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Amount of Selection Applied and Response of Traits in Four Inbred Lines of Beef Cattle

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Frank K. Hoornbeek and Ralph Bogart

INTRODUCTION

Performance, to the animal breeder, means the attainment of maximum reproductive potential and maximum conversion of feed-stuffs to a salable product in the shortest period of time. 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.

Alexander and Bogart (1961) showed that inbreeding of calf had a significant depressing effect on suckling gain, but not on post-weaning rate of gain and feed efficiency. The work of Brinks et al. (1963) indicated that there was a negative effect of inbreeding on growth of cattle from birth to weaning. The success of King (1918; 1919) with inbred rats may be attributed to rigid selection practiced for performance, whereas loss of genetically weaker lines of guinea pigs occurred when Wright and Eaton (1929) practiced inbreeding with no conscious selection. These investigations emphasize the effects of inbreeding on the performance of diverse representatives of the animal world. All of the studies give support to the necessity of a strong selection program whenever inbred lines are maintained.

The study reported herein represents an 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.

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 (1953) up to 800 pounds body weight. Rates of gain during the suckling and postweaning periods, economy of gain, and conformation and condition scores at 500 pounds and at 800 pounds were recorded for each calf. Bull calves remained intact throughout the testing period. Selection was on the basis of preweaning and postweaning performance plus the score for conformation given the animals at 800 pounds, all on an index basis as follows:

$$I = \frac{S - \overline{S}}{{}^{s}S} + \frac{G - \overline{G}}{{}^{s}G} - \frac{F - \overline{F}}{{}^{s}F} + \frac{C - \overline{C}}{{}^{s}C}, \text{ where}$$

S = suckling gain, G = feed test gain, F = feed per unit of gain, and C = score for conformation at the end of the feed test. 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, Clark, and Kieffer (1965), 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,

$$S = \frac{n^{s}{}_{1}s_{1} + n^{s}{}_{2}s_{2} + \ldots + n^{s}{}_{i}s_{i}}{N\overline{A}}$$

On the dam side,

$$D = \frac{n^{d}{}_{1}d_{1} + n^{d}{}_{2}d_{2} + \ldots + n^{d}{}_{i}d_{i}.}{N\overline{A}}$$

For sire and dam combined,

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

where S, D, or P are the selection differentials, $n^{s}{}_{i}$ and $n^{d}{}_{i}$ 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

$$\bar{A} = \frac{n^s{}_i A^s{}_i + n^d{}_i A^d{}_i}{2N}.$$

$\bar{A}$ 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 time trends 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:

	Lionheart line	Prince line	David line	Angus line
Male calves	59	64	61	78
Female calves	64	66	49	111

For the two years in which repeat matings did not occur, the average of the entire calf crop was 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. Performance-trait means were plotted graphically to show trends and yearly variations for suckling gain, postweaning 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.

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

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

Table 1. YEARLY SELECTION DIFFERENTIALS FOR PERFORMANCE TRAITS AND INBREEDING COMPUTED FROM SIRES, DAMS, AND PARENTS COMBINED

Traits	Lionheart			Prince			David			Angus		
	Sire	Dam	P[1]	Sire	Dam	P[1]	Sire	Dam	P[1]	Sire	Dam	P[1]
Suckling gain (lb./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
Postweaning rate of gain (lb./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 (lb./cwt. 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	–.0041	0.0989	0.0562	0.0186	0.0374	0.0662	0.0266	0.0464
Inbreeding (percent)	–.0003	0.0008	0.0002	–.0054	0.0007	–.0023	–.0009	0.0014	0.0002	–.0031	–.0014	–.0022
Generation interval (years)		4.17			3.93			4.17			4.24	
Number of animals 1951-62		123			130			110			189	

[1] Both parents.

interval and number of animals in each line are indicated. The selection differentials, covering the 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 0.0172 pound 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 selection differential of –3.21 for feed per unit of gain indicates that less feed per 100 pounds of gain was selected for at the same time that an increase was selected for in postweaning rate of gain. A higher score, on the basis of the scores of sires and dams, was selected for, amounting to 0.0482 units on a scale of 5 to 15, where the lowest score is 5 and the highest is 15. Except for postweaning rate of gain in the Angus line, 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 increase in preweaning rate of gain of 0.39 pound per day. Selection was also for a total increase in postweaning rate of gain of 0.38 pound per day on 65 pounds less feed per 100 pounds of gain. At the same time, selection for a total increase of 1.17 units in score for conformation was applied.

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

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

Performance of Lines

Differences in performance of the lines by sexes are shown in Tables 2 and 3. Performance prior to the time that selection differentials were computed is presented in Table 2. Average performance 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. This table shows that suckling

Table 2. Means of Performance Traits by Line and Sex Prior to 1951

Traits	Year	Lionheart		Prince		David		Angus	
		Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain (lb./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
Postweaning rate of gain (lb./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 (lb. feed/cwt. gain)	1948	846	1,048	858	1,007	......	......	766	1,265
	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

Traits	Lionheart		Prince		David		Angus	
	Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain (lb./day)	1.77	1.61	1.77	1.57	1.60	1.51	1.97	1.73
Postweaning rate of gain (lb./day)	2.70	1.96	2.64	2.06	2.69	2.16	2.46	1.84
Feed economy (lb. feed/cwt. gain)	706	971	664	854	714	889	788	1,030
Score (units)	12.17	11.96	11.22	11.22	10.70	11.10	11.10	11.10
Inbreeding (percent)	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 of dam (percent)	5.5	6.1	4.9	6.2	9.7	7.1	3.6	3.0

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 David females gained more rapidly than Prince females, which in turn gained at a more rapid 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.

Estimation of Environmental Variation

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.

Since there did not appear to be a general time trend in environmental effects, the data were not corrected for environmental variations.

Response to Selection

The phenotypic time trends in the performance traits and inbreeding from 1951 to 1962 are shown 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 for the four lines are shown in Figures 1 through 16. 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 postweaning rate of gain declined in all cases except for males in the David line and females in the

Table 4. Phenotypic Responses of Traits Yearly from 1951-1962, Determined by Regression of Traits on Years

Traits	Lionheart		Prince		David		Angus	
	Male	Female	Male	Female	Male	Female	Male	Female
Suckling gain (lb./day)	–.020	–.026	–.035	–.007	–.013	–.012	0.008	0.001
Rate of gain (lb./day)	–.019	–.028	–.012	–.040	0.003	–.010	–.024	0.019
Feed economy (lb. feed/cwt. gain)	–7.46	15.25	1.30	12.01	–.35	12.84	11.00	–3.34
Score (units)	0.16	0.10	0.25	0.15	0.08	0.13	0.34	0.38
Inbreeding (percent)		0.70		0.98		0.42		0.62

Angus line. Economy of gain 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 by males.

Effects of Inbreeding

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. For suckling gain, the lower percentages of inbreeding were associated with higher suckling gain for both males and females as shown in Figure 19. Mildly inbred calves gained more rapidly during the postweaning period than noninbred 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. Noninbred 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 in suckling gains associated with inbreeding of dam that was shown by females of the Angus line.

Age of Dam

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; breeders in 1962 averaged 2.5 years older than those in 1951. The same trend was evident for ages of the Prince cows. In the David line, there were older cows at the beginning of the study, 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 the cows of all the lines in later years. In the Angus line, the cows were older at the beginning of the study, average age increased until 1954, and then average age declined until 1959. Subsequent to this date the average age has increased.

Table 5. SUCKLING GAIN BY LINES FOR AGE OF DAM GROUPS

Age of dam	Lionheart Male	No.	Female	No.	Prince 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 Male	No.	Female	No.	Angus 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

Heritability Estimates

Heritability estimates for each trait, given in Table 7, 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 7. HERITABILITY ESTIMATES BY INTRA-SIRE REGRESSION OF OFFSPRING ON DAM, CORRECTED FOR SEX TO MALE BASIS

Traits	Lionheart	Prince	David	Angus[1]
Suckling gain	0.00	0.00	0.00	0.00
Rate of gain	0.29	0.37	0.42	0.22
Economy of gain	0.21	0.46	0.42	0.24
Score	0.16	0.00	0.31	0.10

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

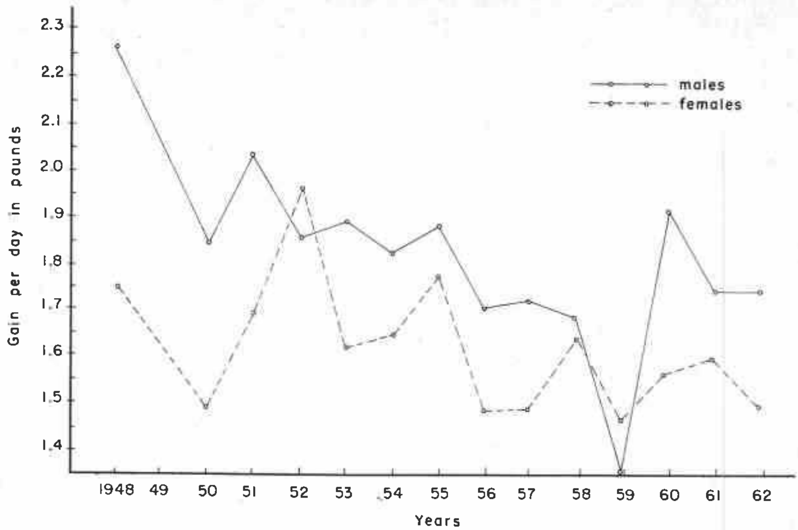

Figure 1. Yearly means by sex of calf for preweaning gain of Lionheart calves.

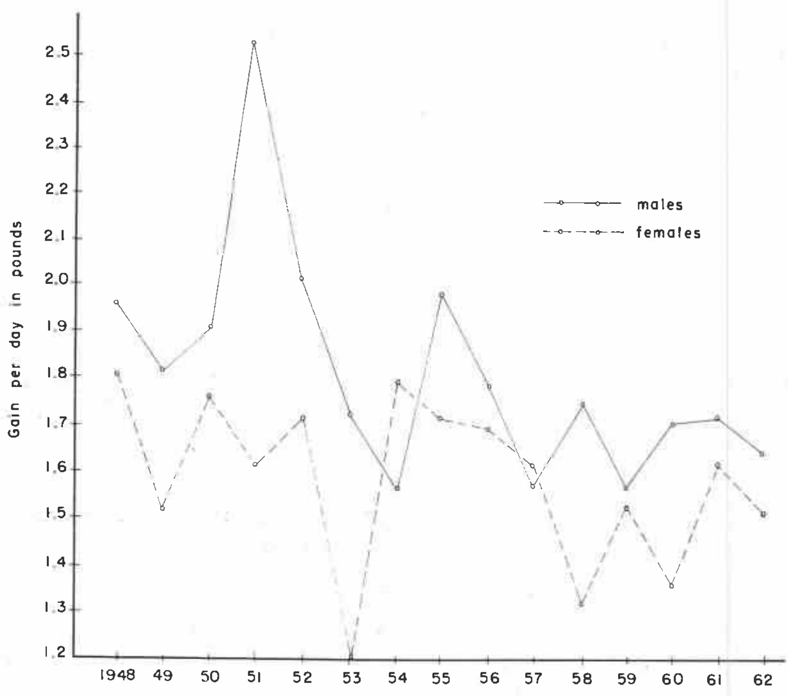

Figure 2. Yearly means by sex of calf for preweaning gain of Prince calves.

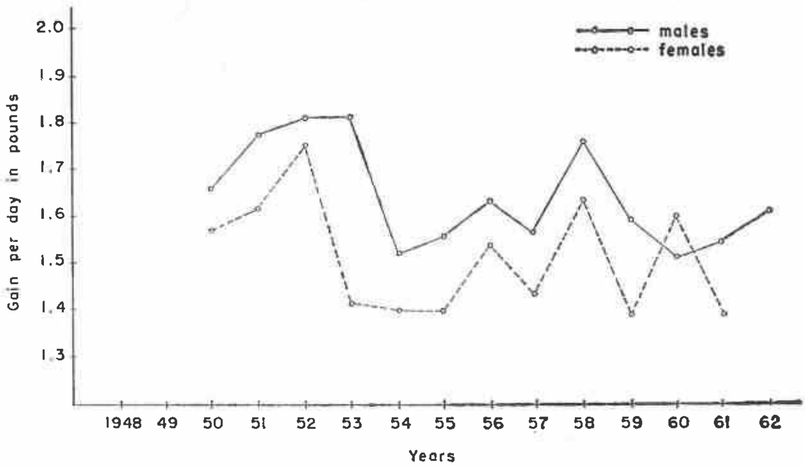

FIGURE 3. Yearly means by sex of calf for preweaning gain of David calves.

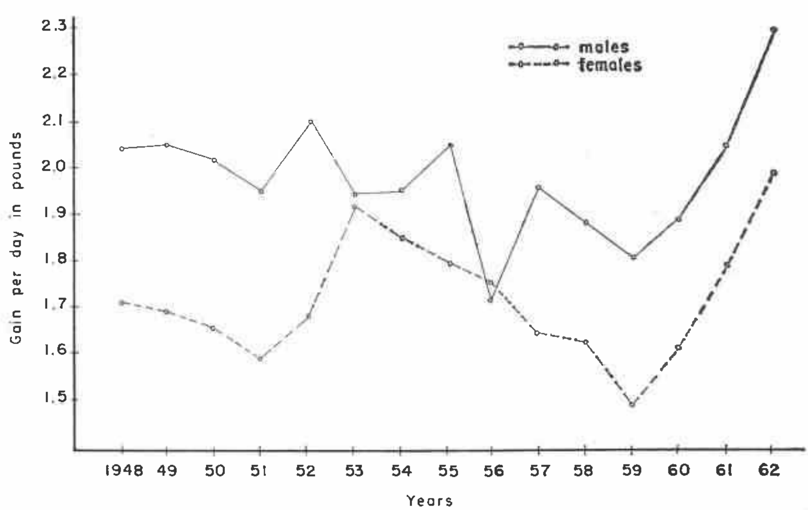

FIGURE 4. Yearly means by sex of calf for preweaning gain of Angus calves.

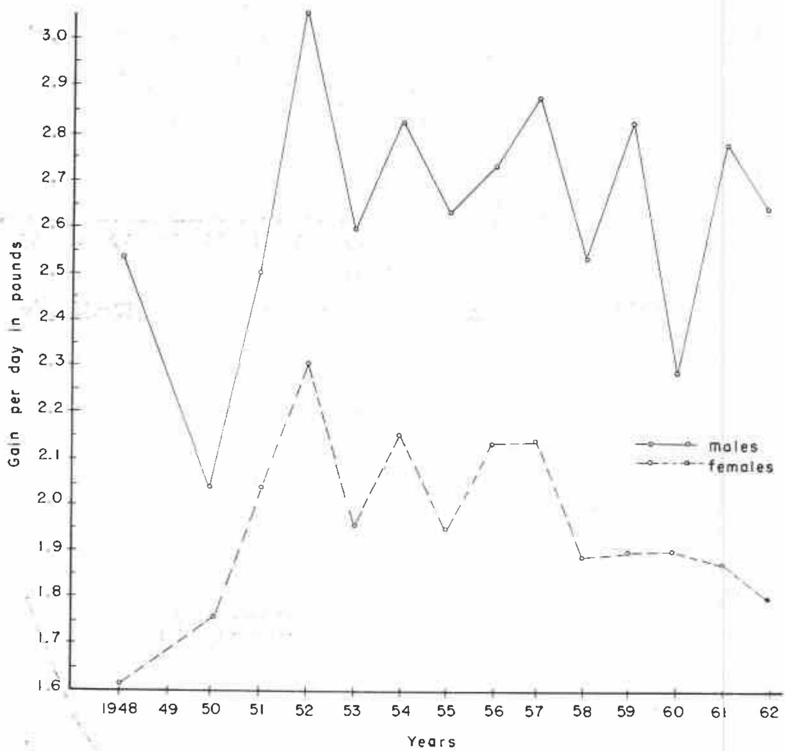

FIGURE 5. Yearly means by sex of calf for postweaning gain of Lionheart calves.

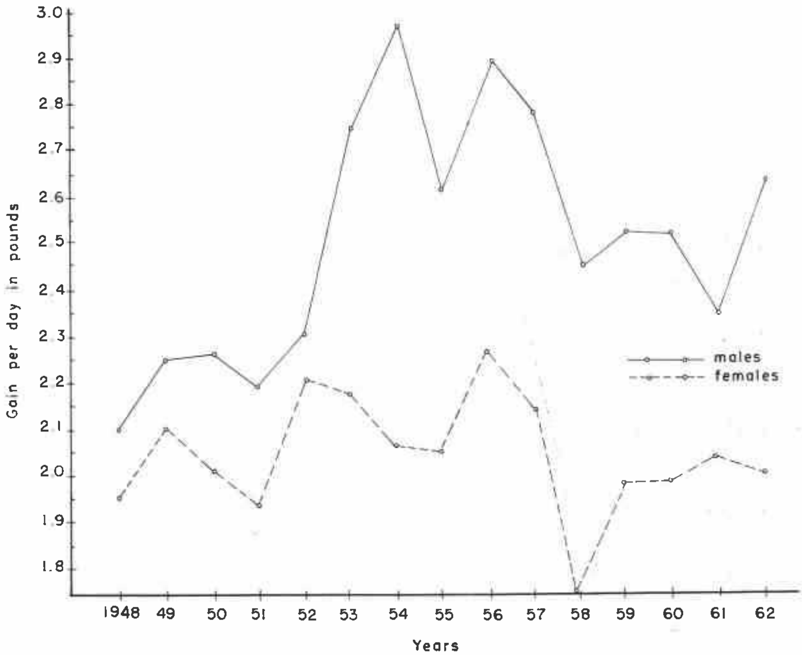

Figure 6. Yearly means by sex of calf for postweaning gain of Prince calves.

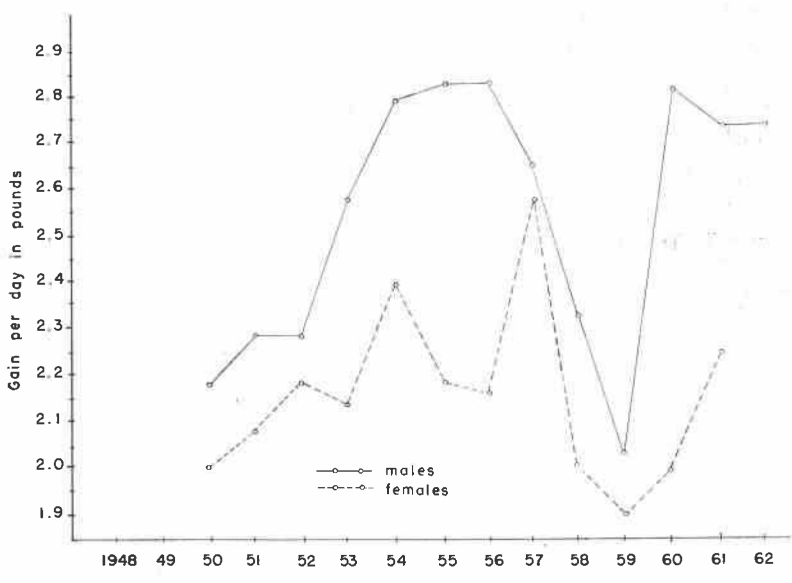

Figure 7. Yearly means by sex of calf for postweaning gain of David calves.

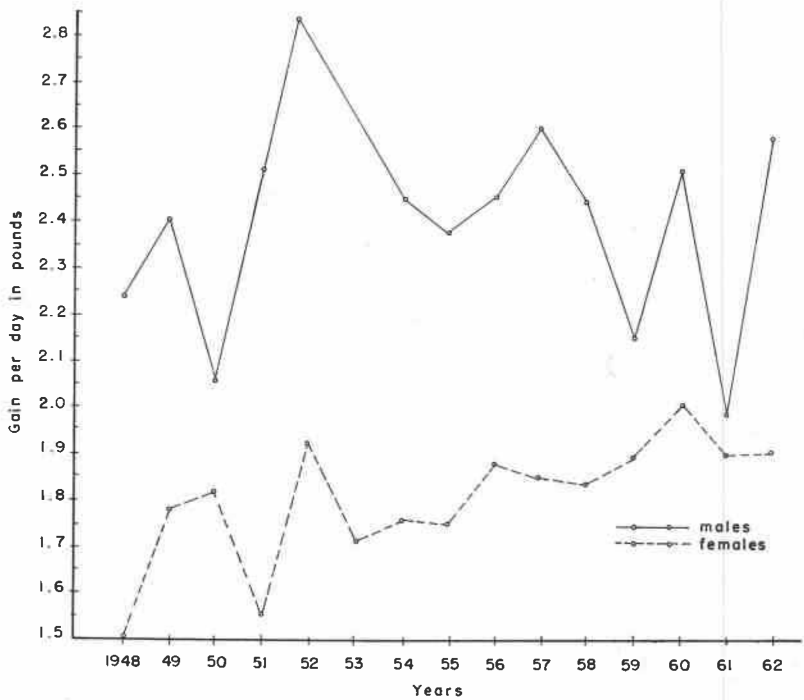

FIGURE 8. Yearly means by sex of calf for postweaning gain of Angus calves.

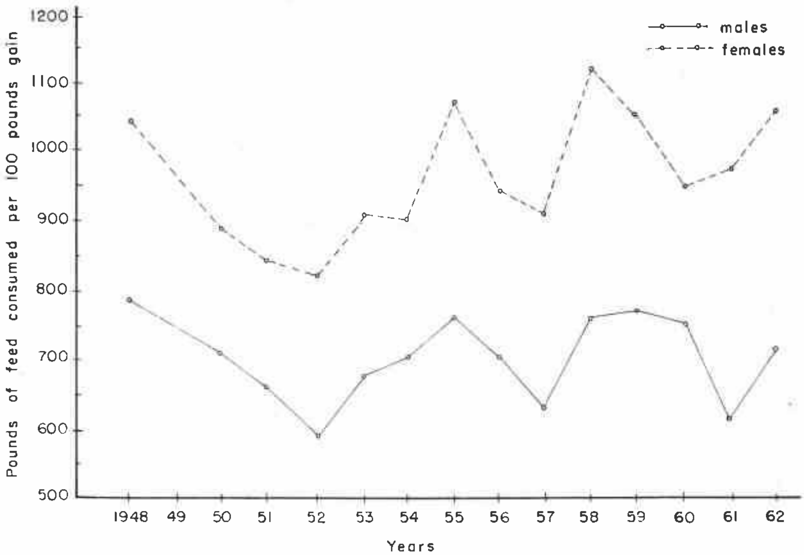

Figure 9. Yearly means by sex of calf for economy of gain of Lionheart calves.

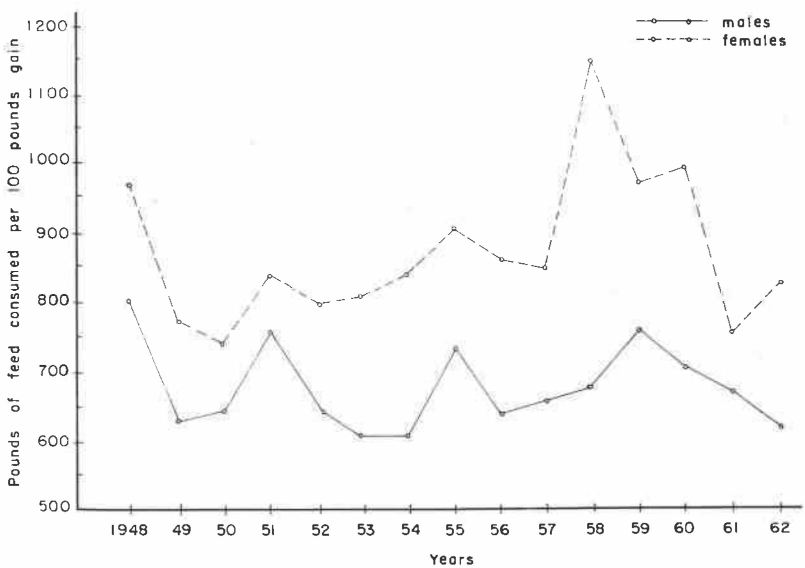

Figure 10. Yearly means by sex of calf for economy of gain of Prince calves.

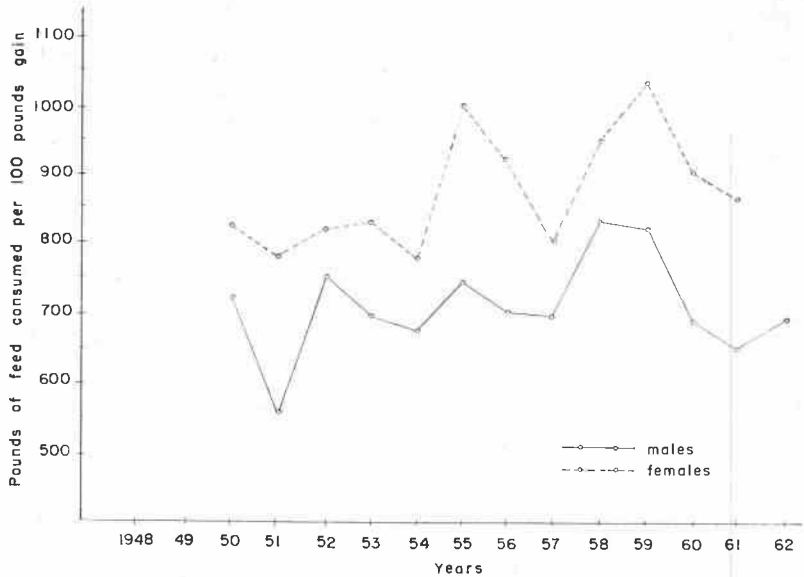

FIGURE 11. Yearly means by sex of calf for economy of gain of David calves.

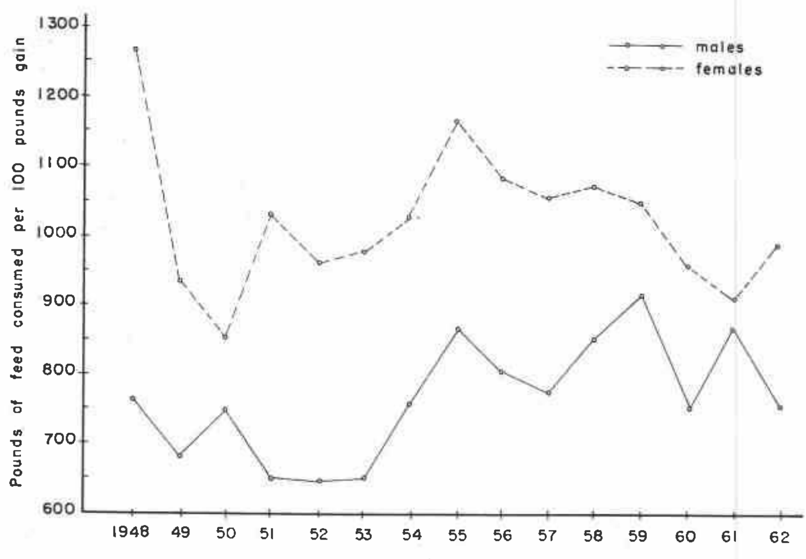

FIGURE 12. Yearly means by sex of calf for economy of gain of Angus calves.

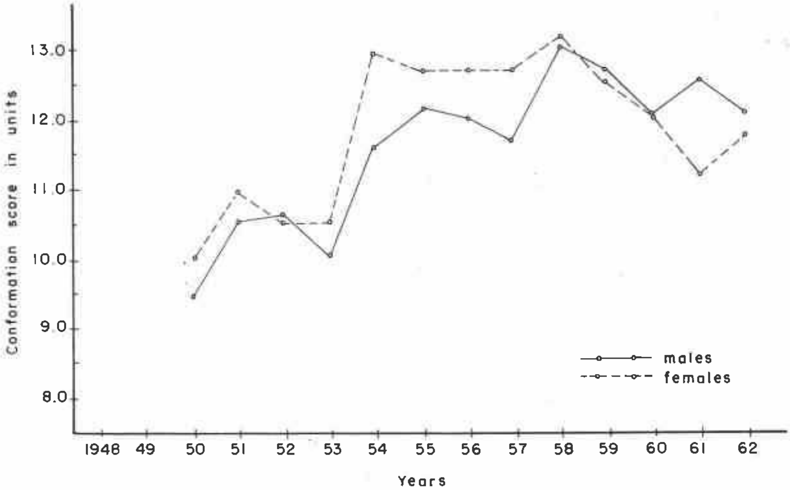

FIGURE 13. Yearly means by sex of calf for conformation score of Lionheart calves.

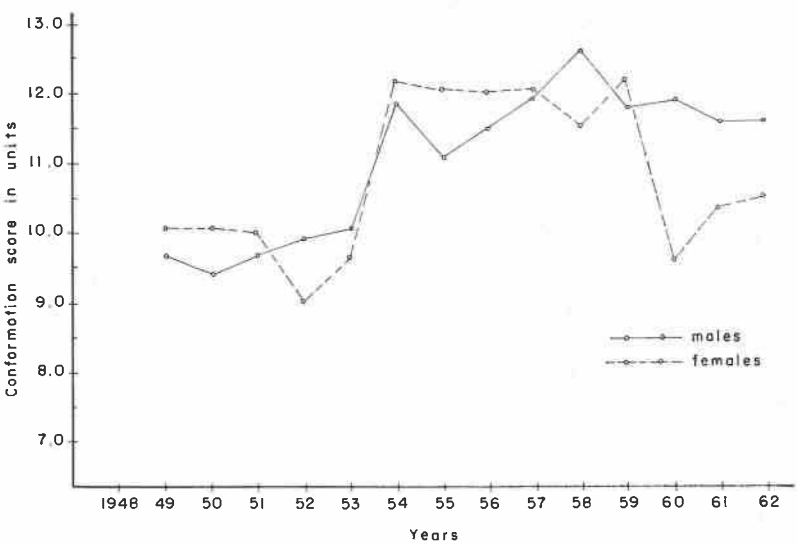

FIGURE 14. Yearly means by sex of calf for conformation score of Prince calves.

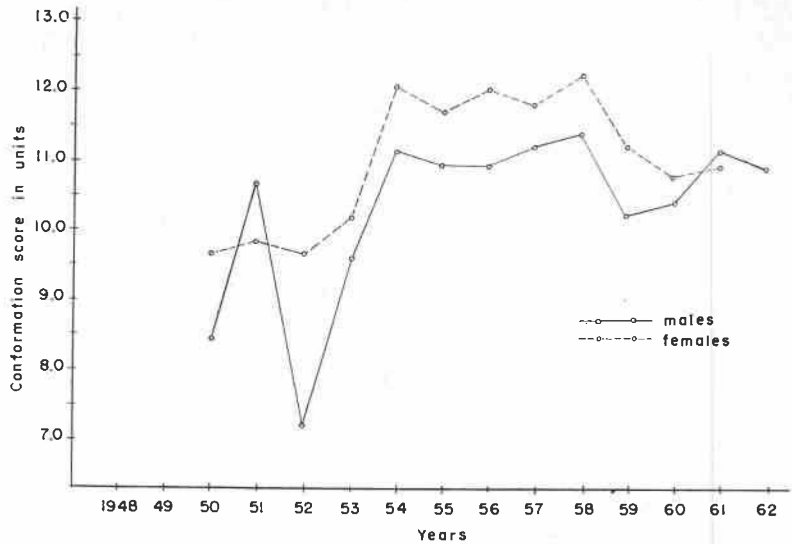

FIGURE 15. Yearly means by sex of calf for conformation score of David calves.

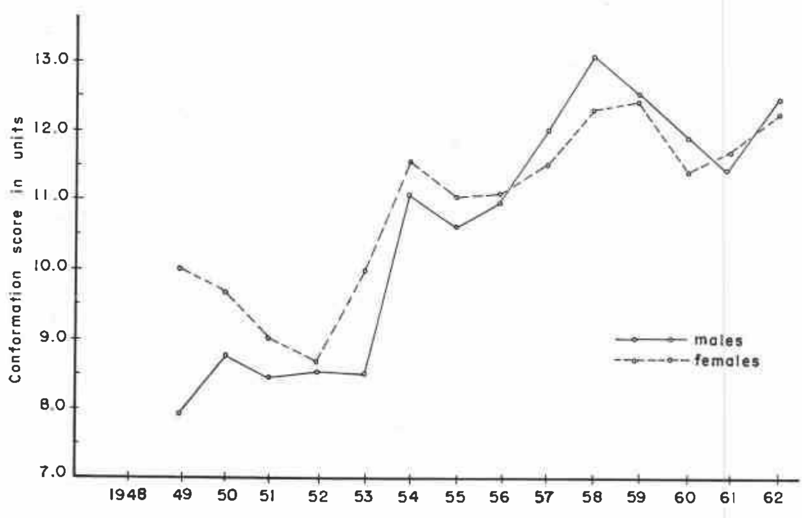

FIGURE 16. Yearly means by sex of calf for conformation score of Angus calves.

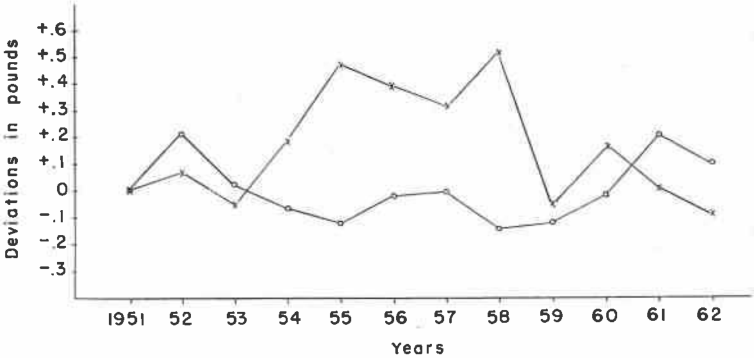

Figure 17. Yearly environmental deviations as estimated by repeat matings.
X = Suckling gain expressed in pounds per day gain deviations.
O = Postweaning rate of gain.

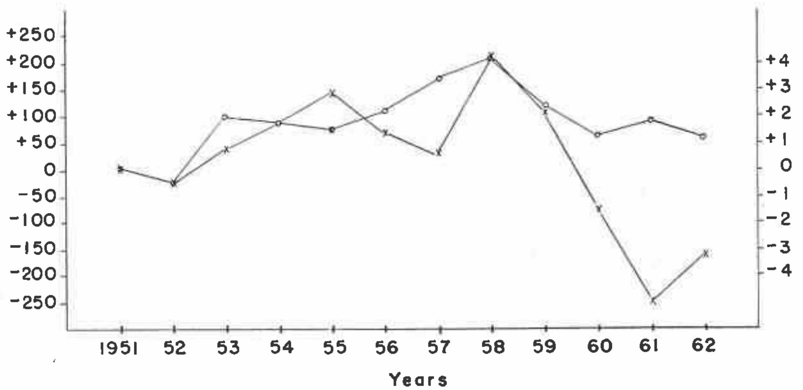

Figure 18. Yearly environmental deviations as estimated by repeat matings.
X = Economy of gain. Left-hand scale is in pounds feed per 100 pounds gain deviations.
O = Score. Right-hand scale is in unit deviations.

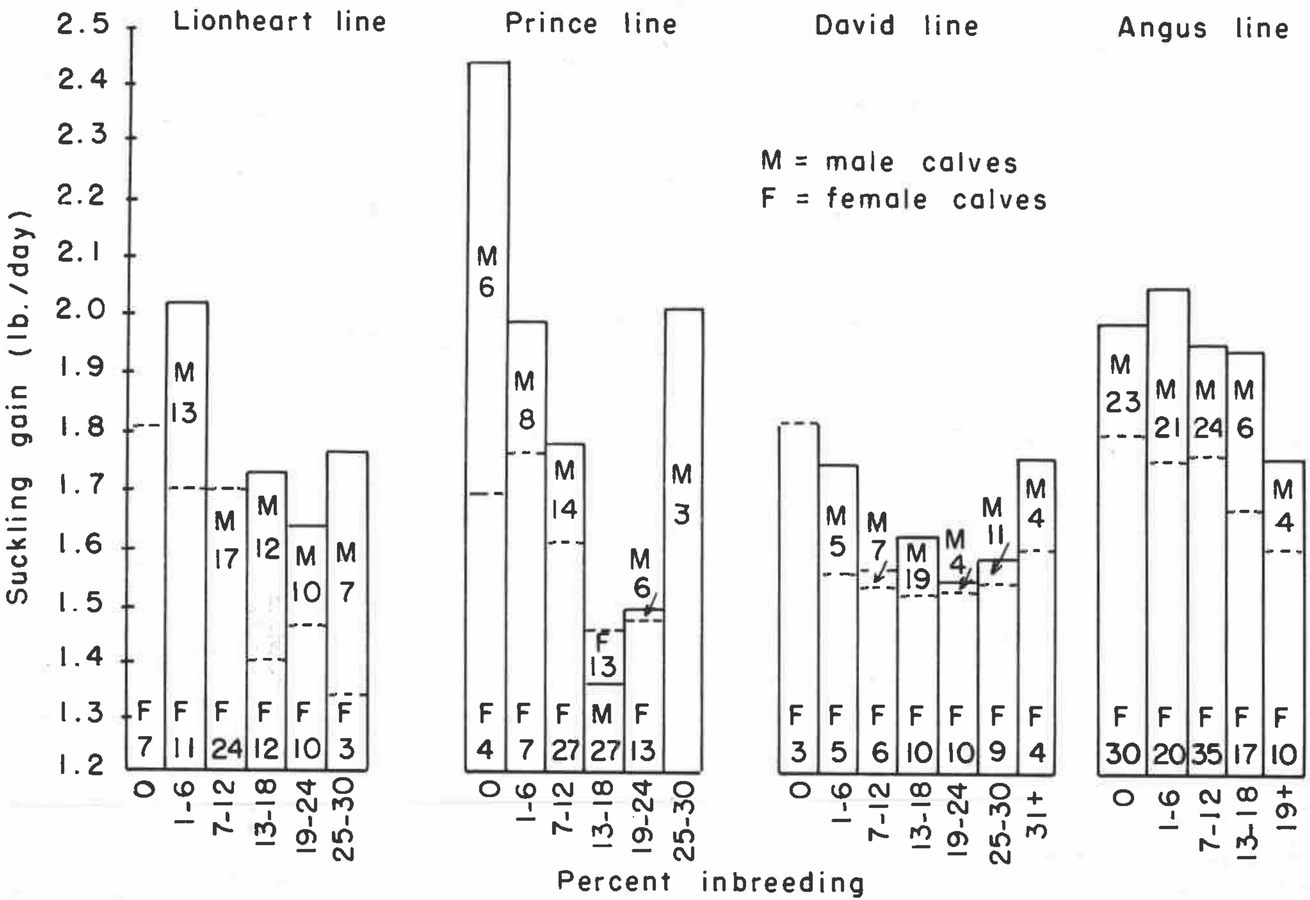

FIGURE 19. Suckling gain means by sexes and lines at different levels of inbreeding of calf.

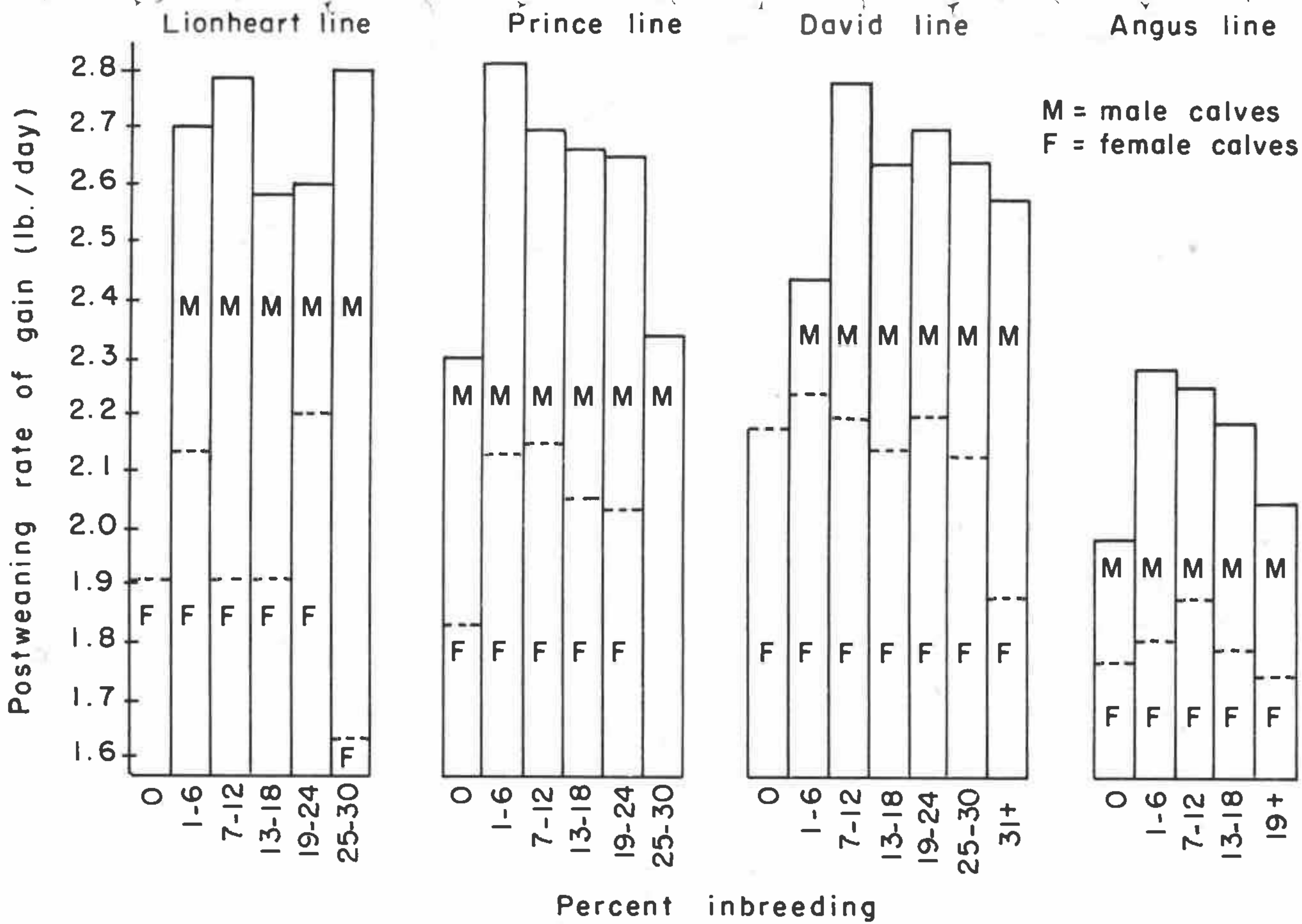

FIGURE 20. Postweaning rate of gain means by sexes and lines at different levels of inbreeding of calf.

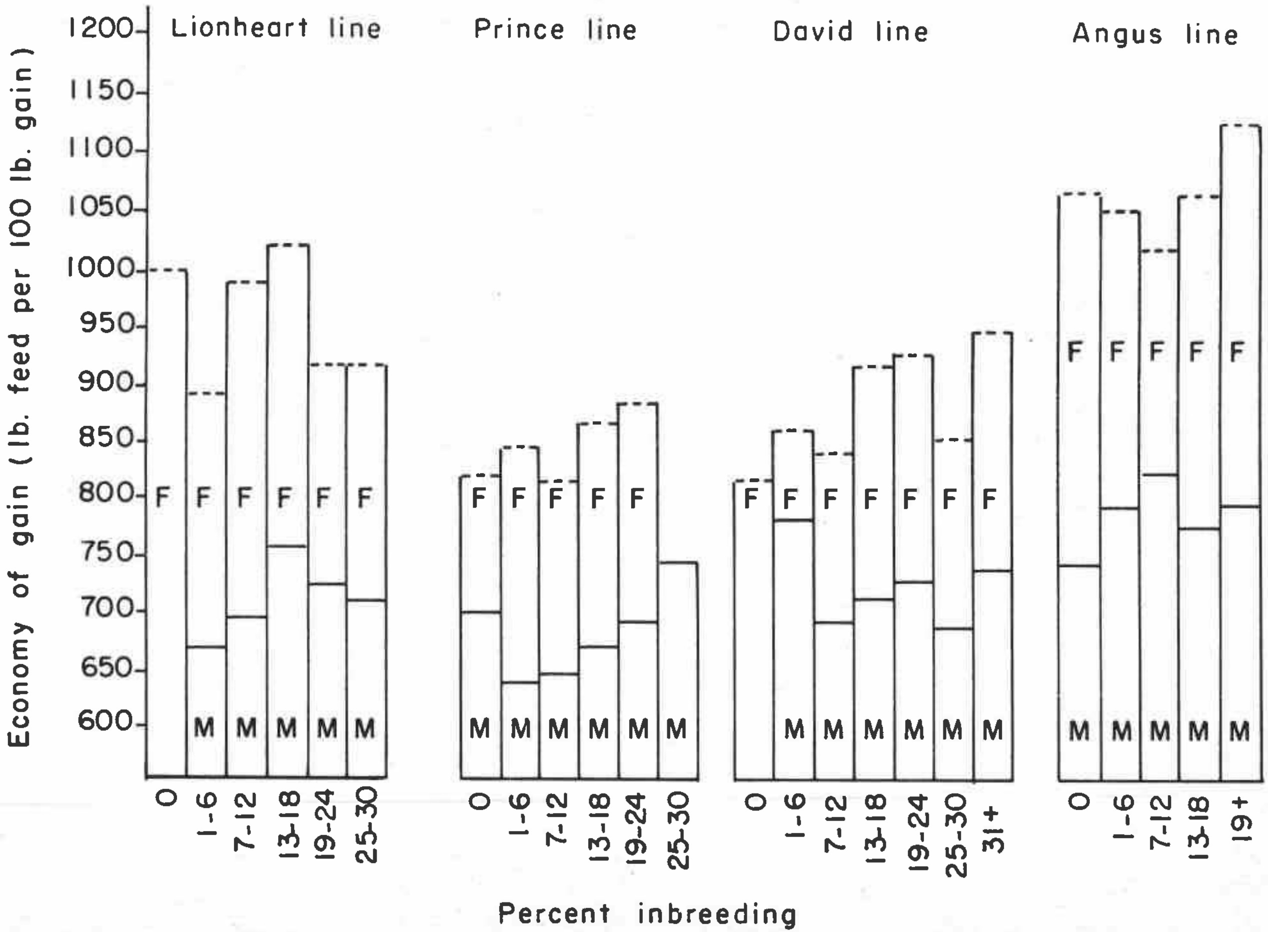

Figure 21. Economy of gain means by sexes and lines at different levels of inbreeding of calf.

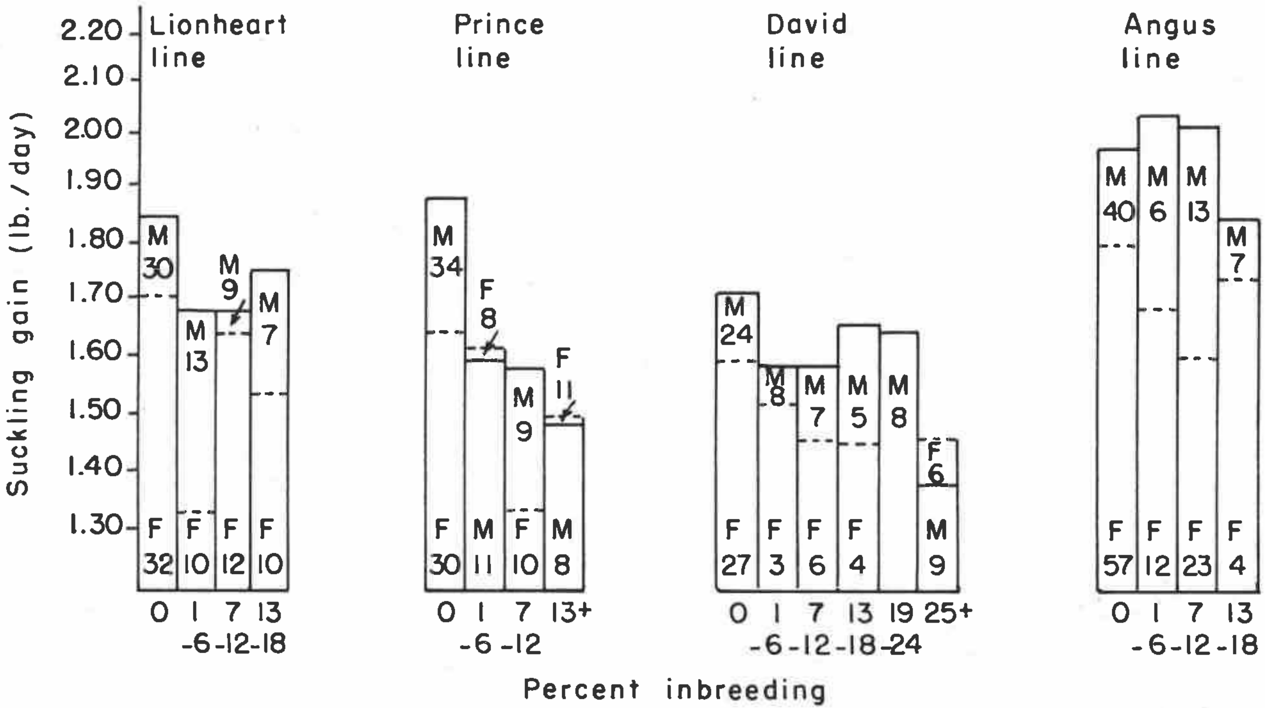

FIGURE 22. Suckling gain means by sexes and lines at different levels of inbreeding of dam.

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, 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 improved performance. Except for postweaning rate of gain in the Angus line, selection was more rigorous on the sire side, a consequence of the lower number of males needed as compared to the higher numbers of females for replacement purposes. This agrees with the results obtained by Flower et al. (1964) but includes additional postweaning evidence. Flower calculated differentials on the sire side only for postweaning growth. In the present study, two cases of negative selection pressure occurred on the dam side of the matings in the Prince line.

Response of Traits

Koch and Clark (1955) 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 (1960) 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.

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 indicate 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. The responses shown in Table 4 indicate that general improvement in all traits has occurred in the Angus line. Score has improved in all lines and inbreeding has increased. The question arises as to the reliability of the estimate of improvement in conformation as indicated by improvement in score because there were changes in personnel doing the scoring over the years and it is not known how much variation occurred in the way different persons scored animals. However, it is felt that selection for improvement in conformation has been effective.

Increased performance in the Angus line coincided with a low average inbreeding coefficient. In 1953, 1954, and 1955, an outside bull was brought into the Angus line and the line was subsequently closed again. This in part 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 postweaning 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 beginning 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.

Swiger et al. (1962) 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 the two stages (the first and second half) 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 confusion that may exist between season of birth and inbreeding. Brinks, Clark, and Kieffer (1963) 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 (1961) studied the effect of inbreeding and selection on performance and noted that year and inbreeding, as well as inbreeding with selection, were confounded. When effects of year and inbreeding were separated, there appeared in every case to be a significant year effect, whereas inbreeding effects were either nonsignificant in excess of the positive effects of selection, or there was a highly significant effect. 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 the age of calves reaching 500 and 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.

Environmental Deviations

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 sizable differences from year to year, cannot be taken into account. This would appear to make a "year" effect determined in any other way 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. Data presented in Figures 17 and 18 are, therefore, subject to the qualifications of gametogenesis and few numbers. Figure 17 shows 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 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. Suckling gain declined with inbreeding in all cases except for David bull calves. This may be due to the absence of male calves with no inbreeding 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.

Results of Inbreeding

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.

It has been determined by Alexander and Bogart (1961) that inbreeding of calf has a depressing effect on preweaning performance, but not on postweaning performance. In the case of David females and Angus males in the present study, postweaning rate of gain declined more than preweaning rate of gain with increased inbreeding. Angus male calves actually showed a positive response in preweaning performance over the 12-year period, which would account for the difference in response associated with inbreeding in this line.

The histograms drawn for postweaning 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 were 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 may have had the same effect.

Inbreeding of dam is considered in the case of suckling gain and the data in Figure 22 show that as the dams became more inbred, suckling gains of their calves declined. It is evident that as inbreeding increased in the later years of the study, the inbreeding of the dams influenced the weaning weights of the calves. In the early phases of the study (Alexander and Bogart, 1961), there was no effect of inbreeding of the dams on the weaning weights of the calves. Brinks, Clark, and Kieffer (1963) 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 (1961), on the other hand, found no significant decrease in suckling gain with increased inbreeding of dam, but did find a positive effect of 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.

Age-of-dam Effects

Flower et al. (1963) 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 (1961) 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 more rapidly 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. (1962) 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. (1963 and 1964) noted the same thing in that little culling of cows was practiced in the selection for performance because of the need for them in the herd; so the age-of-dam constants may be biased because constants for older age groups are too high in comparison with an unselected cow population. Marlowe and Gaines (1958) found that age of dam was the most important source of variation affecting preweaning growth rate. They obtained maximum production from cows in the age group of six to ten years. Brown (1960) also found an increase in calf weight with increases in age of dam up to peak years of production. Koger et al. (1962) found that age-of-dam effects varied significantly with pasture, year, lactation, and breed, and they concluded that indiscriminant use of correction factors, especially for age of dam, may introduce more serious error than working with data which has not been adjusted.

Data in Table 5 indicate 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 effect of a good feed supply on both their production and the gaining ability of their calves. Probably both factors contributed, especially since the dams used were younger and 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. Changes in suckling gains associated with changes in ages of dams can best be illustrated by the data in Table 5. During the years that David cows averaged older, suckling gains generally were higher as can be 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 in that of any of the others.

In the Lionheart line, 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 Lionheart female calves. Environmental influences should not have differentially affected these calves, and the percent inbreeding of the female calves was lower than that in the other Hereford lines (Table 3).

Heritability Estimates of Traits

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 because of the limited number of animals involved. The figures in Table 7 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 condition score. These differences in heritability estimates are substantiated in the literature by Swiger et al. (1962), Taylor et al. (1960), Blackwell et al. (1962), and Shelby et al. (1960).

That environmental effects were more prominent during the preweaning period is evident from the data on repeat matings (Figures 17 and 18). Swiger et al. (1962), using variance components, found at two stations that heritability of birth weight was about .33. Heritability of average daily gain to 130 days of age at one station was estimated at –.16 and at another station at +.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.

Blackwell et al. (1962) 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. (1960) 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.

Analysis of Performance of Lines

An overall 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 Earlscourt 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 tests.

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 University. 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. On some occasions two sires were used.

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 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 generally has performed 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 difficulties with genetic abnormalities in this line. The general pattern for 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 the performance levels of the traits against time or against levels of inbreeding were plotted. Results might be interpreted 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 probably 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 for the re-establishment of synthetic lines.

The size of closed lines is probably strongly associated with the length of time that performance can be expected to improve in a selection program, at least for those traits considered in this study. The optimum number of animals needed for longer term response to selection is not known, but an advantage seems to exist even in the addition of 5 breeding females to a line of 15, and the use of 2 sires instead of 1, based on performance in the Angus line. A wider genetic base certainly contributed to continued response, however. Any inherited abnormalities will offset advantages gained from increased numbers if individuals periodically are born with defects. On the other hand, if the abnormality can be eliminated by culling an entire segment of the line, performance can be expected to be maintained or improved in the remaining segment of the line if there are adequate numbers.

The size of the lines may also influence conscious or unconscious selection for or against an increase in inbreeding. The small size of the lines in this study led to selection for some degree of heterozygosity, as reflected by selection differentials computed on inbreeding as a trait. This heterozygosity is probably more important early in the calf's life, as indicated by an early decline in preweaning performance in the first years of the selection study. It is also important during the postweaning period, as indicated by the decline in performance later in the selection program.

SUMMARY AND CONCLUSIONS

- 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. Differentials were higher on the sire side of the matings because of the small number of sires needed; therefore, a greater selection intensity through the sires was made.

- Since the inception of the lines, performance initially improved, after which there was a plateau followed by a decline. This caused response to selection to be 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. Selection in the Angus line was generally reflected favorably in the response obtained, because of a broader genetic base and more animals from which to select.

Selection against inbreeding on the sire side of the matings was automatically performed in conjunction with selection for increased performance. Again, due to the low selection intensity of 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 lines.

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

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.

Older cows produced more rapidly gaining calves during the preweaning period in all lines except the Lionheart, in which young cows had male calves that gained 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, and older cows again made up the breeding herd in later years. Angus cows followed the same pattern as that shown in the David line. 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 declined, especially in female calves, despite an increase in age of dam.

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

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