages of dam.

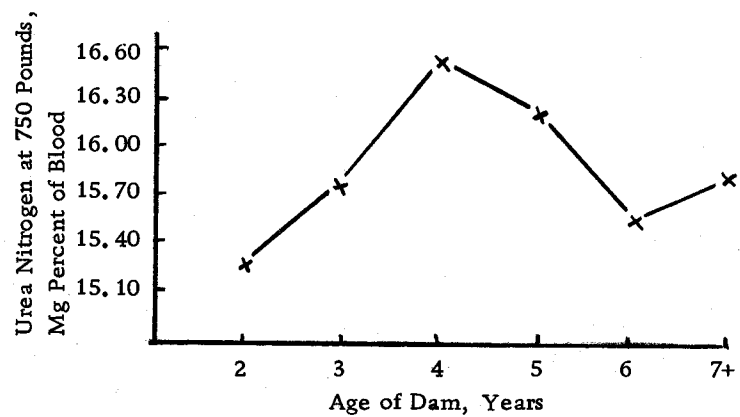
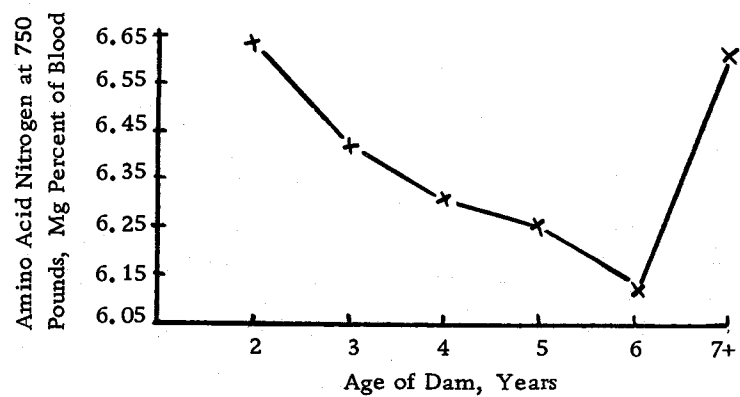
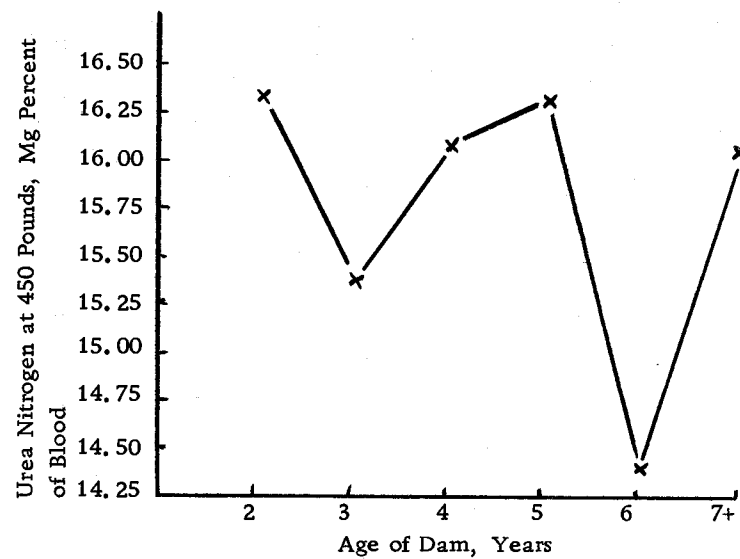
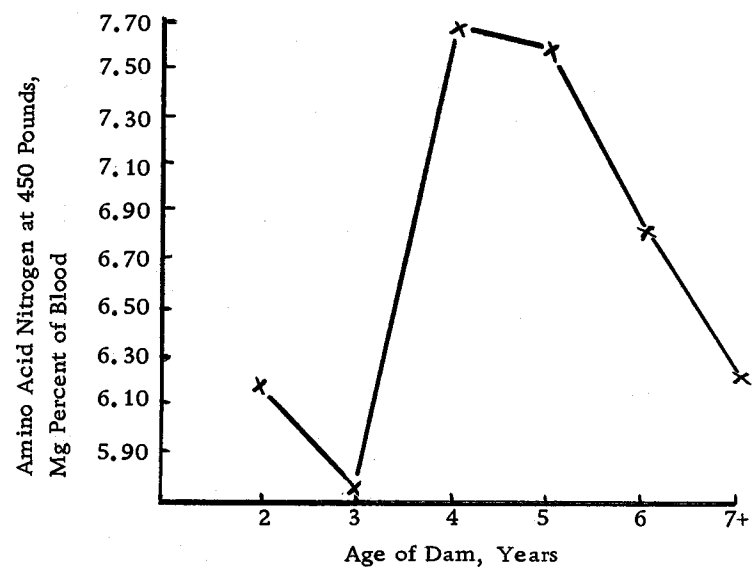


Figure 24. Blood constituents by different ages of dam.

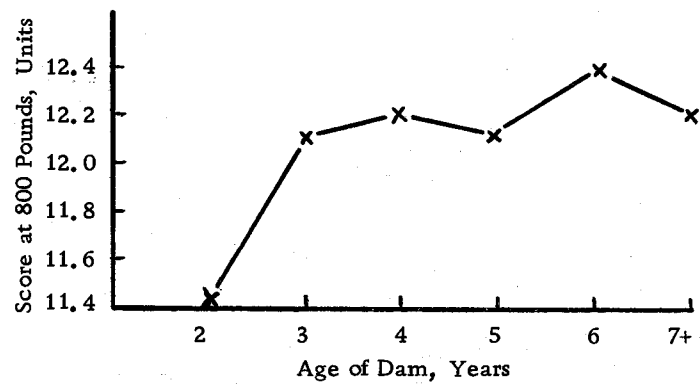
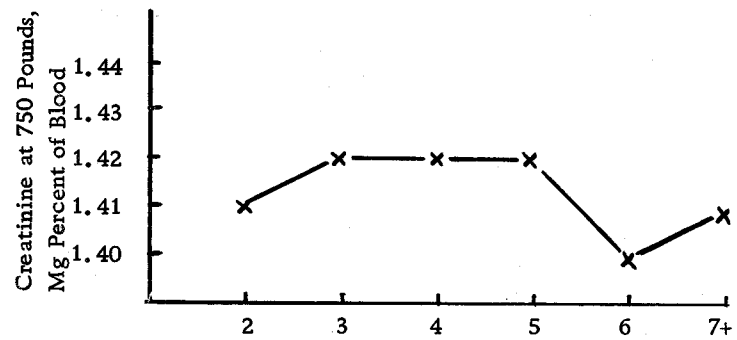
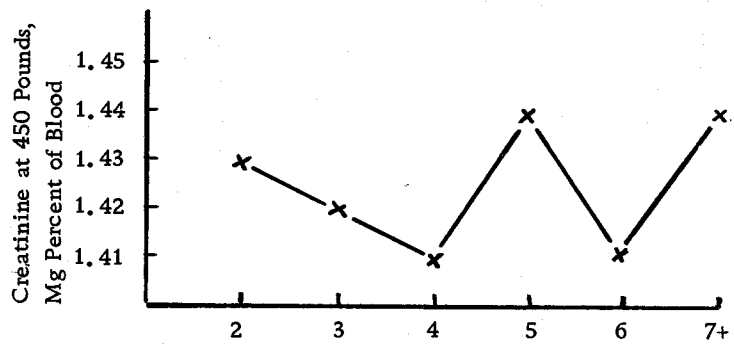


Figure 25. Blood constituents and score by different ages of dam.

Table 12. Factors used to adjust data to a six year age of dam basis.

	Age of Dam					
	2	3	4	5	6	7+
Birth weight	+16	+11	+10	-1	-	+3
Suckling gain	+0.34	+0.05	-0.04	-0.04	-	+0.09
Postweaning rate of gain	-0.01	+0.09	+0.12	+0.08	-	+0.12
Economy of gain	-27	-20	-26	-31	-	-9
Score at 800 pounds	+1.00	+0.30	+0.20	+0.30	-	+0.20
Blood Creatinine						
450 pounds	-0.02	-0.01	-	-0.03	-	-0.03
750 pounds	-0.01	-0.02	-0.02	-0.02	-	-0.01
Blood urea nitrogen						
450 pounds	-1.89	-0.96	-1.68	-1.91	-	-1.56
750 pounds	+0.26	-0.23	-1.05	-0.70	-	-0.22
Blood amino acid nitrogen						
450 pounds	+0.65	+1.10	-0.85	-0.78	-	+0.59
750 pounds	-0.54	-0.32	-0.20	-0.15	-	-0.49

Table 13. Adjusted means of inbred and linecross calves according to the diallel matings.

	Line or Linecross								
	(1x1)	(1x2)	(1x3)	(2x1)	(2x2)	(2x3)	(3x1)	(3x2)	(3x3)
Birth weight	89	85	84	91	89	81	83	81	85
Suckling gain	1.81	1.78	1.66	2.03	1.67	1.74	1.73	1.88	1.64
Postweaning rate of gain	2.88	2.86	3.15	3.02	3.04	2.79	3.20	2.83	2.67
Economy of gain	588	600	535	558	562	584	527	568	618
Score at 800 pounds	12.9	12.6	12.3	13.1	10.9	12.2	12.4	12.3	11.9
Creatinine, 450 pounds	1.40	1.41	1.44	1.38	1.42	1.43	1.38	1.42	1.43
Urea nitrogen, 450 pounds	13.98	14.51	14.46	13.70	15.08	14.39	14.87	13.71	16.59
Amino acid nitrogen, 450 pounds	6.72	6.60	6.71	6.56	7.54	7.10	7.02	6.89	6.55
Creatinine, 750 pounds	1.42	1.41	1.42	1.41	1.39	1.40	1.40	1.40	1.31
Urea nitrogen, 750 pounds	15.74	15.12	16.21	15.61	15.72	14.89	15.79	15.63	14.77
Amino acid nitrogen, 750 pounds	6.30	6.09	6.24	5.74	5.83	5.58	5.93	6.52	6.16

Table 14. Analysis of variance of performance traits.

Source of Variation	D. F.	Mean Squares				
		Birth Weight	Suckling Gain	Postweaning Rate of Gain	Economy of Gain	Score at 800 Pounds
Line of sire	2	108.33	0.035	0.030	256	2.11
Line of dam	2	129.00	0.205	0.195	3656	5.18**
S x D	4	109.72	0.152	0.448**	13854**	3.56**
Genotype	8	114.19	0.136	0.280**	7905**	3.61**
Error	32	75.79	0.099	0.076	1954	0.65
Total	48					

**Significant at $P < .01$.

Table 15. Analysis of variance of blood constituents.

Source of Variation	D.F.	Mean Squares					
		Creatinine at 450 Pounds	Urea at 450 Pounds	Amino Acid Nitrogen at 450 Pounds	Creatinine at 750 Pounds	Urea at 750 Pounds	Amino Acid Nitrogen at 750 Pounds
Line of sire	2	0.005	4.50	1.05	0.015*	0.74	2.18*
Line of dam	2	0.015*	6.75	0.48	0.005	1.20	0.22
S x D	4	---	8.59	1.12	0.010	3.02	0.42
Genotype	8	0.005	7.12	0.95	0.010*	1.99	0.81
Error	32	0.004	3.58	2.56	0.004	1.99	0.64
Total	48						

*Significant at $P < .05$.

Table 16. Performance means by combining ability and inbred vs. linecrosses.

	Birth Weight	Suckling Gain	Postweaning Rate of Gain	Economy of Gain	Score
General combining ability					
Line 1	86	1.80	3.06	555	12.6
Line 2	84	1.86	2.88	578	12.6
Line 3	82	1.75	2.99	553	12.3
Specific combining ability					
(1x2)	88	1.90	2.94	579	12.9
(1x3)	83	1.70	3.18	531	12.3
(2x3)	81	1.81	2.81	576	12.3
All inbred calves	88	1.71	2.86	589	11.9
All linecross calves	84	1.80	2.98	562	12.5

Table 17. Blood constituent means by combining ability and inbred vs. linecrosses.

	450 Pounds			750 Pounds		
	Creatinine	Urea N	Amino Acid N	Creatinine	Urea N	Amino Acid N
General combining ability						
Line 1	1.40	14.38	6.72	1.41	15.68	5.60
Line 2	1.41	14.08	6.78	1.40	15.31	5.98
Line 3	1.42	14.36	6.93	1.40	15.63	6.07
Specific combining ability						
(1x2)	1.39	14.10	6.58	1.41	15.37	5.91
(1x3)	1.41	14.66	6.86	1.41	16.00	6.08
(2x3)	1.43	14.05	6.99	1.39	15.26	6.05
All inbred calves	1.42	15.22	6.94	1.37	15.41	6.10
All linecross calves	1.41	14.27	6.81	1.40	15.54	6.02

Table 18. Performance means by line of sire and line of dam.

		Birth Weight	Suckling Gain	Postweaning Rate of Gain	Economy of Gain	Score
Line of sire, all inbred and linecross calves	1	86	1.75	2.96	574	12.6
	2	87	1.81	2.95	568	12.1
	3	83	1.75	2.90	571	12.2
Line of sire, all linecross calves	1	84	1.72	3.01	567	12.5
	2	86	1.88	2.90	571	12.6
	3	82	1.80	3.02	547	12.4
Line of dam, all inbred and linecross calves	1	88	1.85	3.03	558	12.8
	2	85	1.78	2.91	577	12.0
	3	83	1.68	2.87	579	12.1
Line of dam, all linecross calves	1	86	1.88	3.11	542	12.7
	2	87	1.83	2.85	584	12.5
	3	83	1.70	2.97	559	12.2

Table 19. Blood constituent means by line of sire and line of dam.

		450 Pounds			750 Pounds		
		Creatinine	Urea N	Amino Acid N	Creatinine	Urea N	Amino Acid N
Line of sire, all inbred and linecross calves	1	1.42	14.32	6.67	1.42	15.69	6.21
	2	1.41	14.39	7.06	1.40	15.41	5.72
	3	1.41	15.06	6.82	1.37	15.40	6.20
Line of sire, all linecross calves	1	1.42	14.48	6.65	1.41	15.67	6.16
	2	1.40	14.04	6.83	1.40	15.25	5.66
	3	1.40	14.29	6.96	1.40	15.71	6.23
Line of dam, all inbred and linecross calves	1	1.39	14.18	6.77	1.41	15.71	5.99
	2	1.42	14.43	7.01	1.40	15.49	6.15
	3	1.43	15.15	6.78	1.37	15.29	5.99
Line of dam, all linecross calves	1	1.38	14.28	6.79	1.40	15.70	5.83
	2	1.42	14.11	6.74	1.40	15.38	6.30
	3	1.44	14.42	6.90	1.41	15.55	5.91

Table 20. Analyses of variance of differences due to general and specific combining ability and due to inbred vs. linecross performance.

Source of Variation	D. F.	Mean Squares			
		Postweaning Rate of Gain	Economy of Gain	Score at 800 Pounds	Creatinine, 750 Pounds
General combining ability	2	0.31*	6555*	0.99	--
Error	71	0.08	1966	0.49	--
Total	73				
Specific combining ability	2	0.62**	13110**	1.97	0.00075
Error	34	0.06	1472	0.42	0.00250
Total	36				
Inbreds vs. linecrosses	1	0.23	13612*	6.32*	0.02000*
Error	47	0.09	2386	0.92	0.00383
Total	48				

*Significant at $P < .05$.

**Significant at $P < .01$.

Table 21. Analyses of variance of differences due to variation among lines of dam.

Source of Variation	D. F.	Mean Squares	
		Blood Creatinine at 450 Pounds	Score at 800 Pounds
Dams of all linecross and inbred calves	2	0.015*	5.16**
Error	46	0.003	0.86
Total	48		
Dams of all linecross calves	2	0.005	1.15
Error	25	0.004	0.64
Total	27		
Reciprocal crosses	5	0.006	0.98
Error	31	0.003	0.43
Total	36		

* Significant at $P < .05$.

**Significant at $P < .01$.

Table 22. Correlation coefficients between certain performance traits and blood constituents.

		Suckling Gain	Postweaning Rate of Gain	Economy of Gain	Score	Amino Acid N 450 Pounds	Amino Acid N 750 Pounds	Urea N 450 Pounds	Urea N 750 Pounds	Creatinine 450 Pounds	Creatinine 750 Pounds
Birth weight	(w) ¹	+.07	-.01	+.06	-.04						
	(t)	+.15	+.01	+.11	+.01						
Suckling gain	(w)		-.25	+.20	+.45**	+.34*		-.04		+.10	
	(t)		-.23	+.17	+.46**	+.28*		-.15		-.01	
Postweaning rate of gain	(w)			-.87**	+.13	-.06	+.03	-.17	+.08	+.22	+.14
	(t)			-.88**	+.06	-.02	-.02	-.15	+.20	+.10	+.21
Economy of gain	(w)				-.22	+.02	+.04	+.12	-.23	-.05	-.12
	(t)				-.10	-.02	+.05	+.10	-.32*	-.03	-.20
Amino Acid N 450 pounds	(w)							+.18		+.45**	
	(t)							+.16		+.41**	
Amino Acid N 750 pounds	(w)								+.12		-.18
	(t)								+.14		-.14
Urea N 450 pounds	(w)									-.30	
	(t)									-.22	
Urea N 750 pounds	(w)										+.12
	(t)										+.16

¹(w) = correlation coefficient within subclass

(t) = correlation coefficient ignoring subclass

* Significant at P < .05.

**Significant at P < .01.

DISCUSSION

Differences between the sexes for performance traits show (Table 11) that bull calves weighed heavier at birth, grew more rapidly during both the preweaning and postweaning periods, were more economical in converting feed into gain, and scored higher at 800 pounds. Sex differences in blood urea and amino acid nitrogen are in agreement with previous findings by Bogart et al. (4), and MacDonald, Krueger and Bogart (39). Heifers at 450 and 750 pounds had a higher content of these constituents of the blood than did males. The bulls were more rapid gainers than the heifers at both stages when the blood was sampled. Williams (53, p. 69) concluded that physiologically, females have a decreased protein anabolism compared to bulls, therefore not drawing on the amino acids for growth to the same extent. The excess amino acids are then deaminated resulting in more urea being formed. The creatinine content of the blood has been found by the investigators mentioned above to be highly variable during the growth cycle, and no clear-cut sex differences have been quoted. In the present study, the higher content of creatinine in the blood in males at both weights may indicate a higher percentage of lean body mass in the bulls than in the heifers.

The amount of urea nitrogen in the blood was higher at 750 pounds than at 450 pounds in both sexes. This is in agreement with

increases found between 500 and 800 pounds by Bogart et al. (4) and Williams (53, p. 64-65), but is opposite to the findings of MacDonald, Krueger and Bogart (39, p. 31). Evidently the increased feed consumption that coincides with increased body weight (53, p. 54) accounted for the higher blood urea levels in this study. Decreased protein anabolism and increased fat deposition would explain this higher amount of blood urea. The amino acid and creatinine content of the blood was lower at 750 pounds than at 450 pounds, however. Blood amino acid nitrogen increased in the calves involved in the study by Bogart et al. (4), remained the same in Hereford males and increased in Hereford females in the study reported by MacDonald, Krueger and Bogart (39), and remained the same from 500 to 800 pounds in those animals studied by Williams (53, p. 67), after a significant increase prior to weaning. A significant association between preweaning gain and the blood content of amino acid nitrogen existed as seen in Table 22. This may mean that the good preweaning environment afforded by a good milk supply may have raised blood levels to a level higher at 450 pounds than would be expected under less desirable conditions. Also, at 750 pounds, even though a change in metabolism towards more fat than protein anabolism may have occurred when compared to the rate of protein synthesis of the younger calves, the nitrogen requirements per unit of tissue may have been greater. The increased testosterone

production of bulls at this weight may influence nitrogen retention to a degree great enough to account for the difference in amino acid nitrogen at this weight.

In the analysis of the diallel cross between lines, the adjustment of suckling gain to a six year age-of-dam basis resulted in no significant differences between inbreds or linecrosses. The means shown in Tables 16 and 18 indicate that the David line accounts for the lowest suckling gains in the general and specific combining ability and in the line of dam analyses. Due to other lines of dam being included, it does not account for the lowest mean in the line of sire analysis. In Table 13, the reciprocal differences between crosses involving the David line show it to yield the less rapidly gaining calves during the preweaning period. Linecross calves had higher suckling gains than inbred calves but the difference was not significant. A heterotic effect might be expected in preweaning rate of gain, but a greater increase would be expected in gains of calves from linecross cows. The linecross calves here are subjected to the same preweaning environment as the inbred calves, except for chance deviations resulting from better milking cows within the inbred group of dams. When the calves were weaned and reached 450 pounds, analyses of the blood constituents revealed a significant difference in creatinine due only to variations between lines of dam. If creatinine in the blood is an indication of lean body mass

(8, p. 353), then the lower blood creatinine of calves born to Lionheart cows (Table 19), which were better milkers, than of calves born to the poorer milking David cows, reflects a possible difference in the ratio of fat to lean in these young calves. Calves from the poorer milking David cows could conceivably have a larger percentage of lean than calves from Lionheart cows. In Table 13, the reciprocal difference shown between the Lionheart x David cross is in favor of a higher blood creatinine level in calves born to David cows.

At the postweaning stage when the genotype of the calf determined its rate of gain to the greatest extent, significant general and specific combining ability differences occurred in rate and economy of gain. The difference in performance agrees with what would be expected on the basis of performance of the inbred lines themselves and the magnitude of the heritability estimates in the previous study. Most of the variation in the postweaning performance is due to the additive effect of genes. Accumulation of desirable genes is reflected in the differences of performance in the inbred lines and performance in crosses involving these lines would be expected to generally coincide with the inbred line performance. The Lionheart and David lines have been the best gainers during the postweaning period. In Table 16, the general combining means of these lines are similar to the performance histories of these lines. The Prince line was lowest

in the general combining ability analysis. Specific combining ability differences in rate of gain favored crosses between the most rapidly gaining Lionheart and David lines. The Prince x David cross was the lowest performing cross among specific crosses, which may be an indication that some nonadditive gene action contributed to the better performance of the Lionheart x David crosses. This is indicated because of more genetic diversity between the two lines. Genetic diversity would not be as marked between the Prince and David lines, as indicated in the history of the lines in Part I of this study. The lack of higher performance from the Lionheart and Prince cross even though genetic diversity would be expected to be as great as between the Lionheart and David lines, may be due to the higher inbreeding of the David line. This would result in the fixation of more desirable genes and be reflected in the performance of crosses involving this line. Compensation for preweaning gains may have some influence on the results of all crosses, but in Table 16 it can be seen that although this appears in the case of the Lionheart x David cross, the Prince x David cross performed poorly during both the preweaning and postweaning periods. The nonsignificant negative association between suckling gain and postweaning rate of gain (Table 22) probably indicates compensation soon after weaning. This effect should become less marked during the later stages of the feed test.

The difference between linecross and inbred calves was not

significant for postweaning rate of gain, although linecrosses were the more rapid gainers.

Referring to Table 18, the discussion pertaining to rate of gain seems to be contradicted in the line of sire analysis when all inbred and linecross calves were included. This is because of the high performance of the inbred Prince calves in this study during the postweaning period. The small number of inbred Prince calves probably enhanced this chance variation. The analysis of sire differences excluding the inbred calves conformed to the previous conclusions concerning better performance of the Lionheart and David lines.

The analyses of differences in economy of gain were similar to those for postweaning rate of gain, but there was a significant difference between linecross and inbred calves in addition to differences in general and specific combining ability. This is probably a function of the economy of gain contributed by the Prince line to the linecross calves which, although gaining at a slower rate (Table 18) gained nearly as economically as calves sired by the Lionheart bulls. Therefore, even though there is a high association between rate and economy of gain (Table 22), a difference exists between lines for these two traits. It was shown in Part I of this study that the Prince line had the most economical gains.

Differences in specific combining ability existed for score at

800 pounds, due to higher scores being given to calves of the Lionheart x Prince cross. This is not surprising, as calves of the David line have scored lower in the past and this is reflected in the scores of calves resulting from crosses with the David line. Line-cross calves scored significantly higher than inbred calves due to the lower scores given the inbred Prince and David calves (Table 13). Differences between lines of dam also were due to the lower scores given these two groups of inbred calves. Poorer gaining calves during the preweaning period scored lower at 800 pounds. The highly significant positive association between suckling gain and score is the result of scoring the poor gaining calves of crosses involving the David line lower. This is also in keeping with the past criticism of conformation of the David line as indicated by score.

The significant difference in blood creatinine levels at 750 pounds due to variation between lines of sire was caused by the low levels in inbred David calves. In this study, this group of calves gained the poorest during the postweaning period. Although this is contrary to the discussion of better gaining David calves at this stage of the growth cycle, this was a small group of calves and, like the Prince calves, may have represented chance deviations. The slower gain or possibly less total lean in the carcass evidently was reflected in the blood creatinine levels. The high levels of blood creatinine in the calves sired by the Lionheart bulls reflect

the higher rates of gain of these calves and possibly a larger amount of lean body mass. The significant difference between inbred and linecross calves for blood creatinine was also due to the low levels in the blood of David inbreds.

Significant sire differences existed for blood amino acid nitrogen at 750 pounds, due to the low content in calves sired by Prince bulls (Table 19). This may be a function of efficiency of feed conversion by Prince sired calves, although no significant differences existed between economy of gain or rate of gain in the line of sire analyses.

A significant negative association was found between economy of gain and urea nitrogen at 750 pounds. This association, which means that the animals with a higher feed requirement per unit of gain had less urea nitrogen in the blood, is contradictory to what would be expected if ammonia, which is formed in the rumen passes through the rumen wall and is converted to urea in the liver. Higher amounts of feed ingested would lead to the greater possibility of excess ammonia being formed and converted to urea via this pathway. The blood collections were made in the morning approximately 12 hours after the evening feeding and prior to the morning feeding so that the effects of food ingestion should have been minimal on all blood constituents. At 450 pounds the association between blood urea nitrogen and subsequent feed consumption was positive (though not

significant), as would be expected if more efficient converters of feed drew on the amino acid supply for growth resulting in less being available for conversion to urea. The non-significant negative association of postweaning rate of gain with blood amino acid nitrogen at 450 pounds substantiates this theory. The reason for the reversal of associations at 750 pounds is not evident.

Postweaning rate and economy of gain were highly associated (Table 22) even though differences in economy of gain exist between lines, with the Prince line being the most economical converter of feed to gain (Part I of this study). A selection program within a line of breeding could be effective using rate of gain as an index of feed economy. Between lines of breeding, however, there is the possibility that an advantage could be had by selection on the basis of economy of gain as well as rate of gain, especially in the formation of a new line where the maximum in both is desired.

A highly significant positive association between blood creatinine at 450 pounds and blood amino acid nitrogen at the same weight was found and might be expected if much of the milk protein is converted to creatine, and indirectly, creatinine (10, p. 130-131). The non-significant negative association between blood creatinine at 750 pounds and blood amino acid nitrogen may indicate that animals with more lean tissue are drawing more heavily on the amino acid supply of the blood. The higher creatinine levels in these

animals reflect the increased amount of lean.

SUMMARY AND CONCLUSIONS

1. A complete diallel cross among the Lionheart, David and Prince Hereford lines was made in 1963. Performance data and blood samples were collected from the calves resulting from this cross. Performance traits and constituents of the blood were analyzed in order to detect differences due to line of sire, line of dam, sire x dam interaction, and genotypes. Appropriate general and specific combining ability, line of sire, line of dam and inbred vs. linecross analyses were performed when differences were found. Coefficients of correlation were computed between certain performance and blood constituent data.

2. Bull calves contained lower levels of blood amino acid and blood urea nitrogen and more blood creatinine than heifer calves at both 450 and 750 pounds, probably due to increased protein anabolism, less deamination of unused amino acids to urea, and a greater percentage of lean body mass. A highly significant positive association existed between suckling gain and the amino acid nitrogen content of the blood at 450 pounds, reflecting the effect of the pre-weaning nutrition on the calves.

3. Blood urea nitrogen increased from 450 to 750 pounds in both sexes and blood amino acid nitrogen and blood creatinine decreased between these two weights. Increased food consumption

probably accounted for increased urea formation. The lower amino acid nitrogen content could have been due to a higher nitrogen retention per unit of tissue, influenced by an increased testosterone output in bull calves.

4. Differences in the lines for general and specific combining ability existed for postweaning rate and economy of gain and coincided with differences observed in the histories of the lines involved in the crosses, with the calves from matings involving the Lionheart and David lines gaining the most rapidly in the general combining ability analysis. The specific crosses between the Lionheart x David cattle performed better than those of the Lionheart x Prince cattle. The genetic diversity between the Lionheart and David and Lionheart and Prince lines should have been comparable, but a higher rate of inbreeding in the David line may have caused better response in the Lionheart x David cross. Compensation for poor preweaning growth could have been a factor for those calves born to David cows, but the specific cross of Prince x David cattle performed poorly both during the preweaning and postweaning periods.

5. Linecross calves were more economical in feed use than inbred cattle, probably due to the effect of the Prince line on the linecrosses. This line has been more efficient in past studies even though not having the highest rate of gain of the three lines.

6. Linecross calves scored higher than inbred calves due to

the high scores given the calves from the Lionheart x Prince crosses. Score at 800 pounds and suckling gain were highly associated due to the lower gaining inbred David and the David cross calves during the preweaning period being the same calves that scored lowest at 800 pounds.

7. Blood creatinine differed due to line of sire variations at 750 pounds, with inbred David calves being low in blood creatinine and in turn the poorest in rate of gain in this study. The less rapid gain evidently resulted in less lean tissue and less creatinine in the blood compared to faster gaining, more muscular animals. At 450 pounds, on the other hand, a significant difference in blood creatinine was due to variation between lines of dam. More creatinine was found in the blood of calves from David dams, in this case probably due to a greater percentage of lean than was contained by calves gaining more rapidly on a greater milk supply during the preweaning period.

8. A significant difference existed at 750 pounds for blood amino acid nitrogen due to line of sire differences. The lower blood amino acid nitrogen in linecross calves which contained Prince breeding may be a function of efficiency of feed conversion by Prince sired calves, although no significant differences existed for line of sire in the rate and economy of gain analyses.

9. A highly significant association was found between post-weaning rate and economy of gain. Urea nitrogen at 750 pounds and

pounds of feed per 100 pounds gain were negatively correlated. A highly significant association existed between blood creatinine and amino acid nitrogen at 450 pounds.

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