ABSTRACT

GENETIC PARAMETERS IN STRAIGHTBRED AND CROSSBRED BEEF CATTLE POPULATIONS

by Richard John Dunn

The data included records on 375 steers and 362 heifers, born over a four year period, 1960 to 1963 inclusive, at the Fort Robinson Beef Cattle Research Station in northwestern Nebraska. The calves were from 80 cows each from the Angus, Hereford, and Shorthorn breeds, and were the progeny of 17 Angus, 16 Hereford, and 16 Shorthorn sires. The cows were randomized to breeding pastures each year so that each sire was bred to twice as many cows of his own breed as to each of the other two breeds. Traits studied were birth weight, weaning score, and adjusted 200-day weight (steers and heifers); adjusted final weight, marbling score, final carcass grade, fat thickness, rib-eye area, and actual cutability (steers); and adjusted 550-day weight (heifers).

The experimental design included new sires each year which caused a hierarchal design with sires nested within breed of sire and year, but cross classified with breed of dam. Steers and heifers were analyzed separately for all traits.

Variance components for all traits were obtained from analysis of variance tables. A least-squares and maximum likelihood general purpose program was used to compute the following estimates of genetic parameters and standard errors:

1. Components of genetic variance and covariance were calculated for each of the mating types. There were no differences in the sire components between the straightbreds and crossbreds, indicating similar additive genetic variance in the two groups.
2. Heritability estimates were obtained for the various traits by the paternal half-sib correlation method. Separate analyses were published for the pooled within straightbred, and pooled within crossbred groups. The analyses yielded heritability estimates from 0.15 to 0.85 with most standard errors between 0.3 and 0.4. No difference was noted between the crossbreds and straightbreds. The heritability estimates were large enough to indicate that mass selection should produce improvement in the traits.
3. Genetic and phenotypic correlations for the pooled within straightbred analyses are presented. Standard errors, in general, varied from 0.3 to 0.4. The high genotypic and phenotypic correlations among traits associated with weight (birth and 200-day weight, final weight, 550-day weight, rib-eye area, and actual cutability) were the most important from an economic standpoint.

Results indicate that mass selection for traits associated with weight in the purebred population should give simultaneous improvement in these traits. Adjusted 200-day weight (steers and heifers), ad-

justed final weight (steers), and 550-day weight (heifers) were recommended as traits to emphasize in a mass selection program.

4. Estimates of the correlations between the genetic ability of a sire to produce the same trait in straightbred and crossbred progeny, and between his genetic ability to produce one trait in the straightbred population, and another trait in the crossbred population, were high. It was concluded that mass selection in the purebred populations that make up a cross would be as effective in improving commercial production in the crossbreds as it would be in improving commercial production in a breeding program where the purebred bulls were bred to commercial cattle of their own breed.

GENETIC PARAMETERS IN
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BEEF CATTLE POPULATIONS

By

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DEDICATION

To Mom and Dad for their unending inspiration, encouragement, love, and sacrifice.

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INTRODUCTION

The beef cattle breeder of today is getting caught in a "cost-price squeeze". He needs to identify those animals in his herd, or other herds, which will add the most improvement in the traits that will contribute to productive efficiency and better beef carcasses. He must then utilize these animals in effective breeding plans that will help him make [illegible] improvement in his herd. This, in turn, will provide increased profits and a better means of living for these beef cattle breeders, the packers and retailers of beef, and will supply the consumer with an appealing, high-quality, nutritious product at a reasonable cost. As Gregory (1965) states: "One segment of the beef cattle industry cannot be divorced from the other segments. From a long term standpoint, there is an interdependence among them. The commercial producer is interested in cows with a long productive life that wean a high percentage of heavy, high grading calves; the feeder desires rapid and efficient feedlot gains; and the packer and retailer are interested in the maximum amount of edible portion per unit of live or carcass weight. The consumer expects this edible portion to be tender, flavorful and juicy".

Beef cattle scientists need more basic knowledge on genetic parameters in order to recommend better breeding and selection methods and plans to these breeders. Measurement procedures for economically important traits and reliable estimates of their genetic parameters (heritabilities, genetic correlations, heterosis, etc.) are fundamental in the search for this basic knowledge. As these measurement procedures are developed, one must consider the relationship of the measures to the trait being studied, the heritability of the measurements, their genetic correlations with other traits being studied, and the relative economic value of the trait being studied. This information is essential to the future potential of beef cattle breeding in this age of efficient, scientific agriculture.

Heterosis has been observed in some of our domestic animals for many years. Several studies are presently in progress to study the influence of heterosis in beef cattle. Several recent studies have used the British breeds because they are the ones most frequently used for production of beef in the northern two-thirds of the United States. The influence of heterosis is estimated by comparing the crossbreds with the average of the straightbreds sired by the same bulls and out of comparable cows. The difference between the crossbreds and straightbreds is due to non-additive gene effects. In general, crossbreeding has resulted in about 3% increase in growth rate up to about 18 months of age, in favor of the crossbred cattle. Heterosis in carcass traits apparently is important only in those traits that are associated with growth of the animal (Gregory *et al*., 1965, 1966a, 1966b, 1966c; Gaines *et al*., 1966, 1967; Brinks *et* al., 1967; and Vogt et al., 1967.)

Beef cattle scientists are generally in agreement that the amount of genetic change of economically important traits in domestic animals, such as beef cattle, depends largely on the size of the genetic variances and the heritabilities of the traits studied.

The heritability estimate is a key to improving the population by breeding methods. It is considered one of the most important parameters in animal breeding. Lush (1948) states it as follows: "A characteristic is not inherited as such. The thing inherited is the ability to respond in a given manner to a given environmental circumstance. The observed phenotype is the net result of these inherited potentialities and the environmental circumstances, such as nutrient supply, temperature, diseases, accidents, etc. which they encounter. Between the genes which are transmitted and the observed phenotype of the plant or animal is a considerable gulf of time and of chemical and physiological processes in which the genes interact with environmental substances, forces and conditions, and also with the primary and secondary products of each other. The complete story of all that happens in this period includes the whole subject matter of embryology and the physiology of growth and development." Reviews reveal only one estimate of heritability between straightbred and crossbred beef cattle (Miquel and Cartwright, 1963), but in the last 20 years numerous studies have been made, providing heritability estimates for economic traits, in straightbred and purebred beef cattle. These studies reveal that heritability of birth and weaning weight, and conformation scores are moderately high, and post-weaning growth rate and carcass traits are highly heritable. Warwick (1958) concluded that beef cattle differ in their inherent productivity and that those differences are rather high in heritability. Gregory (1961) reported that heritabilities for most of the economically important traits, except fertility, seem high enough for selection to be reasonably effective.

If selection pressure is applied to more than one trait at the same time, progress is affected by the genetic interrelationship among the important traits, the amount of selection practiced, and the generation interval. In order to prepare effective breeding plans, estimates of genetic, environmental, and phenotypic parameters for traits of economic importance are needed. Accurate estimates of genetic correlations allow us to predict direct and correlated responses in one trait resulting from selection for another single trait. There are only a few estimates of genetic correlations between traits, and studies on correlated responses in the literature. This is mainly because of the great amounts of data that are necessary to provide reliable estimates of these genetic correlations among the important performance traits. Gregory (1961) feels that to date no important genetic antagonisms have been shown among important performance traits, but we have not shown experimentally that mass selection is an effective breeding program for these traits.

If non-additive gene action is a major source of genetic variance, selection on the basis of purebred or straightbred performance may not be effective for improving the performance of the crossbreds. The research by Gregory, using these data, show that most of the traits exhibit hybrid vigor, therefore some non-additive gene action must be involved.

Comstock (1960), referring to swine, stated the need for estimates of genetic variance among crossbred sire families, and the regression of crossbred sire progenies on purebred sire performance. If this is low, selection for purebred performance will be proportionately ineffective for crossbred improvement. If negative genetic correlations are important, he felt that the effective genetic variance among crossbred sire families may be considerably greater than that within the breeds.

To evaluate the expected progress in a crossbred population when selection is practiced in a purebred population, estimates of genetic variances and covariances from contemporary purebred and crossbred data in beef cattle are needed. These estimates are not in the literature. These are crucial questions that must be answered if crossbreeding becomes a more important force in our future beef breeding programs.

The objectives of this study were:

1. Obtain estimates of the heritability of economically important live- animal and carcass traits in a straightbred beef cattle population.
2. Obtain estimates of the heritability of economically important live- animal and carcass traits in a crossbred beef cattle population.
3. Obtain estimates of genetic variances and covariances from contemporary straightbred and crossbred data in beef cattle.
4. Study the effect of genetic variances and covariances from contemporary straightbred and crossbred beef cattle data on the effectiveness of selection for genetic improvement in beef cattle.
5. Estimation of interrelationships of straightbred and crossbred progeny performance in the same trait, and between one trait in the straightbred population, and another trait in the crossbred population.
6. To obtain estimates of specific genetic parameters in straightbred and crossbred populations of beef cattle for various economic traits, and to use these estimates to predict trait response to indirect selection within populations of similar genetic makeup.

REVIEW OF LITERATURE

Information is very limited in beef cattle breeding research regarding differences in heritability estimates between straightbred and crossbred populations, genetic correlations between productivity of traits in straightbred and crossbred populations, and covariances between progeny performance of traits in crossbreds, straightbreds, and between the two populations.

Some studies have been made in swine. This is probably because crossbreeding research in swine has been conducted longer than in beef cattle.

Enfield and Rempel (1962) made a study to estimate the covariance of sire effects in purebred and crossbred populations of swine. These covariance estimates were: weaning weight, -2.42 ± 3.67; average daily gain, 0.0040 ± 0.0018; and backfat probe, 0.0005 ± 0.0007. The authors stated that the genetic progress that can be made in improving crossbred performance by selection within pure lines can be estimated if the following is known: (a) selection intensity in the purebreds, (b) phenotypic variance of the selection criterion in the purebreds, and (c) the covariance of sire effects in the populations under selection and the population cross. They concluded that practicing mass selection in both sexes of both purebred populations that make up a cross, would make the expected improvement of the crossbreds the product of the average selection differential in the purebreds, and the ratio of four times the covariance of sire effects, divided by the phenotypic variance in the purebreds. They made estimates of this ratio which they felt were somewhat analagous to heritability in the purebred populations. These were: weaning weight, -.17; average daily gain, 0.42; and backfat probe, 0.07.

Taylor et al. (1965) studied genetic correlations between straightbred and crossbred swine. The straightbred and crossbred daughters of 35 boars were composed of straightbred daughters having crossbred litters, daughters retained to propagate their strain, and crossbred daughters. Traits studied were: litter size and litter weight at birth, 21, and 56 days. Three variance components and two covariance components involving comparisons of crossbred daughters with both of the other types of daughters were estimated for each trait. One-half of the variance components were negative, but, in general, they were smaller than the corresponding covariance components of the same sign. Only the covariance components for litter weight at 21 days and one for litter weight at 56 days were positive. Only three genetic correlations were obtained since some negative variance components were obtained. A positive genetic correlation of 0.18 was obtained for litter weight at 21 days when comparing crossbred daughters to straightbred daughters. For litter weight at 56 days the correlation was 0.61 between crossbred and straightbred daughters and -.38 for crossbred daughters and straightbred daughters having crossbred litters. They concluded that since most of the covariance components were negative, non-additive gene effects may be important sources of variation in the traits studied.

Stanislaw, et al. (1967) studied progeny records of 99 purebred boars that sired both purebred and crossbred litters. The heritability estimates for 56-day weight, postweaning daily gain, and probed backfat thickness in the purebreds were 0.03 ± .06, 0.28 ± .06, and 0.55 ± .12, respectively. The corresponding estimates within the crossbreds were 0.19 ± .09, 0.39 ± .10, and 0.47 ± .13. The genetic correlations within the purebreds between 56-day weight and postweaning daily gain, 56-day weight and backfat thickness, and postweaning daily gain and backfat thickness, were 0.29 ± .50, -.05 ± .53, and -.07 ± .18, respectively. Within the crossbreds the corresponding correlations were 0.20 ± .21, 0.61 ± .16, and -.39 ± .18. The authors concluded that improvement in postweaning growth rate and probed backfat must come almost entirely from selection pressure applied to these traits, but in the crossbred it appeared that postweaning daily gain could be increased by selection for either 56-day weight or less backfat. The sire components of covariance were 1.61, 0.0013 and 0.0023 for 56-day weight, postweaning daily gain and probed backfat thickness, respectively.

Robison, et al. (1964) studied boars with both purebred and crossbred progeny to obtain preliminary estimates of the effectiveness of selection in purebred populations for achieving improvement in crossbred populations. Genetic correlations between purebred and crossbred progeny means for the two breeds of boars were 0.22 and 0.72 for 140-day weight and 0.21 and $>$1.00 for backfat at 140 days. They concluded that selection for purebred performance would not be effective for improving the crossbreds.

Louca and Robison (1967) estimated components of variance and covariance from records on purebred and crossbred pigs sired by 76 boars. Heritability values from paternal half-sib correlations were estimated for birth weight, 154-day weight, litter size at birth, weaning, and 154 days, and backfat probe. The authors quoted these estimates as 0.17 ± 0.42, 0.09 ± 0.29, and 0.05 ± 0.20 for birth weight, 0.35 ± 0.34, 0.14 ± 0.15, and 0.33 ± 0.18 for backfat probe, and 0.70 ± 0.41, 0.81 ± 0.35, and 0.65 ± 0.24 for 154-day weight in the purebred boars, barrows, and gilts, respectively. Corresponding values for the crossbred barrows and gilts were 0.01 ± 0.05 and 0.03 ± 0.05 for birth weight, 0.03 ± 0.04 and 0.00 ± 0.04 for 154-day weight and 0.22 ± 0.06 and 0.09 ± 0.05 for backfat probe. The comparison of the components of variance in the two breeding groups led the authors to suggest that non-additive gene action was involved. Both studies indicated to the authors that selection on the basis of purebred performance would not be effective for improving crossbred performance and that selection for specific combining ability should provide a better means for utilizing heterosis experienced in crosses. Genetically, birth weight was negatively correlated with backfat probe and positively correlated with weight at 154 days. Weight at 154 days was negatively correlated with backfat probe. The authors felt that, in general, the magnitude and direction of associations among traits were high enough to suggest that simultaneous improvement in all traits would be possible.

Only one reference comparing heritabilities in crossbred and purebred (or straightbred) beef cattle was found in the literature. Miquel and Cartwright (1963) compared heritabilities for birth weight, weaning weight, and feedlot gain from 10 years of data on Herefords (H), Brahmans (B), and various crosses of the two breeds: B sire x H dam, F_1's (BH), H x B F_1's (HB), backcrosses to H sires (HF_1) and backcrosses to B sires (BF_1). They adjusted their data for effects of sex, year, and age of dam with least squares analysis. Heritability estimates by the paternal half-sib method for birth weight were: H, 0.15; B, 0.16; BH, 0.55; HB, 0.50; HF_1, 0.26; and BF_1, 0.20. Heritability estimates for weaning weight were: H, 0.24; B, 0.44; BH, 0.25; HB, 0.22; HF_1, 0.07; and BF_1, 0.19. Estimates for feedlot gain were: H, 0.74; B, 0.23; BH, 0.90; HB, 0.00; HF_1, 0.42; and BF_1, 0.70. The authors noted that the estimated genic variance and heritability ranked in the same order for all characters with one minor exception. They concluded that selection would be roughly as effective in crossbreds as in purebreds.

One study was also located in the literature that dealt with heritability estimates and genetic correlations between straightbred and crossbred lambs. Bassett and Shelton (1966) studied birth weight, slaughter score, and 120-day weight of lambs out of straightbred ewes, and sired by rams of the same breed, and rams of two other mutton breeds. Heritability estimates for birth weight were 0.60 for the adjusted data in the straightbred lambs, and 0.24 and 0.03 for the crossbred lambs. Estimates of heritability of adjusted 120-day weight for the straightbred lambs were 0.47 and 0.39, as compared with 0.25 and 0.45 for the crossbred lambs. Estimates of heritability for adjusted slaughter score were 0.29 and 0.33 for the straightbred lambs, and 0.21 and 0.19 for the crossbred lambs. The two estimates include data which were both adjusted and not adjusted for environmental effects as determined by least-squares analysis. In only one instance did the crossbred data give a higher estimate of heritability than the straightbred data. The genetic correlation between birth weight and 120-day weight in the crossbred data was 0.87. This was the highest value found in the study. The authors did not quote other genetic correlations.

The literature contains numerous studies of heritability estimates for economic traits in straightbred and purebred beef cattle. There are, also, a few estimates of genetic correlations between economic traits in straightbred and purebred beef cattle. Warwick (1958) attempted to summarize studies which were known to have been reported up until that time. Those heritability estimates, related to this study, are given in table 1.

Table 1. Heritability estimates for beef cattle characters (Warwick, 1958)

Character	No. of estimates	Av. of estimates	Range of estimates
		%	%
Birth weight	15	41	11-100
Weaning weight	26	30	-13-100
Post-weaning feedlot gain	13	45	19-70
Post-weaning pasture gain	6	30	9-43
Carcass traits:			
Carcass grade	5	34	-30-84
Rib eye area	3	69	69-72
Conformation grades:			
Weaning	16	26	0-53
Slaughter	5	39	-13-63

Warwick also summarized the genetic interrelationship of traits in beef cattle that had been studied prior to his summary. Results prior to 1958 showed one study indicating a negative relationship between maternal abilities and post-weaning gaining ability; another giving positive genetic correlations for gains of steers through three seasons, including a winter feeding period, grazing for a summer, and a second winter feeding period; and one with positive genetic correlations between gains in consecutive 84-day periods of a 252-day feeding period. Observed positive genetic, but negative environmental correlations between weaning score and subsequent feedlot gains were found by one group of workers. Several others studied genetic relationships among grade and gains at various periods. Only a few reports on genetic correlations had appeared at that time due to the large bodies of data required for precise estimates.

Warwick's summary has been used as a base for this review. No attempt has been made to duplicate the literature cited in his summary.

Table 2 is an attempt to summarize heritability studies since Warwick completed his summary in 1958, including estimates related to this study. Only heritability estimates obtained by the paternal half-sib method are included. The estimate is a simple arithmetic average of the values reported by the research workers. No attempt has been made to adjust values to number of head of cattle included, variance of the estimate, etc. Where a worker reported more than one value (different sexes, different breeds, different planes of nutrition, etc.) one combined average value was obtained. Again, this was a simple arithmetic average with no adjustment made. If the author gave a pooled estimate, this was the one used. Thus, the summary contains one estimate per trait, per report, with each receiving equal weight.

Table 2. Heritability estimates for beef cattle characters

Character	No. of estimates	Av. of estimates	Range of estimates	References
		%	%	
Birth weight	17	44	11-100	61,95, 46, 84, 90,82, 67, 6 , 49, 4, 80, 43, 77,50, 24, 33, 70,48.
Weaning score	27	37	5-70	10, 47,99, 3, 100, 85, 82, 72, 63, 67, 6, 78, 49, 18, 60, 36, 57, 62, 80, 55, 12, 69, 23, 91, 34, 50, 70, 48.
Weaning weight	40	35	-12-100	61, 97, 10, 68, 46, 47, 84, 99, 90, 3, 100, 85, 82, 67, 6, 78, 64, 86, 36, 9, 88, 35, 89, 4, 57, 80, 79, 21, 76, 55, 43, 20, 12, 69, 23, 42, 77, 50, 24, 70.
Final feedlot weight	17	57	2-100	81, 84, 99, 5, 3, 100, 85, 82, 86, 9, 8, 88, 21, 19, 58, 13, 70.
Marbling score	2	47	31-63	9, 23,
Final carcass grade	9	57	0-135	10, 13, 3, 82, 56, 17, 21, 20, 23.
Fat thickness	8	48	24-74	13, 82, 86, 9, 17, 21,20, 23.
Rib eye area	9	58	12-156	13, 82, 56, 9, 17,44,21,20,23.
Actual cutability	1	23		23.
Long yearling pasture weight	10	40	10-71	97, 3, 85, 66, 6,36,59,76,58,70

Several summaries of heritability estimates have been made since Warwick's. Gregory (1961) presented a summary almost identical to that of Warwick. He did not identify the references included in each trait. Clark et al., (1963) included two tables of heritability estimates, but he did not obtain an average value for each trait. Most of his references were included in the summary by Warwick, but he included a few later studies.

Table 3 is a summary of genetic correlations reported for cattle since 1958. Warwick (1958) presented a brief discussion of the work up to that time, but did not present actual values.

Petty and Cartwright (1966) prepared a summary of genetic and environmental statistics for growth and conformation traits of young beef cattle. A number of the traits were the same ones studied in this work. They presented weighted averages of paternal half-sib estimates, as well as unweighted ones. The estimates were averaged by weighting them with either the number of sires included in each estimate or the estimated number of sires based on the average number of offspring per sire in the other estimates of that trait. Genetic correlations were given, with appropriate sire-weighted averages determined by the "Z" transformation method using the number of sires or the estimated number of sires involved in the estimate when the actual number was not given. These summaries are presented in tables 4 and 5. The authors tried to select the most independent and pertinent

Table 3. Genetic correlations for beef cattle characters.
(Genetic correlations are to the right of the diagonal with the top number being the number of estimates, the middle number being the av. of the estimates, and the bottom number the range. References are at the left of the diagonal.)

	Birth wt.	Weaning score	Weaning wt.	Final feedlot wt.	Marbling score	Final carcass grade	Fat thickness	Rib-eye area	Actual cutability	Long yrlg. pasture wt.
Birth wt.		7 .003 -.40-.99	9 .54 .16-.99	4 .60 .44-.78		1 -.43	1 -.16	1 -.01		1 .60
Weaning score	5,82,6 72,67, 70,48.		15 .08 -.81-.72	6 .29 -.19-.69	1 -.15	4 .34 -.70-1.17	1 -.03	2 .16 .08-.24	1 -.25	2 -.34 -.08-(-.61)
Weaning wt.	77,46,5 84,82,6 67,24,70	11,47,99,70 3,100,85,82, 67,23,12,55,	6, 5,36.	9 .72 .33-.98	1 .06	4 .58 -.04-.92	3 .02 -.29-.91	2 .20 .01-.40		5 .53 .18-.81
Final feedlot wt.	84,5, 82,70	99, 5,70, 100,82,3	84,99,3, 100,82,5, 86,88,70			2 .52 .16-.88	2 .30 .18-.42	1 .07		
Marbling score		23	23			1 .94	1 .85	1 -.11		
Final carcass grade	82	11,3, 23,82	11, 3, 23, 82	3, 82	23		3 .75 .23-1.03	3 .01 -.35-.48		
Fat thickness	82	82	82, 86, 23	82, 86	23	82, 17, 23		3 .34 .08-.63	1 .86	
Rib-eye area	82	82, 23	82, 23	82	23	82, 17, 23	82, 17, 23			
Actual cutability		23					23			
Long yrlg. pasture wt.	6	3, 6	3, 85, 6,36,76							

Table 4. Summary of heritability averages obtained by paternal half-sib method (Petty and Cartwright, 1966)

Trait	No. of estimates	Unweighted average	Weighted average	Off. per sire, weighted average
Birth weight	21	.44	.44	16
Weaning score	24	.34	.36	16
Weaning weight	30	.33	.32	14
Final feedlot weight	15	.56	.62	10
Yearling pasture weight	9	.39	.41	10

Table 5. Summary of genetic correlation averages. (Petty and Cartwright, 1966)

Correlation between	Overall r_G	Weighted r_G	Off. per sire weighted average
Birth weight - Weaning weight	.58	.58	21
Birth weight - Weaning score	-.01	.36	13
Birth weight - Final feedlot weight	.61	.64	--
Weaning weight - Weaning score	.24	.39	13
Weaning weight - Final feedlot weight	.75	.79	11
Weaning weight - Yearling pasture weight	.46	.67	12
Weaning score - Final feedlot weight	.47	.43	--
Weaning score - Yearling pasture weight	-.08	-.03	10

information available. The summary varies from the ones included in this study since it contains selected references dating back to the first studies (1946). Thus, it contains references cited in Warwick's summary, as well as those presented in this study.

In general, the review of literature summary of heritabilities in this study is higher than those of Warwick (1958) and Gregory (1961), averaging about 9% higher in the traits included in all summaries. The study is in rather close agreement, however, with the summary of genetic statistics given by Petty and Cartwright (1966), including both heritabilities and genetic correlations. There are some differences in the data included, as was discussed earlier, but in a number of the heritability estimates and genetic correlations, the majority of the references used were identical in both cases. In some cases they organized the material in a slightly different manner than that done in this study. The present summary also contains some additional references not included by Petty and Cartwright, or published after their study.

At best, heritability estimate averages and genetic correlation averages presented can only be used as a guide, but they probably give as good an overall picture as anything presently available. All summaries combined represent over 100 studies, and include a high percentage of the work done since 1946, when the first estimates were made. We must realize, however, that the values may be biased by many yet undetermined factors. Some of the estimates are based on too few estimates to give the type of accuracy and confidence useful estimates should have. It is hoped that these summaries may be of value to research workers to compare their future estimates with, and for them to use in formulating breeding plans in beef cattle.

MATERIALS

Data for this study were obtained from an experiment designed by Gregory et al. (1965, 1966a, 1966b and 1966c) to evaluate the effects of heterosis on traits of economic value in beef cattle.

The plan of the experiment was described by Gregory et al. (1965, 1966a, 1966b, 1966c). The experiment began in 1957. High grade heifer calves were purchased from Angus, Hereford and Shorthorn breeders in Nebraska, Montana and Colorado. All females were outbred and randomly selected from large populations of their respective breed. The three breeds were chosen because they are the most important ones used for beef production in the United States. The plan was to obtain calves of each breed from a number of sources.

Table 6 contains the design of the experiment, showing the total number of sires, dams and calves by subgroup. The numbers vary slightly from those shown by Gregory since all calves not having complete data recorded on them were dropped from this study. This was necessary for the computing of genetic correlations and covariances.

Table 6. Experimental design showing the total number of sires, dams and calves by subgroup.

Dams		Breed of sire and number of offspring						
		Hereford		Angus		Shorthorn		Total
Breed	No.	M[a]	F[b]	M	F	M	F	offspring
Hereford	80	63	53	35	25	34	35	245
Angus	80	29	37	55	56	26	39	242
Shorthorn	80	33	33	34	27	66	57	250
Total	240	125	123	124	108	126	131	737

[a] M = male, [b] F = female

The original experimental design included eighty females of each of the three breeds. These females produced four calf crops (1960, 1961, 1962 and 1963). Because all females were the same age each year, calves produced during the four years were out of 3-, 4-, 5-, and 6-year-old dams, respectively. Females not calving in any given year were removed from the experiment.

The design of the experiment included using four bulls of each breed per year. This was revised slightly, with three Angus bulls being used in 1960, and six in 1963. This made a total of 16 Hereford bulls, 17 Angus bulls, and 16 Shorthorn bulls. These bulls were obtained from breeders or experiment stations in Montana, Wyoming, Colorado, North Dakota, Nebraska, Kansas, Oklahoma, Iowa and Missouri. A deliberate attempt was made to obtain bulls from different sources. Some of the sires were inbred, but the inbreeding was low. The sires represented a cross-section of their respective breed. The females were randomly allotted to breeding pastures, with twice as many being exposed to bulls of their own breed as to each of the other breeds.

Site of the experiment was the Fort Robinson Beef Cattle Research Station, Crawford, Nebraska. The station is located in the Mixed Sandy and Silty Tableland of northwestern Nebraska. The average rainfall in the area varies from about 15-18 inches per year, and the native range vegetation is made up of short and intermediate grasses.

The management of the experimental herd included a calving season extending from approximately February 10 to May 1, with the majority of calves being dropped between February 20 and March 31. Calves ran with their dams on native pasture until weaning time, which was the first week in October each year. Calves averaged from 200 to 210 days of age at weaning time. All calves from each calf crop were weaned on the same day. Birth weight was recorded on each calf within 24 hours of birth. All male calves were castrated and all calves with horns were dehorned at the time they were weighed. The weaning weight was recorded in October. All weaning weights were adjusted to a constant age of 200 days, by multiplying the average daily gain by 200 and adding the birth weight. A committee evaluated the beef conformation of each calf at the time they were weaned. The scoring system used is listed in table 7. Most of the calves were given the choice grades.

All the heifers from each year were run together with the exception of the breeding season of their dams. Those dropped in 1960 and 1961 were managed for calving as 3-year-olds. They were fed 1 pound of a 40% supplement per head per day on native range during the first winter. The ration was planned to produce gains of approximately 0.5 pound per day during the 196-day wintering period from weaning in October until April. The following summer the heifers were grazed on native summer range for a grazing season of 154 days.

The heifers from the last two calf crops (1962 and 1963) were managed for calving as 2-year-olds. They were grazed on limited native range the first winter, but received about 5 pounds of concentrate feed per head per day in addition to a liberal feeding of hay. This program was planned to produce a daily gain of about a pound during the 196-day period. These heifers were grazed during the following summer on a short and intermediate grass range similar to that used with the first two crops of heifers.

Following weaning, all steer calves were fed for a post-weaning period of 252 days. Weaning weight and date were used as initial weight and the base date for the feeding period. A growing-fattening ration with approximately 65% TDN was fed to the steers. The 1960 steers were group fed, while the 1961, 1962 and 1963 steers were on a program of individual self-feeding. The feeding program for the individually fed steers consisted of a 2- to 3-week conditioning period, followed by the use of individual self-feeders for the rest of the 252-day period. The steers were randomly assigned to their individual feeder, and were tied to their feeder overnight except the 1963 steers which were fed part of their feed during the day.

The feeding program consisted of a pelleted ration in 1960 and 1961, and one that was ground and mixed in 1962 and 1963. During most of the years about 1.5 pounds of long grass hay per steer was fed free choice to the group before they were fed their individual grain ration. Plenty of bunk space was available for the hay and it was readily consumed. Ample water was available to the steers in their group lots when they were not in their individual feeding area. All steers were slaughtered at the end of the 252-day feeding period each year at an average age of 452 days.

Carcass measures and grades were obtained on all four calf crops in a commercial beef cooler. Detailed carcass cut-out data, using the right side of each carcass, were obtained on calves from the 1961, 1962 and 1963 calf crops. Processing of wholesale cuts was on the basis of boneless, closely trimmed cuts (not over 0.3 inch of fat on any surface). Retail product, fat trim and bone were weighed and recorded.

All cuts were boneless with the exception of the loin which contained the vertical and spinous processes, and the rib which contained approximately 6 inches of the rib bones. The same cut-out procedure was used on all carcasses. Data was adjusted to a complete carcass basis by multiplying the cut-out values obtained from the right side of each carcass by two.

Beef cooler carcass data were obtained by official graders of the U. S. Department of Agriculture.

Actual cutability was not obtained for the steers produced in 1960. This was estimated from the percent retail cuts estimated by the USDA equation, using data from the other three calf crops as a guide. A list of the traits used in this study is shown in table 7.

Table 7. Description of the traits used in this study.

Item	Description
Steers and Heifers (Preweaning):	
Birth weight	Actual birth weight
Weaning score	7 = low good, 8 = av. good, 9 = high good, 10 = low choice, 11 = av. choice, 12 = high choice, 13 = low prime, 14 = av. prime, 15 = high prime
200 day weight	Average daily gain birth to weaning x 200 + birth weight
Steers (Postweaning):	
Adjusted final weight	Actual final weight minus actual weaning weight + 200 day weight
Marbling score	0 = tr. 1 = sl-, 2 = sl, 3 = sl+ 4 = sm-, 5 = sm, 6 = sm+ 7 = mt-, 8 = mt, 9 = mt+ 10 = md-, 11 = md, 12 = md+ 13 = sl.ab.-, 14 = sl.ab., 15 = sl.ab.+ 16 = md.ab.-, 17 = md.ab., 18 = md.ab.+ 19 = ab- 20 = ab
Final carcass grade	7 = low good, 8 = av.good, 9 = high good, 10 = low choice, 11 = av. choice, 12 = high choice, 13 = low prime, 14 = av.prime, 15 = high prime
Fat thickness	A single measurement taken 3/4 the distance of the longest axis of the rib-eye recorded to the nearest .01 inch.
Rib-eye area	Square inches
Actual cutability	Lbs. of boneless closely trimmed beef from the round, loin, rib and chuck.
Heifers (Postweaning):	
Adjusted 550 day weight	550 day weight minus actual weaning weight + 200 day weight

STATISTICAL METHODS

The statistical analyses of the data to measure the effects of heterosis were explained by Gregory *et al*. (1965, 1966a, 1966b, 1966c). Because the cattle used in that study and this study are identical, with a few exceptions, the analyses done by Gregory were not repeated.

Variance components for all traits studied were obtained from analysis of variance tables.

The experimental design included a new crop of sires each year which caused a hierarchal design with sires nested within breed of sire and year, but cross-classified with breed of dam. Year and sires were random effects, with the other main effects being fixed. Steers and heifers were analyzed separately for each trait. This was necessary primarily for the analysis of post-weaning traits and correlations between pre- and post-weaning traits because of different management after weaning.

Since the same set of females were used throughout the study, age of dam was confounded with years. Traits affected by age of dam cause the mean squares for years to be augmented by the age of dam effects.

Method of Analysis:

The following general model was used to analyze the data in the study, except where otherwise noted.

General Model:

$$Y_{ijklmo} = \mu + y_{ij} + s_{ijklm} + e_{ijklmo}$$

μ = an effect common to all animals

i = trait

y_{ij} = an effect common to all animals calved in the j^{th} year.

s_{ijklm} = an effect common to all calves sired by the m^{th} sire of the k^{th} breed of sire when mated to the l^{th} breed of dam in the j^{th} year.

e_{ijklmo} = the random experimental error.

General Design of the Experiment:

Table 8 is used to explain the general design of the experiment.

Explanation of information in cells of table 8:

This table is an example of several that were used in the analysis. This is an example of steer calves from Hereford sires, and using one combination of two traits as an example: birth weight and yearling weight. A similar one was used for heifer calves from Hereford sires for these two traits. Similar tables were used for each pair of traits, in each sex, and in each sire breed group (Hereford, Angus, and Shorthorn), except where otherwise noted.

Each cell (A to O) in the table was made up of mean squares or covariances including the following sources:

Source:

Years
Sires/Years
Calves/Sires/Years

Each cell in the table included the following information:

Table 8. Example of the analysis of the data, steer calves, Hereford sires.

	Trait	Birth weight (BW)				Yearling weight (YW)				Covariance (BW) (YW)			
	Year	1960	1961	1962	1963	1960	1961	1962	1963	1960	1961	1962	1963
	Sire	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n	1,2-n
	Straightbred Hereford (HH)	A				B				C			
Crossbreds	Hereford-Angus (H-A)	D				E				F			
	Hereford-Shorthorn (H-S)	G				H				I			
	Covariance (HH) (H-A)	J				K				L			
	Covariance (HH) (H-S)	M				N				O			

A, B	Heritability of the traits birth weight (bw) and yearling weight (yw) in the straightbred Hereford population.
C	Genetic correlation between production of the traits (bw) and (yw) in the straightbred Hereford population.
D, E	Heritability of the traits (bw) and (yw) in the Hereford-Angus crossbred population.
F	Genetic correlation between production of the traits (bw) and (yw) in the Hereford-Angus crossbred population.
G, H	Heritability of the traits (bw) and (yw) in the Hereford-Shorthorn crossbred population.
I	Genetic correlation between production of the traits (bw) and (yw) in the Hereford-Shorthorn crossbred population.
J	Correlation between the genetic ability of a sire to produce straightbred Hereford progeny and his genetic ability to produce Hereford-Angus crossbred progeny for the trait (bw).
K	Correlation between the genetic ability of a sire to produce straightbred Hereford progeny and his genetic ability to produce Hereford-Angus crossbred progeny for the trait (yw).

L*	Correlation between the genetic ability of a sire to produce the trait (bw) in straightbred Hereford progeny and his genetic ability to produce the trait (yw) in a Hereford-Angus crossbred population (and vice versa).
M	Correlation between the genetic ability of a sire to produce straightbred Hereford progeny and his genetic ability to produce Hereford-Shorthorn crossbred progeny for the trait (bw).
N	Correlation between the genetic ability of a sire to produce straightbred Hereford progeny and his genetic ability to produce Hereford-Shorthorn crossbred progeny for the trait (yw).
O*	Correlation between the genetic ability of a sire to produce the trait (bw) in straightbred Hereford progeny and his genetic ability to produce the trait (yw) in a Hereford-Shorthorn crossbred population (and vice versa).

* Due to the many combinations of traits involved, a limited number were selected to study (birth weight, adjusted weaning weight, adjusted final weight (steers) and 550-day weight (heifers), and actual cutability). These traits were selected because they seemed to be the most important economically. Since adjusted final weight and 550-day weight were thought to be the most important single traits

studied, the correlations involved combinations of the other three traits with adjusted final weight and weight at 550 days of age.

Estimates of genetic parameters and standard errors of the estimates were obtained by use of the Least-Squares and Maximum Likelihood General Purpose Program (LSMLGP) written by Walter R. Harvey, Ohio State University, who assisted in the computations of the analyses on this portion of the data. Details are given by Harvey (1960, 1964). The program subroutine, which computes these genetic parameters, calculates estimates that are identical to those obtained by the Henderson (1953) Method 3.

The standard errors calculated by this program are approximate because no allowance is made for adjustments of data for the effects of fixed factors. They thus afford only minimum estimates of the standard errors (standard errors are at least as large as these). Formulas used in the program to obtain estimates of these standard errors are modifications of those given by Swiger et al., (1964) and Tallis (1959).

The following model was used for computing estimates of heritability and genetic correlations from paternal half-sibs:

$Y_{ijkl} = \mu + y_{ij} + s_{ijk} + e_{ijkl}$

μ = an effect common to all calves.

i = trait

y_{ij} = an effect common to all calves calved in the j^{th} year.

s_{ijk} = an effect common to all calves by the k^{th} sire in the j^{th} year.

e_{ijkl} = the random experimental error.

Dickerson (A. S. A. P., 1960) and Lush (1948) have described the expected composition of variances and mean squares. Table 9, from Dickerson, summarizes these.

Methods of estimating variance and covariance components with unequal sub-class numbers have been outlined by Hazel *et al.* (1943), Henderson (1953), and King and Henderson (1954).

Paternal half-sib heritability estimates and genetic correlations for traits within a mating type were computed using the analysis of variance form shown in table 10.

The form is similar to that used by Hazel *et al.* (1943). Sums of squares and cross products were computed in the usual manner.

The within sire component $V(W_i)$ expresses the variation between individual offspring by the same sire. The between sire component $V(S_i)$ expresses the differences between the true averages of sire groups. Therefore, offspring from different sires have an expected variance $V(W_i) + V(S_i)$. The subscript i denotes the trait being studied. The between sire

Table 9. Expected composition of variances and regression coefficients for autosomal inheritance in non-inbred strains, with no assortive mating. (From Dickerson (A.S.A.P., 1960))

Component of variance	σ^2_A	σ^2_D	σ^2_{AA}	σ^2_{AD}	σ^2_{DD}	σ^2_{AAA}	σ_{MG}	σ^2_M	σ^2_C	σ^2_E	σ^2_{GE}	σ^2_W
Sire, S	.25	0	>.0625	0	0	.016	0	0	0	0	<.25	0
Dam, D	.25	.25	>.1875	>.125	>.0625	>.109	1	1	1	0	<.25	0
Sibs, F	.50	.75	<.7500	<.875	<.9375	<.875	0	0	0	1	>.50	0
Within Ind., W	0	0	0	0	0	0	0	0	0		0	1
σ^2_T = S + D + F + W	1.00	1.00	1.000	1.000	1.000	1.000	1	1	1	1	1	1

σ^2_A = variance from average effects of genes.

σ^2_D = variance from dominance deviations from average gene effects.

σ^2_{AA} = variance from two-loci interactions of av. effects.

σ^2_{AD} = variance from two-loci interactions of av. effects with dominance deviations.

σ^2_{DD} = variance from two-loci interaction of dominance deviations.

σ^2_{AAA} = variance from three-loci interaction of average effects, etc.

σ^2_M = variance from genetic variation in direct maternal effects.

σ^2_{MG} = covariance between total genetic deviations in the <u>transmitted</u> and the <u>direct maternal</u> effects.

σ^2_C = variance from environment that is alike for full sibs, but differs between families from different dams.

σ^2_E = variance from environment that is alike for all observations of one animal, but differs between animals.

σ^2_{GE} = variance from interaction of genotypes with different samples of environments (years, locations, generations, etc.)

σ^2_W = variance from environmental differences among observations on same animal including interaction of genotypes with environmental variations within samples.

Table 10. Analysis of variance and covariance for computing heritabilities and genetic correlations.

Source	d.f.	Expected Mean Squares	Expected Covariance
Years	p-1		
Sires/Years	p(n-1)	$V(W_1) + k_oV(S_1)$	$Cov(W_1W_{1'}) + k_oCov(S_1S_{1'})$
Calves/Sires/ Years	pn(k-1)	$V(W_1)$	$Cov(W_1W_{1'})$
Total	pnk-1		

component is multiplied by k_o which signifies the average number of calves per sire group.

Where unequal numbers of calves per sire group are present, k_o is expressed by Hazel and Terrill (1945) as:

$$k_o = \frac{(\varepsilon k)^2 - \varepsilon(k)^2}{\varepsilon k(n-1)}$$

where:

k = number of offspring per sire

n = number of sires

The between sire component $(V(S))$ is calculated from the formula, $\frac{1}{k_o}(MS_{\text{between sires}} - MS_{\text{within sires}})$.

Hazel and Terrill (1945) outlined relationships between components of variance and the genetic and environmental variance for different systems of mating (non-inbred in this study):

Source	Component	Non-inbred populations
Variance of offspring	V(S)	$(\frac{1}{4})$V(G)
	V(W)	(3/4)V(G)+V(E)
	V(S)+V(W)	V(G)+V(E)

This says, in effect, that the variance component for between sires, V(S), is considered to be an estimate of $\frac{1}{4}$ of the genic variance, and the variance component for within-sires, V(W), is considered to be non-genic variance plus 3/4 of the genic variance.

The genic variance, V(G), includes all the variance that can be ~~attributed~~ to the average effects of the individual genes. The non-genic variance, V(E), includes the effects of environment, dominance and epistasis.

In random mating populations, the contribution of the various underlying correlations of different genic effects to the phenotypic half-sib correlation are as follows: $r_{GG} = \frac{1}{4}$, $r_{DD} = 0$, and r_{II} seems to be about 1/16 for two-gene interactions, 1/64 for three-gene interactions, etc. (Lush, 1948).

In this study, the phenotypic variance of each calf is made up of the genic variance plus the environmental variance. This can be symbolized as follows:

$$V(P) = V(G) + V(E)$$

The components of variance and covariance in this study can be attributed to (1) differences between calves by different

sires and (2) differences between calves by the same sire.

The estimates of the components of variance and covariance for our problem were derived as follows: (methods of Hazel et al., 1943):

Variance

Genic Variance - $V(G)$:

$$V(G_i) = 4.0\ V(S_i)$$

$V(S_i)$ = variance between sires for the ith trait

Variance among calves by the same sire - $V(W)$:

$$V(W_i) = 3/4\ V(G_i) + V(E_i)$$

$V(W_i)$ = within sire variance for the ith trait.

Non-genic Variance - $V(E)$:

$$V(E_i) = V(W_i) - 3/4\ V(G_i)$$

Phenotypic Variance - $V(P)$:

$$V(P_i) = V(G_i) + V(E_i)$$

Covariance

Genic Covariance:

$$Cov(G_iG_{i'}) = 4.0\ Cov(S_iS_{i'})$$

Covariance among calves by the same sire:

$$Cov(W_iW_{i'}) = 3/4\ Cov(G_iG_{i'}) + Cov(E_iE_{i'})$$

Non-genic covariance:

$$Cov(E_iE_{i'}) = Cov(W_iW_{i'}) - 3/4\ Cov(G_iG_{i'})$$

Phenotypic covariance:

$$Cov(P_iP_{i'}) = Cov(G_iG_{i'}) + Cov(E_iE_{i'})$$

Discussions of heritability are given by Lush (1940, 1948, 1949). Of the methods described in these articles, the paternal half-sib method is applicable to this study. The general procedure for computing heritability by this method is as follows: First, subtract the environmental component from their observed resemblance. Second, multiply the result by four. Third, correct for any deviations from random mating. This estimate includes the genic variance, a small amount of the epistatic variance, but none of the dominance variance. It includes nothing from the maternal environment because paternal half-sibs are used. Tallis and Klosterman (1959) discuss the factors that influence heritability estimates obtained by the paternal half-sib method.

Heritabilities within each of the breeding groups were computed as follows:

$$\frac{4V(S_1)}{V(W_1) + V(S_1)}$$

The estimates of heritability of the traits pooled for the different breeding groups in the straightbred population and pooled for different breeding groups in the crossbred population were computed using pooled variance components. These were obtained by adding together the $V(S_1)$ and the $V(W_1)$ for the different breeding groups within the straightbred population and within the crossbred population.

The same procedure as discussed earlier was then used. The computer program used in obtaining these estimates was written by Marsha Spieler, graduate student in Animal Husbandry at Michigan State University.

Methods for estimating genetic, environmental, and phenotypic correlations have been developed and described by Hazel, et al. (1943).

The following formula was used to obtain the genetic correlation between two traits in a single population:

$$r_{G_iG_{i'}} = \frac{(\mathrm{Cov}\ S_iS_{i'})}{\sqrt{V(S_i) \cdot V(S_{i'})}}$$

where:

$\mathrm{Cov}\ S_iS_{i'}$ = covariance between sire effects for the two traits (i and i').

$V(S_i)$ = the between sire component of variance for the ith trait.

$V(S_{i'})$ = the between sire component of variance for the i'th trait.

The method of computing the correlation between the genetic ability of a sire to produce straightbred progeny and his genetic ability to produce crossbred progeny was complicated because of the unequal numbers encountered in the data (k being different for the two groups).

A method suggested by Robison (1967) was used to obtain the covariances needed to estimate the correlation between the genic value of a sire for producing straightbred and crossbred calves. The covariance between the straightbred and crossbred calves by a sire was computed simply as the covariance between the progeny means of the two groups. Robison thought that the method seemed clear for equal numbers, but left some doubt when used with unequal numbers. His comparison of the method with one using an adjustment for unequal numbers (Robertson, 1962) resulted in essentially the same results. Thus, he felt that this method would do a reasonably good job of estimation. Comstock (1961) suggested this simple covariance when he estimated the covariance of sire effects in his population under selection and the population cross by using the simple covariance between straightbred and crossbred half-sib family means taking the two kinds of families by pairs having common sires.

The covariance of sire effects of sires bred to their own breed (straightbred progeny) and bred to one of the other two breeds (crossbred progeny) was estimated using the following general formula ($\text{Cov}\ \bar{S}_{pi}\bar{S}_{ci}$):

$$\frac{\sum_{jm} \bar{Y}_{ijklm.}\ \bar{Y}_{ijkl'm.} - \sum_{j} \frac{(\bar{Y}_{ijkl..})(\bar{Y}_{ijkl'..})}{n_j}}{(\sum n_j - 4)}$$

where:

i = trait

j = year

k = breed of sire

l = breed of dam

m = sire

n_j = number of sires in j^{th} year

An example to symbolize how the covariance of sire effects for sires bred to their own breed, and bred to other breeds, for a given trait, is given below. We are using trait #1 (birth weight), and Hereford sires with calves out of Hereford and Shorthorn dams:

$$\frac{\sum_{jm} \bar{Y}_{1\,jHHm.}\,\bar{Y}_{1\,jHSm.} - \sum_{j} \frac{(\bar{Y}_{1\,jHH..})(\bar{Y}_{1\,jHS..})}{n_j}}{(\sum_j n_j - 4)}$$

When a covariance of sire effects was studied for one trait in the straightbred progeny, and another in the crossbred progeny (and vice versa), the following procedure was used. The example used is trait #1 (birth weight) in the progeny sired by Hereford sires and out of Hereford dams, and trait #4 (yearling weight) in the progeny sired by Hereford sires and out of Shorthorn dams (and vice versa):

$$\frac{\sum_{jm} \bar{Y}_{1\,jHHm.}\bar{Y}_{4\,jHSm.} - \sum_{j} \frac{(\bar{Y}_{1\,jHH..})(\bar{Y}_{4\,jHS..})}{n_j}}{(\sum_j n_j - 4)} \quad +$$

$$\frac{\sum_{jm} \bar{Y}_{4\,jHHm.}\bar{Y}_{1\,jHSm.} - \sum_{j} \frac{(\bar{Y}_{4\,jHH..})(\bar{Y}_{1\,jHS..})}{n_j}}{(\sum_j n_j - 4)} \Big/ 2$$

The formula used to estimate the correlation between the genetic ability of a sire to produce straightbred progeny and his genetic ability to produce crossbred progeny for a single trait, or one trait in one population and one in the other population (and vice versa) was as follows:

$$r_{G_{pi}G_{ci}} = \frac{\text{Cov}\ \bar{S}_{pi}\ \bar{S}_{ci}}{\sqrt{V(S_{pi}) \cdot V(S_{ci})}}$$

where:

$\text{Cov}\ \bar{S}_{pi}\ \bar{S}_{ci}$ = covariance between the progeny means of the straightbred calves ($\bar{S}_p$) and crossbred calves ($\bar{S}_c$) for the i^{th} trait.

$V(S_{pi})$ = the between sire component of variance for straightbred calves by a sire for the i^{th} trait.

$V(S_{ci})$ = the between sire component of variance for crossbred calves by a sire for the i^{th} trait.

Progeny means were computed using One-Way Analysis of Variance with Unequal Number of Replications Permitted (UNEQI Routine) which was programmed by Donald F. Kiel, and the description written by William Ruble, Donald F. Kiel, and Mary E. Rafter, Agricultural Experiment Station, Michigan State University.

The covariances between the progeny means of straightbred calves and crossbred calves by the same sire, within years, were computed, as explained earlier, using a modification of the subroutine of the BASTAT Program prepared by William Ruble, Agricultural Experiment Station, Michigan State University.

The between sire components of variance for straightbred and crossbred calves by a sire were obtained from the Least Squares and Maximum Likelihood General Purpose Program (LSMLGP) written by Walter Harvey, Ohio State University.

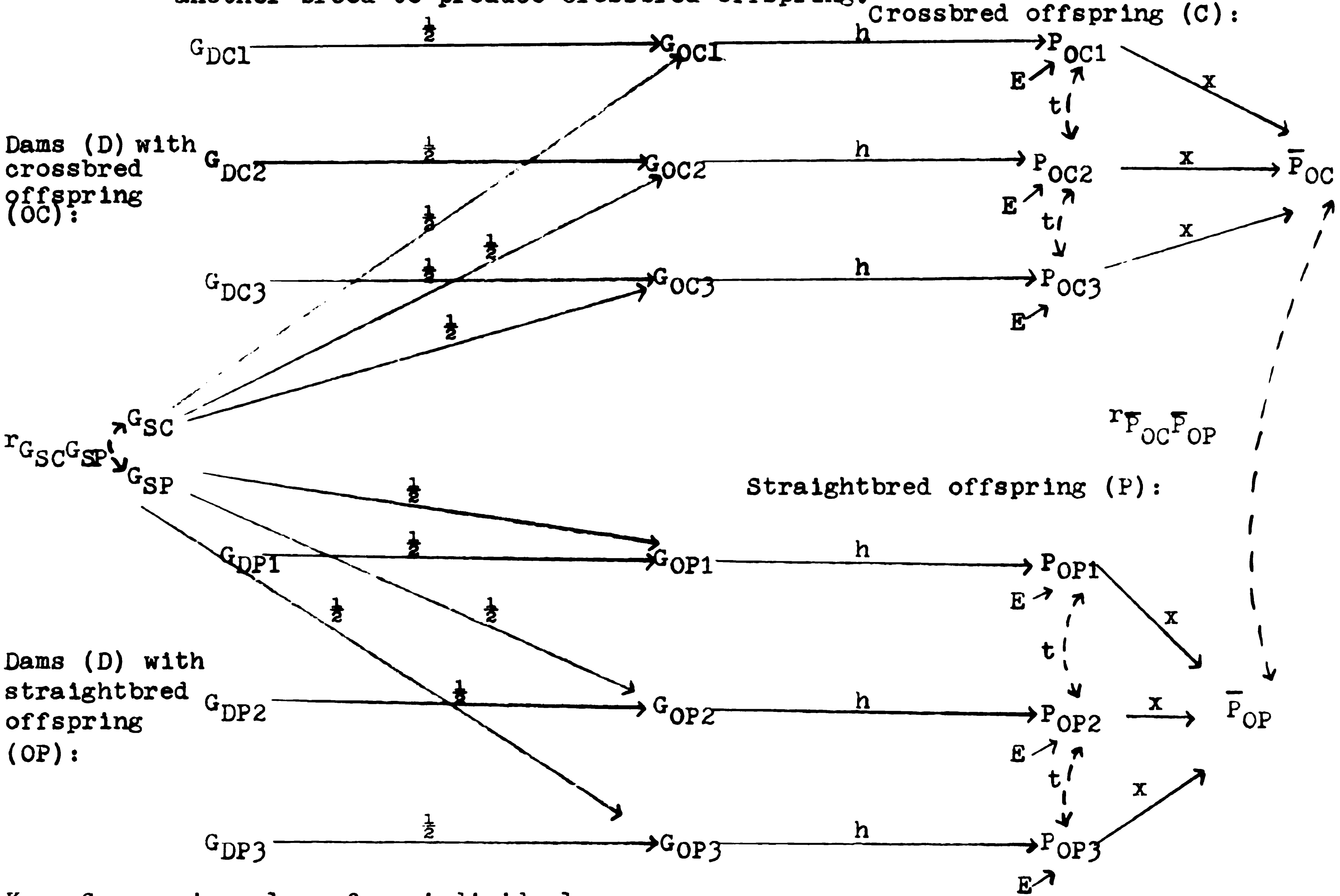
The program for computing the correlations between the genetic ability of a sire to produce straightbred progeny and his genetic ability to produce crossbred progeny for a single trait, or one trait in one population and another trait in the other population was written by W. T. Magee, Animal Husbandry Department, Michigan State University.

This correlation between the genetic ability of a sire to produce straightbred progeny and his genetic ability to produce crossbred progeny can be shown more clearly using a path coefficient diagram.

Since the biometric relations between individuals can be described in terms of correlations or variances, we can illustrate them by using the method of path coefficients. This method was described and used by Lush (1948).

Figure 1 is a path coefficient diagram illustrating the correlations involved when a straightbred sire is mated to several cows of his own breed, and to cows of one of the other two breeds. The illustration shows the bull being mated to three cows of his own breed, and to three cows of one of the other breeds since the average number of offspring per sire group in our study was between three and four (for steers $k_o = 3.64$ and for heifers $k_o = 3.33$). The path between the genic value of a parent and its offspring is $\frac{1}{2}$ in a random mating population in which neither the parent nor offspring is inbred.

Figure 1. A path coefficient diagram showing the correlations involved when a sire is mated to several cows of his own breed to produce straightbred offspring, and cows of another breed to produce crossbred offspring.



Key: G = genic value of an individual
P = observed phenotype
$\bar{P}$ = average phenotype
t = correlation between the phenotype of half-sibs.
h = $\sqrt{\text{heritability}}$
E = non-genic effects (contains the effects of environment, dominance, and epistasis.)

RESULTS AND DISCUSSION

Values for the variance components between sires and within sires and the covariance between the sire averages for straightbred and crossbred calves, by sexes, are shown in tables 11a, 11b, and 12. Table 11a includes the covariance between sire averages for straightbred and crossbred calves including all traits where the covariance of another trait with yearling weight was calculated. Table 11b includes the covariance between sire averages for straightbred and crossbred calves, including the traits where the covariance among different traits was not calculated. Table 12 includes the components of variance for between sires and within sires for different mating types and pooled averages for straightbred and crossbred calves.

Petty and Cartwright (1966) have summarized weighted averages of genetic variance estimates in purebred and straightbred beef cattle for birth weight, weaning weight, weaning score, final feedlot weight, and yearling pasture weight. The genetic variances obtained in this study agree reasonably well with those obtained by Petty and Cartwright, but, in general, are slightly smaller.

Table 11a. Covariance between sire averages for straightbred and crossbred calves including all traits where the covariance of another trait with yearling weight was calculated.

Trait (Straightbreds)	Mating type c		No. of sires		Trait (Crossbreds)						
	Sire-Dam	Sire-Dam	M[a]	F[b]	Birth wt. M	Birth wt. F	Adj. weaning wt. M	Adj. weaning wt. F	Adj.fn. wt. M	550-day wt. F	Actual cut. M
Birth weight	55	57	14	15	15.27	9.25			37.56	88.57	
	77	75	14	15	2.82	3.73			-3.15	46.05	
	66	65	14	14	17.42	4.63			-25.14	78.51	
	55	56	14	15	8.69	3.69			104.03	72.10	
	77	76	16	15	4.66	6.18			154.98	5.08	
	66	67	16	14	19.67	-1.55			106.74	45.90	
Adj. weaning wt.	55	57	14	15			-75.6	111.9	-123.5	428.3	
	77	75	14	15			-49.8	-75.8	-6.8	26.9	
	66	65	14	14			224.0	131.2	478.4	-557.6	
	55	56	14	15			-29.6	113.2	-134.6	241.3	
	77	76	16	15			443.1	14.3	1148.5	-228.8	
	66	67	16	14			525.9	7.9	961.4	279.3	
Adj. final wt. (M) 550-day wt. (F)	55	57	14	15	70.89	6.21	-63.3	-18.6	184.4	356.0	
	77	75	14	15	-17.36	-14.99	10.2	6.8	-249.8	328.6	94.7
	66	65	14	14	-32.06	-131.35	438.5	125.1	1291.6	-707.4	-96.5
	55	56	14	15	47.46	-19.62	408.0	-158.4	850.2	-101.6	80.7
	77	76	16	15	13.69	-7.74	710.9	7.6	2152.6	-146.0	176.1
	66	67	16	14	-15.13	-28.62	669.6	352.6	816.5	956.2	294.7
											287.3
Actual cutability	55	57	14						62.8		27.68
	77	75	14						-18.4		-6.63
	66	65	14						129.5		21.00
	55	56	14						197.5		40.01
	77	76	16						351.0		53.22
	66	67	16						158.0		48.10

[a] M = male calves

[b] F = female calves

[c] 5 = Hereford, 6 = Angus, 7 = Shorthorn

Table 11b. **Components of covariance between sire averages for straightbred** and crossbred **calves including the traits where the covariance among different traits was not calculated.**

Mating type^c		No. of sires		Covariances					
				Weaning score		Marbling score	Fn. car. grade	Fat thick.	Rib-eye area
Sire-Dam	Sire-Dam	M^a	F^b	M	F	M	M	M	M
55	57	14	15	0.000	0.226	1.079	0.152	0.000	-.070
77	75	14	15	0.102	0.039	1.209	-.054	-.002	0.158
66	65	14	14	0.247	0.232	4.114	1.060	0.010	0.110
55	56	14	15	0.202	0.030	0.033	0.008	0.000	0.027
77	76	16	15	0.156	0.129	1.519	0.138	0.001	0.166
66	67	16	14	-.026	0.391	-1.135	-.192	-.001	0.210

[a] M = male calves
[b] F = female calves

[c] 5 = Hereford, 6 = Angus, 7 = Shorthorn

Table 12. Components of variance for between sires (V(S)) and within sires (V(W)) for different mating types and pooled averages for straightbred and crossbred calves.

Mating type[c]	Source of	Trait					
		Birth weight		Weaning score		Adj. wean. wt.	
Sire - Dam	variance	M[a]	F[b]	M	F	M	F
55	V(S)	6.84	8.55	0.066	0.047	-208.0	187.7
	V(W)	56.08	64.58	0.642	0.441	1859.3	1271.7
66	V(S)	25.14	2.57	0.146	0.113	431.3	294.1
	V(W)	53.32	56.76	0.477	0.541	1294.2	1148.5
77	V(S)	4.85	6.98	0.021	-.068	70.8	218.1
	V(W)	25.67	26.95	0.629	0.825	1629.7	1107.6
56	V(S)	-21.60	-6.47	0.052	0.133	198.4	-110.3
	V(W)	84.67	72.06	0.661	0.605	1209.4	1606.0
57	V(S)	-1.46	40.42	0.070	0.117	583.0	76.3
	V(W)	66.29	46.16	0.482	0.535	1439.7	951.8
65	V(S)	28.64	22.20	0.147	-.062	-151.9	-262.7
	V(W)	54.95	54.75	0.710	1.159	1241.8	1445.2
67	V(S)	52.73	-.52	0.297	0.694	753.7	614.4
	V(W)	45.01	25.75	0.278	0.486	739.1	672.4
75	V(S)	-8.29	38.61	-.142	0.006	-765.9	420.4
	V(W)	44.62	27.55	0.808	0.855	2771.5	1216.2
76	V(S)	-6.31	-9.48	0.050	-.034	180.3	-191.1
	V(W)	44.05	50.08	0.617	0.580	1095.1	1042.3
Averages Pooled	V(S)	12.28	6.03	0.078	0.031	98.0	233.3
Straightbreds	V(W)	45.02	49.43	0.583	0.602	1594.4	1175.9
Averages Pooled	V(S)	7.28	14.11	0.079	0.142	132.9	91.2
Crossbreds	V(W)	56.58	46.06	0.593	0.703	1416.1	1155.6

[a] M = male calves [c] 5 = Hereford, 6 = Angus, 7 = Shorthorn

[b] F = female calves

Table 12 (Cont.). Components of variance for between sires (V(S)) and within sires (V(W)) for different mating types and pooled averages for straightbred and crossbred calves.

Mating type Sire - Dam	Source of variance	Trait						
		Adj. fn. wt. M	Adj. 550-day wt. F	Marbling score M	Fn. carcass grade M	Fat thick. M	Rib-eye area M	Actual cut. M
55	V(S)	152.1	-229.6	1.357	0.122	0.001	0.183	38.11
	V(W)	5987.3	3770.2	8.833	2.178	0.021	0.854	133.37
66	V(S)	2785.9	1177.2	2.463	0.626	0.004	0.053	41.51
	V(W)	5525.2	2485.0	6.558	0.677	0.010	0.837	152.18
77	V(S)	993.3	366.1	-.356	-.043	0.002	0.117	6.06
	V(W)	5628.1	2421.5	10.058	0.788	0.026	0.463	184.71
56	V(S)	2071.8	264.8	0.211	0.271	0.007	-.220	-31.31
	V(W)	2607.7	2313.0	6.983	0.739	0.023	1.381	255.93
57	V(S)	-568.1	229.0	0.479	0.116	-.000	0.195	70.40
	V(W)	8858.0	3229.4	5.004	0.658	0.025	1.472	153.10
65	V(S)	423.8	67.0	1.010	0.281	0.020	-.131	35.76
	V(W)	4620.0	3192.6	7.425	1.333	0.011	1.007	117.07
67	V(S)	1365.1	3194.7	0.940	0.073	0.006	0.082	8.42
	V(W)	4488.1	2575.3	4.852	0.755	0.013	0.840	115.08
75	V(S)	-1440.7	1353.9	1.891	0.118	0.004	-.146	-23.72
	V(W)	4370.8	2498.7	5.842	1.154	0.013	0.883	140.12
76	V(S)	2839.9	334.6	-6.094	-.726	-.004	0.255	104.84
	V(W)	3617.0	2521.1	14.117	1.550	0.023	0.839	73.08
Averages Pooled Straightbreds	V(S)	1310.4	437.9	1.155	0.235	0.002	0.118	28.56
	V(W)	5713.5	2892.2	8.483	1.214	0.019	0.718	156.75
Averages Pooled Crossbreds	V(S)	782.0	907.3	-.260	0.022	0.006	0.006	27.40
	V(W)	4760.3	2721.7	7.370	1.032	0.018	1.070	142.40

Table 13 contains the paternal half-sib heritability estimates for the straightbred and crossbred steer and heifer calves, and the genetic and phenotypic correlations for the straightbred steer and heifer calves. The original statistical analyses of the data contained a separate analysis for each mating type and sex (18 separate analyses), as well as the pooled analysis separately for each sex. The k_o was very small (3.64 for steers and 3.33 for heifers), and the degrees of freedom for sires was 13 to 15, therefore, the standard errors of both the heritability estimates and the genetic correlation estimates were large, making them of little use as point estimates. The reason for classifying the data into such small groups was to get the variance components needed to calculate the genetic correlations between the performance of the straightbred and crossbred progeny by a sire. The pooled within straightbred and crossbred analyses for each sex were useful for showing trends. The pooled analyses still have rather large standard errors because k_o is small, most values being between 0.3 and 0.4. The sampling errors for the separate analyses were considered too large to justify publishing them.

Values greater than one are found in the table. It is impossible for a true heritability or genetic correlation to be greater than one. These estimates above one result from sampling errors. They are presented to make it possible to obtain an unbiased average of values. It was not possible to calculate certain genetic correlations because of some negative sire components of variance.

Table 13. Heritabilities for the straightbred and crossbred steer and heifer calves, and genotypic and phenotypic correlations for the straightbred steer and heifer calves. (Heritabilities appear on the diagonal, genetic correlations are to the right of the diagonal, and phenotypic correlations are to the left of the diagonal.)

		Trait												
		Birth wt.		Wean. score		Adj. wean. wt.		Adj. fn. wt.	550-day wt.	Marb. score	Fn.car. grade	Fat thick.	Rib-eye area	Actual cut.
Trait	Mating type	M^c	F^d	M	F	M	F	M	F	M	M	M	M	M
Birth wt.	C^b	0.46	0.94											
	P^a	0.85	0.47	-.34	0.03	0.91	0.84	0.65	0.74	-.73	-.42	-.59	0.64	0.77
Wean. score	C			0.47	0.67									
	P	0.07	0.20	0.42	0.15	-.42	-.20	-.42	-.07	0.69	0.25	0.13	0.17	-.50
Adj. wean. wt.						0.34	0.29							
	P	0.51	0.64	0.33	0.36	0.18	0.67	1.14	0.92	-.35	0.09	0.23	1.20	1.23
Adj. fn. wt. (M), 550-day wt. (F)	C							0.56	1.00					
	P	0.51	0.60	0.14	0.24	0.74	0.79	0.71	0.51	-.03	0.18	0.13	0.92	0.91
Marb. score	C									-.15				
	P	-.12		0.17		0.11		0.12		0.42	0.95	1.00	-.38	-.48
Fn. car. grade	C										0.03			
	P	-.13		0.21		0.14		0.21		0.85	0.56	0.61	-.19	-.40
Fat thickness	C											0.94		
	P	-.01		0.26		0.28		0.41		0.32	0.34	0.39	-.27	-.24
Rib-eye area	C												0.02	
	P	0.26		0.12		0.34		0.42		-.06	-.03	-.05	0.60	0.95
Actual cutability	C													0.65
	P	0.51		0.19		0.67		0.84		0.09	0.12	0.32	0.59	0.59

^{a}P = straightbred, ^{b}C = crossbred, ^{c}M = male, ^{d}F = female

The numbers available in this study are too small to give meaning to point estimates. Tallis and Klosterman (1959) found that the number of offspring per sire played a very important part in determining sizes of errors of estimate. Extensive data are needed since estimates are subject to large sampling errors. They have published a table giving the minimum number of animals needed to estimate heritability with a certain standard error. In referring to this review of literature heritability summary, for example, it is found that traits in this study have had average values from 35% to 60% when studied by other research workers on large numbers of data during the past 20 years. Using weaning weight as an example, and referring to the table, it is seen that to obtain a standard error of 0.05 would require about 306 sire groups, 13 offspring per sire, or about 3,978 offspring. A standard error of 0.15 would require 35 sire groups, 13 offspring per sire, or about 455 offspring.

Tallis (1959) has also prepared a table giving the optimum sizes of progeny groups for the estimation of genetic correlations with ($n > 1000$). An example using this table will be the genetic correlation between weaning weight and final weight (genetic correlation average of 0.72 on 9 estimates quoted in this review of literature). Tallis' table discloses that the optimum size of progeny groups would be about 7, with about 143 sires, making a total of 1,000 offspring.

When the data were pooled within sexes for the straight-

bred calves, all of the heritability estimates and most of the genetic correlations are within the range of estimates reported by previous research workers. In a number of cases they are quite close to the average estimates reported in the Review of Literature summary. Very few previous estimates of genetic correlations are available on the carcass traits. The phenotypic correlations are in reasonably close agreement with the summary by Petty and Cartwright (1966).

This study did not indicate any differences between the heritability estimates of the straightbred and crossbred calves by a sire, indicating that selection should be as effective in the crossbreds as the straightbreds. This was in agreement with the only other study in the literature comparing heritabilities in crossbred and straightbred beef cattle (Miquel and Cartwright, 1963). They concluded that the estimated genic variance and heritability ranked in the same order for all characters with one minor exception. Bassett and Shelton (1966), working with heritability estimates and genetic correlations between straightbred and crossbred lambs, found only one instance where the crossbred lambs provided a higher estimate of heritability than the straightbred lambs. Louca and Robison (1967) quoted higher heritabilities for purebred pigs than for crossbred pigs in the traits they studied, but the heritabilities given by Enfield and Rempel (1962) for swine data did not seem to indicate any definite trend.

In order to obtain the correlation between the genetic ability of a sire to produce a given trait in straightbred progeny and his genetic ability to produce the same trait in crossbred progeny, and the correlation between the genetic ability of a sire to produce one trait in straightbred progeny, and another trait in crossbred progeny (and vice versa), the components of covariance between the progeny means in tables 11a and 11b were used along with the sire components of variance in table 12. The method used is discussed in the section on Statistical Methods.

Tables 14 and 15 contain these correlations for the steer and heifer calves by mating types and pooled by sexes. As discussed earlier, k_o is small, and the degrees of freedom for sires is too small to make useful point estimates, but the values obtained should indicate trends.

The pooled values for the correlations are high in both sexes, with the correlations being higher for the steers than for the heifers. Out of the 17 pooled correlations, possible to compute, in both sexes, about half have a value of 1.0 or greater, with several others being higher than 0.8. This indicates, in these data, that the correlation of a sire's genic ability to sire straightbred and crossbred calves is probably high.

Since so many of the estimated correlations among the genetic values of the sires were above one, it seemed advisable to make other calculations to determine if the pro-

Table 14. Correlations between the genetic ability of straightbred beef cattle sires to produce straightbred steer progeny (S) and their genetic ability to produce crossbred steer progeny (C) for the same trait, and for one trait in the straightbreds and another in the crossbreds (and vice versa).

Mating type[c] Sire-Dam	Mating type[c] Sire-Dam	No. of sires	Birth wt. (S) Birth wt. (C)	Wean. score (S) Wean. score (C)	Adj. wean. wt. (S) Adj. wean. wt. (C)	Adj. fn. wt. (S) Adj. fn. wt. (C)	Marb. score (S) Marb. score (C)	Fn. car. grade (S) Fn. car. grade (C)	Fat thick. (S) Fat thick. (C)	Rib-eye area (S) Rib-eye area (C)	Actual cut. (S) Actual cut. (C)
55	56	14	B[a]	3.45	B	1.52	0.06	0.04	0.00	B	B
55	57	14	B	0.00	B	B	1.34	1.28	B	-.37	0.54
56	65	14	0.65	1.69	B	1.19	2.61	2.53	1.12	B	0.54
66	67	16	0.54	-.12	0.92	0.42	-.75	-.90	-.20	3.18	2.57
77	75	14	B	B	B	B	B	B	-.71	B	B
77	76	16	B	4.81	3.92	1.28	B	B	B	0.96	2.11
Pooled			1.21	1.45	1.52	0.83	B	2.57	0.37	3.82	1.09

[a] B = Correlation not calculated because of negative sire component of variance.

[c] 5 = Hereford, 6 = Angus, 7 = Shorthorn

Table 14 (Cont.) Correlations between the genetic ability of straightbred beef cattle sires to produce straightbred steer progeny (S) and their genetic ability to produce crossbred steer progeny (C) for the same trait, and for one trait in the straightbreds and another in the crossbreds (and vice versa).

Mating type Sire-Dam	 Sire-Dam	Birth wt. - adj. fn. wt. (S & C)	Adj. wean. wt. - adj. fn. wt. (S & C)	Actual cutability - adj. fn. wt. (S & C)
55	56	B	B	3.04
55	57	B	B	B
66	65	-.14	0.97	0.42
66	67	0.16	0.74	0.98
77	75	B	B	B
77	76	B	1.90	0.99
Pooled		0.36	1.08	0.84

Table 15. Correlations between the genetic ability of straightbred beef cattle sires to produce straightbred heifer progeny (S) and their genetic ability to produce crossbred heifer progeny (C) for the same trait, and for one trait in the straightbreds and another in the crossbreds (and vice versa).

Mating type[c] Sire-Dam	Mating type[c] Sire-Dam	No. of sires	Birth wt. (S) Birth wt. (C)	Wean. score (S) - Wean. score (C)	Adj. wean. wt. (S) - Adj. wean. wt. (C)	Adj. 550-day wt. (S) - Adj. 550-day wt. (C)	Birth wt. - Adj. 550-day wt. (S & C)	Adj. wean. wt. - Adj. 550-day wt. (S & C)
55	56	15	B[a]	0.38	B	B	6.13	1.59
55	57	15	0.50	3.05	0.93	B	B	B
66	65	14	0.61	B	B	-2.52	-.30	-2.19
66	67	14	B	1.40	0.02	0.49	0.19	0.32
77	75	15	0.23	B	-.25	0.47	0.11	0.03
77	76	15	B	B	B	-.42	B	-2.05
Pooled			0.47	2.64	0.35	0.18	0.14	0.11

[a] B = Correlation not calculated because of negative sire components of variance.

[c] 5 = Hereford, 6 = Angus, 7 = Shorthorn

cedure followed had a bias in it. One value which could be used is the phenotypic correlation between the averages per sire for straightbred and crossbred offspring. The first step in this procedure was to graph several of these to get a visual appraisal of the relationships involved.

Two examples of these are sire progeny means, by years, for adjusted weaning weight in the steers for Shorthorn sires bred to Shorthorn and Angus cows and similar means, by years, for adjusted 550-day weight in the heifers for Angus bulls bred to Angus and Hereford cows. These are shown in figures 2 and 3. These two relationships were selected as examples since they represent one of the largest positive correlations, and one of the largest negative correlations in traits.

By visual analysis, it can be seen that the correlation in figure 2 is highly positive, and that the correlation in figure 3 could give us a negative value.

Phenotypic correlations were not obtained between the progeny of a sire bred to cows of his own breed to produce straightbred progeny and to cows of one of the other two breeds to produce crossbred progeny for all traits used in the study, but the two examples above were done on a hand calculator for illustrative purposes.

A phenotypic correlation of 0.62 was computed for adjusted weaning weight between progeny means of straightbred steer calves from Shorthorn bulls bred to Shorthorn cows and progeny means of crossbred steer calves from the Shorthorn bulls bred

Figure 2. Sire progeny means, by years, for the trait adjusted weaning weight (in pounds) in steers. Shorthorn sires (7) on Shorthorn (7) and Angus (6) dams.

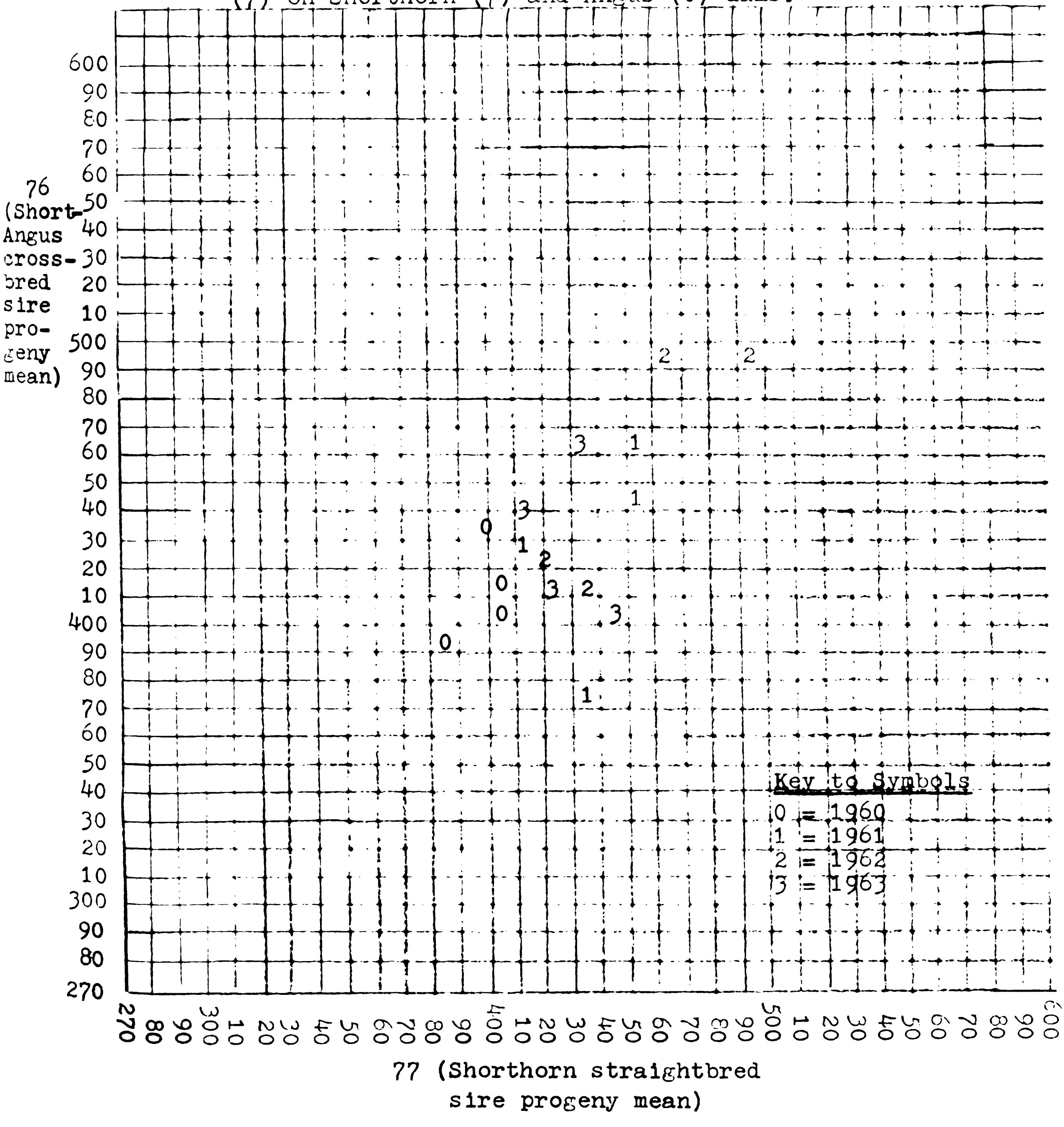
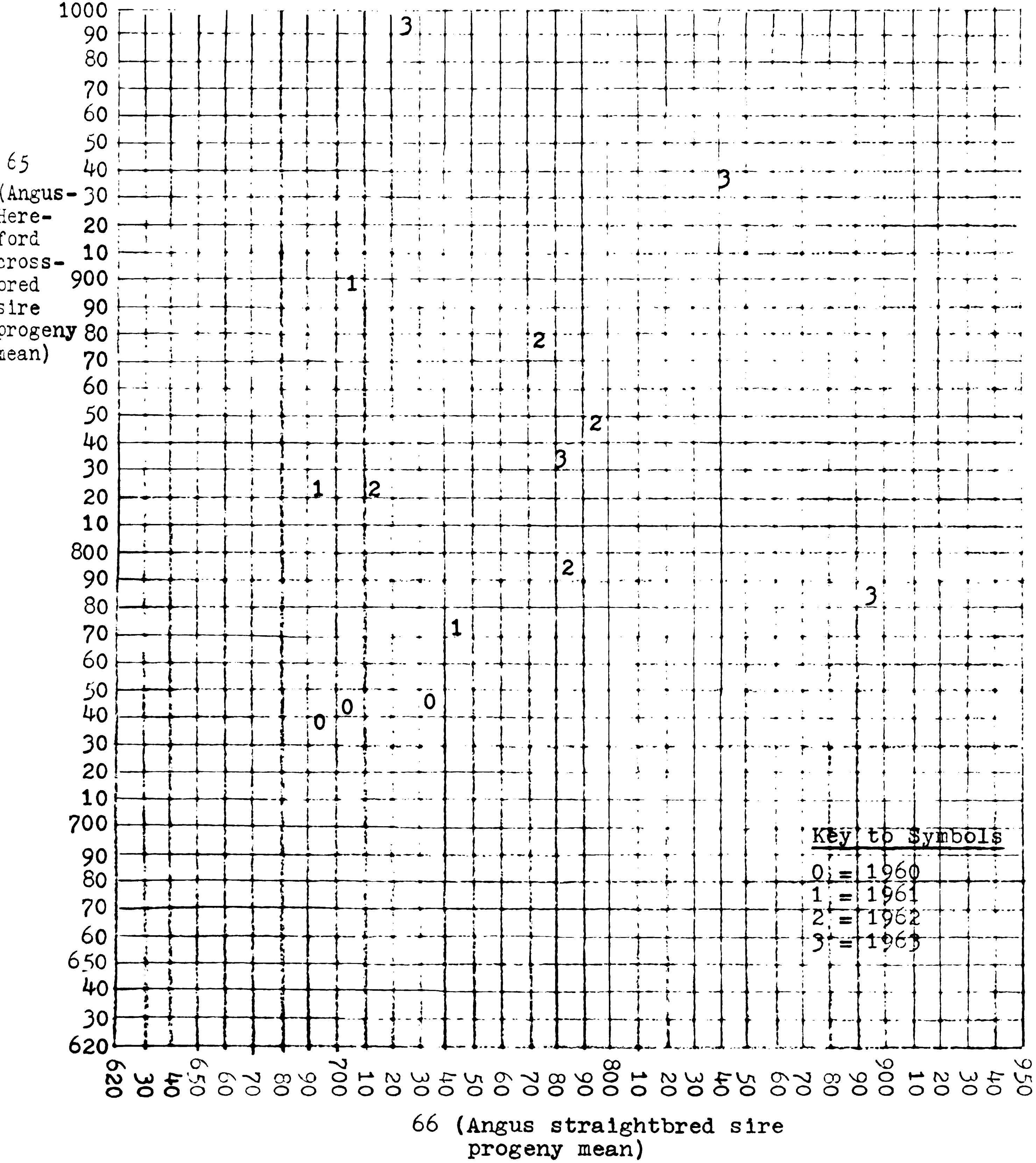


Figure 3. Sire progeny means, by years, for the trait adjusted 550-day weight (in pounds) in heifers. Angus sires (6) on Angus (6) and Hereford (5) dams.



to Angus cows. Likewise, a phenotypic correlation of -.29 was computed for 550-day adjusted weight between progeny means of straightbred heifers from Angus bulls bred to Angus cows and progeny means of crossbred heifers from the Angus bulls bred to Hereford cows. The phenotypic correlations were product moment correlations among the sire averages.

In order to check the model and statistical procedures for determining the correlations involved when a sire is mated to several cows of his own breed to produce straightbred offspring, and mated to several cows of another breed to produce crossbred offspring, with an average being obtained on each of the progeny groups, a path coefficient diagram, as shown in figure 1, was drawn.

The methods of Lush (1948) are used in computing the phenotypic correlation by the path coefficient diagram method. As illustrated in figure 1, the correlation between the genic value of a parent and its offspring is one-half. For the heritability estimate for weaning weight the one chosen was the average of 0.35 from table 2. This is the best point estimate available at the present time for beef cattle. The value of the path between the phenotype of one offspring by a sire and the average phenotype of several progeny by a sire is given by Lush as:

$$x = \frac{1}{\sqrt{n\left[1 + (n-1)\,t\right]}}$$

where t = the correlation between the phenotypes of individual offspring by a sire

($t = \frac{1}{4}$ of heritability in half-sibs)

n = number of offspring by a sire.

The paths in figure 1 show the relationship between the observed phenotypic correlation and the biological cause of the correlation. This relationship is as follows:

$$r_{\bar{P}_{op}\bar{P}_{oc}} = n^2 \left[(r_{G_sG_o})^2 \, h^2 \, x^2 \, r_{G_{sp}G_{sc}} \right]$$

where:

$r_{\bar{P}_{op}\bar{P}_{oc}}$ = the correlation between the genic value of a sire and the genic value of his offspring.

h^2 = heritability

n and x = (defined earlier)

$r_{G_{sp}G_{sc}}$ = the correlation between the genetic ability of a sire to sire straightbred offspring and his genetic ability to sire crossbred offspring.

If the correlation between the genetic ability of a sire to sire straightbred offspring and his genetic ability to sire crossbred calves for adjusted weaning weight is equal to 1.00, as this study would indicate, working through the problem gives a correlation of 0.21. This can be defined as an estimate of the expected phenotypic correlation between progeny means of straightbred and crossbred calves by a sire for weaning weight. Since this value is only about one-third of the product moment correlation computed from the actual progeny means, it indicates that the sampling errors have made this observed covariance among sire averages different than the true covariance.

This adds confidence to the belief that the values in tables 17 and 18 are not above 1.00 because of mistakes in developing the procedure to estimate them, rather than a procedural bias.

The statistical analyses of the data used in the experiment, to measure the effects of heterosis, were explained by Gregory et al. (1965, 1966a, 1966b, 1966c). These calculations were not repeated in this experiment, but a summary of the appropriate parts will be discussed since their results have a direct bearing on the results and discussion of this experiment.

In Gregory's analysis of variance, years were highly significant ($P < .01$) for birth weight (heifers), weight at 200 days (steers and heifers), weaning score (steers and heifers), 550-day weight (heifers), rib-eye area, carcass grade, actual cutability, fat trim, and adjusted final weight (steers). All interactions involving years were relatively unimportant. Gregory interpreted this to mean that, within the range of environments of the 4 years at one location and within the genotypes of the breeds of sires and dams, genetic-by-environment interactions were not important for the traits studied, however, year effects were highly significant. In this study sires are nested within years. This nesting prevents the sires from interacting with years (since a nested factor cannot interact with a factor of a larger classification).

Gregory's interactions between breed of sire and breed of dam were significant ($P < .01$) for birth weight and 200-day weight (both sexes), 550-day weight (heifers), final weight, and rib-eye area (steers). Gregory stated that these significant interactions reflected the importance of heterosis on these traits. The heterosis effect was highly significant ($P < .01$) for all pre-weaning traits (birth weight, weaning weight at 200 days, and weaning conformation score) for both sexes, adjusted final weight (steers), 550-day weight (heifers), and most carcass traits associated with or affected by weight. The effects of heterosis decreased with increasing age. Interactions of sires with breed of dam were not significant for any of the traits studied, indicating that the difference in heterosis effects between sires of the same breed were not important. When Gregory compared this interaction with that between breed of sire and breed of dam it indicated to him that heterosis was due to the effects of the breed of sire, rather than to the effect of sires within breeds.

In the analysis of variance done by Gregory, difference between sires within breed of sire and year were highly significant ($P < .01$) for birth weight and weaning score (steers and heifers), and significant ($P < .05$) for 200-day weight in the heifers. In the 1962-63 heifers sire differences for 550-day weight were highly significant. In the steers, final weight, actual cutability, and fat trim showed highly significant differences among sires, while rib-eye area and carcass

grade showed significant differences. These sire differences within breeds indicated to Gregory that additive genetic variance was important on the traits studied.

Gregory et al. (1965, 1966a, 1966b, 1966c) have given least-squares means and constants for breed of sire, breed of dam and interactions for each sex, and means for sexes combined, estimated by an analysis of least-squares. For this reason the means for the groups shown in their paper are not listed here.

In this study, means of progeny of individual sires and standard deviations within sexes were computed for each of the sires when bred to cows of their own breed and to cows of each of the other two breeds. Allowing for certain missing cells, this added up to 137 averages in the steers (on 9 individual traits) and 138 averages in the heifers (on 4 individual traits). Partly because of the size of this table (1785 averages for individual traits), and since it does not directly apply, in itself, to the final results, it was not included. These means of progeny of individual sires were computed for use in obtaining the covariances needed to estimate the correlation between the genic values of a sire for producing straightbred and crossbred calves, discussed earlier.

APPLICATION

Basic knowledge on genetic parameters is necessary in the improvement of livestock through better breeding and selection methods. These parameters are calculated from a particular population at a particular time. They may or may not be the same for another population or another period of time.

Even though a deliberate attempt was made to obtain heifer calves from several sources and an attempt was made to obtain bulls from different sources, the sample used in this study is not representative of the Angus, Hereford and Shorthorn breeds. Also, the breeds used in the experiment cannot be considered a random sample of all beef cattle breeds. Thus, all statements made in reference to these data, cannot be expected to hold true for all beef cattle. Also, as mentioned earlier, the average number of offspring per sire, and degrees of freedom for sires are too small to give useful point estimates. All comments must be on the basis of trends.

The paternal half-sib heritability estimates computed in this study agree reasonably well with the average estimates summarized in the Review of Literature. These estimates represent many thousands of cattle, and over 100 studies during the past 20 years.

The heritabilities in this study ranged from 0.15 to 0.85 with only two of the 13 values below about 0.40. Values for these traits from this Review of Literature summary ranged from 0.23 to 0.58. Research workers have concluded that the heritabilities for the pertinent traits are high enough for selection to be reasonably effective (Gregory, 1961). Results from this study agree with this conclusion.

In this study, there did not appear to be any difference in the heritability estimates between the straightbred and crossbred calves. This was in agreement with the study of Miquel and Cartwright (1963) discussed earlier. Also, there were no apparent differences in the estimated sire components between the straightbred and crossbred calves. This information would lead to the same conclusion as Miquel and Cartwright made when they concluded that selection would be roughly as effective in crossbreds as in the purebreds (straightbreds in this study).

In general, the pooled within straightbred analyses, by sexes, indicate high genetic correlations (0.64 to 1.23) between the traits pertaining to weight, rib-eye area, and actual cutability. The phenotypic correlations follow the same pattern except for the correlations between rib-eye area and the other traits (0.26 to 0.59). Weaning score is negatively correlated genetically with all traits pertaining to weight and actual cutability (0.0 to -.50), and is slightly correlated with final carcass grade, fat thickness, and rib-eye area (0.13 to 0.25), while being more highly correlated with marbling score (0.69). Phenotypic correlations of weaning score with the other traits are also low, varying from

0.07 to 0.36, with the highest values being between weaning weight and weaning score. The carcass traits, marbling score, final carcass grade, and fat thickness are highly correlated genetically with each other (0.61 to 1.00), negatively correlated genetically with birth weight, rib-eye area, and actual cutability (-.24 to -.73) and slightly correlated with the other traits for weight (0.09 to 0.23). Phenotypic correlations for these traits follow the same pattern with negative correlations (-.01 to -.12) with birth weight and rib-eye area, and moderate correlations with the other traits.

One of the main objectives of this study was the estimation of interrelationships of straightbred and crossbred progeny performances in the same trait, and between one trait in the straightbred population and another trait in the crossbred population. These correlations between the genetic ability of a sire to sire straightbred and crossbred progeny for one trait, and his ability to sire one trait in the straightbred progeny, and another in the crossbred progeny, were high, with many being greater than one. Between one-third and one-half of the values could not be computed because of negative sire variance components. Values were higher in the steers than in the heifers. No explanation can be given for this. Only 13 out of 108 correlations were negative. In the steers only 10 out of 72 individual correlations, and 2 of the 12 pooled correlations were below 0.50. In the heifers, one-third of the 36 individual correlations, and 5 of the 6 pooled correlations were below 0.50. No trends among correlations were noted on the basis of specific mating types. The only pooled correlation low in both steers and heifers is the one between birth weight and adjusted final weight. It would seem that traits measured in both sexes would need to be low in both sexes to be significant as it is hard to visualize that there should be any biological differences between a bull's ability to sire steers and heifers. The correlation for fat thickness (measured only in the steers) is also much lower than the other values.

This study indicates that the correlation between a sire's genetic ability to sire straightbred and crossbred progeny for one trait, and his ability to sire one trait in the straightbred progeny, and another in the crossbred progeny is high. Thus, a sire that sires good straightbred calves should also sire good crossbred calves (and vice versa) when bred to comparable cows.

Mass selection has been the most common method for improving livestock. This is the method in which animals are selected on their own phenotypic values. Only the production traits (birth weight, weaning weight and score, and final weight) can have direct selection applied to them. Other traits (carcass traits) require another system, such as sib-selection.

By selecting calves with heavy weaning weights and final weights, it should be possible to produce heavy cattle which make rapid and efficient gains in the feedlot, and will produce a maximum amount of edible portion per unit of carcass weight. Indications are that adjusted weaning weight and adjusted final weight would be the best criteria to use in mass selection. The associations among the traits concerned with weight are high enough to recommend that simultaneous improvement in all of these traits would be possible.

Gregory *et al*. (1965, 1966a, 1966b, 1966c) have analyzed the influence of heterosis in the cattle used in this experiment. In general they found that crossbreeding has resulted in about a 3% increase in growth rate up to about 18 months of age, in favor of the crossbred cattle. Heterosis seems to be important only in carcass traits that are associated with the growth of the animal. Heterosis has been measured by comparing the crossbred offspring by a sire with the straightbreds out of comparable cows. The difference between the crossbreds and straightbreds is due TO non-additive gene effects. Other studies (quoted earlier) have found similar advantages, in favor of the crossbreds.

If future experiments continue to observe heterosis in beef cattle, it is probable that the majority of the commercial cattle production in the future will be made up of crossbred cattle. If this is the case, one of the main questions will be : Will practicing mass selection in both sexes of both purebred populations that make up a cross be effective in improving the performance of the crossbred offspring? This question is one of the most important ones trying to be answered in this study.

Results of this study indicate that:

1. There are no differences in the heritability estimates between the straightbred and crossbred calves, thus the effectiveness of selection would be roughly the same in the crossbreds and the straightbreds.
2. Heritability estimates for the traits studied seem high enough so that mass selection for them should be effective.
3. The associations among the traits concerned with weight are high enough to recommend that simultaneous improvement in all of them would be possible.
4. Indications are that the correlations between the genetic ability of a sire to sire straightbred and crossbred offspring for one trait, and his ability to sire one trait in the straightbred progeny, and another trait in the crossbred progeny are high.

Thus, it can be concluded that simultaneous mass selection for traits associated with weight in the purebred population should be effective for improving the crossbred population.

The rate at which the crossbred performance can be improved by mass selection in both sexes of both purebred populations that make up a cross can be expressed using the following formula:

mean in the crossbred population $= (r_{G_pG_c} \sqrt{h^2p}\, \sigma_{G_c} (z/b))$

where:

$r_{G_pG_c}$ = the correlation between the genic value of the purebred and the genic value of the crossbred.

h^2p = heritability in the purebred population.

z/b = selection intensity.

σ_{G_c} = the standard deviation of genic values of the crossbred population.

If the correlation between the genic value of the purebred and the genic value of the crossbred is near 1.0 (as this study would indicate) it can be seen, from the above formula, that mass selection in both sexes of the purebred population that make up a cross will be as effective in improving commercial crossbred performance as if the selection were practiced   improving commercial straightbred performance.

SUMMARY

The data included records on 375 steers and 362 heifers, born over a four year period 1960 to 1963 inclusive, at the Fort Robinson Beef Cattle Research Station in northwestern Nebraska. The calves were from 80 cows each from the Angus, Hereford, and Shorthorn breeds, and were the progeny of 17 Angus, 16 Hereford, and 16 Shorthorn sires. The cows were randomized to breeding pastures each year so that each sire was bred to twice as many cows of his own breed as to each of the other two breeds. Traits studied were birth weight, weaning score, and adjusted 200-day weight (steers and heifers); adjusted final weight, marbling score, final carcass grade, fat thickness, rib-eye area, and actual cutability (steers); and adjusted 550-day weight (heifers).

The experimental design included a new crop of sires each year which caused a hierarchal design with sires nested within breed of sire and year, but cross classified with breed of dam. Steers and heifers were analyzed separately for all traits.

Variance components for all traits were obtained from analysis of variance tables. A least-squares and maximum likelihood general purpose program was used to compute estimates of genetic parameters and standard errors.

The results of the study were as follows:

1. Components of genetic variance and covariance were calculated for each of the mating types. There were no differences in the sire components between the

straightbreds and crossbreds, indicating similar additive genetic variance in the two groups.

2. Heritability estimates were obtained for the various traits by the paternal half-sib correlation method. Separate analyses were obtained for each mating type x sex sub-group (18 separate analyses), and pooled within straightbred, and pooled within crossbred analyses were obtained for each of the sexes. The separate analyses were subject to large sampling errors because of limited offspring per sire group, and small degrees of freedom for sires. They were not published. The pooled analyses yielded heritability estimates from 0.15 to 0.85 with most standard errors between 0.3 and 0.4. No difference was noted between the crossbreds and straightbreds. The heritability estimates were large enough to expect improvement in the traits with mass selection. The results indicate that the same type of selection programs used to improve straightbred populations would also be effective in improving crossbred populations.
3. Genetic and phenotypic correlations were obtained for the same groups as discussed in 2, except for the pooled within crossbred group, which was not computed. The within straightbred analyses, by sex, are published. Some of the genetic correlations could not be computed because of negative sire components of variance. Standard errors, in general,

varied from 0.3 to 0.4. The traits associated with weight (birth and 200-day weight, final weight, 550-day weight, rib-eye area, and actual cutability) were highly correlated both genetically and phenotypically with each other. Weaning score was negatively correlated genetically, and slightly correlated phenotypically, with the above mentioned traits, and slightly correlated both genetically and phenotypically with the other carcass traits (marbling score, final carcass grade, and fat thickness). These carcass traits were highly correlated, genetically, with each other, and negatively correlated with birth weight, rib-eye area, and actual cutability. Their phenotypic correlations with birth weight and rib-eye area were negative, and they were moderately correlated with the other traits studied.

Results indicate that a selection program based on mass selection would be effective in improving traits associated with weight in the straightbred population. The size and direction of association among traits associated with weight, would suggest that simultaneous improvement in all of these traits would be effective. Adjusted 200-day weight (steers and heifers), adjusted final weight (steers), and 550-day weight (heifers) were recommended as traits to emphasize in a mass selection program.

4. Correlations were obtained between the genetic ability

of a sire to produce the same trait in straightbred and crossbred progeny, and between his genetic ability to produce one trait in the straightbred population, and another trait in the crossbred population. In general, the correlations were high. Many were greater than 1 due to sampling errors. Due to unequal numbers of offspring per sire, the covariance was computed simply as the covariance between straightbred and crossbred progeny means. Sire components of variance were obtained from the program used to obtain the genetic correlations. A path coefficient diagram was used to illustrate the relationships involved.

In general, the correlations were high indicating, despite large sampling errors, that the expected values of the correlations in this study are near 1.00. This would indicate that selection in purebreds that are used in a crossing program would be effective in improving the performance of the crossbreds.

5. A formula was proposed to measure the expected response in the crossbred population, from mass selection in the purebred populations that make up the cross. If the correlation between the genic value of the straightbred and the genic value of the crossbred is near 1.00, as this study indicates, it was concluded that mass selection in the purebred populations that make up a cross would be as effective in improving commercial production in the crossbreds as

it would be in improving commercial production in a breeding program where the purebred bulls were bred to commercial cattle of their own breed.

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