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**RESPONSE OF FEEDLOT AND CARCASS CHARACTERISTICS TO
SELECTION AND CROSSBREEDING**

Michigan State University

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RESPONSE OF FEEDLOT AND CARCASS
CHARACTERISTICS TO SELECTION
AND CROSSBREEDING

by

Donna Jo Cox

A DISSERTATION

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ABSTRACT

RESPONSE OF FEEDLOT AND CARCASS CHARACTERISTICS TO SELECTION AND CROSSBREEDING

by

Donna J. Cox

Efficiency of production by beef cattle producers depends to a large extent on the effective use of selection and crossbreeding. Genetic and phenotypic correlations and heritabilities have been estimated for marbling score, yield grade, average daily gain, loin eye area, internal fat (KPH), carcass grade, fat thickness, final weight and yearling weight from records obtained at the Lake City Experiment Station in Lake City, Michigan. The estimated parameters can be used by producers as an aid to effectively using their resources. In addition, the effect of selection was investigated by comparing the performance of unselected Hereford steers to the feedlot and carcass traits of Herefords selected for yearling weight.

More desirable feedlot gains and heavier slaughter weights characterized the selected Herefords in comparison to the unselected group of Hereford steers. In addition, the selected Herefords were more desirable in their overall muscling.

When dairy cross steers were compared to beef crossbred steers, the steers with dairy pedigrees outweighed the traditional beef steer for both yearling and final weights, although they did not gain as quickly while they were in the feedlot.

Donna J. Cox

A significant improvement was observed in the growth traits and total amount of muscling due to crossbreeding. In addition, the crossbred steers produced leaner carcasses which resulted in more desirable yield grades.

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INTRODUCTION

Beef cattle producers in the United States are divided into two segments--seedstock producers and commercial beef producers with the latter comprising a high proportion of the beef cattle producers. Commercial cattlemen attempt to breed cattle in such a way as to achieve the "ultimate" goal of the industry--to produce the fastest growing cattle on the least amount of feed with carcasses that have the greatest amount of edible portion per unit of carcass weight. In addition, it is necessary that the edible portion be pleasing to the consumer. Two genetic tools available to commercial cattlemen are selection and crossbreeding. Cundiff (1970) asserted if nonadditive and additive genetic variation both are important, then improvement should be maximized by combining systematic crossbreeding with selection within and among breeds.

It is desirable for the breeder to have a realistic idea of how quickly the various characteristics of interest can be changed genetically. Numerous estimates of potential progress from certain selection programs are available. These estimates depend, to a large degree, on the estimated heritabilities and correlations among selected traits of economic importance. It is important to attempt to estimate accurately the genetic and phenotypic parameters of traits required for a particular selection program.

Crossbreeding has been used successfully for the introduction of certain desirable genes into a population that would have otherwise been absent. Much of the classic work with crossbreeding in the United States was done in the Southwest, where Brahmans were crossed with British breeds of cattle. Subsequently, numerous European breeds have been utilized for crossbreeding purposes in the United States.

Simmental numbers within the United States have increased rapidly in recent years and are now recognized as an important beef breed. Consequently an increasingly greater percentage of crossbreeds boast some Simmental breeding. The breed is widely recognized as one that produces a large amount of muscling in a moderate to large frame in comparison to the smaller British breeds with somewhat more average muscling. It would be interesting to compare feedlot and carcass performance of steers sired by Simmental bulls to those sired by a traditional beef breed, the Hereford.

In recent years, the use of restricted maximum likelihood (REML) has gained popularity among dairy scientists as a tool for estimating the variance components necessary for estimation of heritabilities by the paternal half-sib correlation method. Little work has been done in the beef cattle field to make use of this relatively new estimation procedure. It would, therefore, seem appropriate to estimate the components utilizing REML methodology and compare these to estimates previously reported.

The data presented in this study were collected at the Lake City Experiment Station in Lake City, Michigan. They are a portion of data from a long-term crossbreeding program designed and implemented by W.

T. Magee. The base cow population consisted of 200 Hereford cows. Breeding in the herd involved Angus, Charolais and Simmental breeds as well as the Hereford breed. Only the data from the steer calves were utilized in this study.

The objectives of this study were:

- 1) To compare steers sired by Simmental bulls selected on yearling weight to steers sired by Hereford bulls also selected on yearling weight.
- 2) To compare steers selected for yearling weight with those unselected for yearling weight; both sired by Hereford bulls.
- 3) To estimate the heritabilities and phenotypic and genetic correlations of selected feedlot and carcass traits in beef cattle selected for yearling weight.
- 4) To compare the estimates of heritabilities obtained using REML to previously reported estimates.

LITERATURE REVIEW

For several years germ plasm available for beef production in the United States was essentially limited to three British breeds and a representative of the Zebu breeds - Shorthorn, Angus, Hereford and Brahman. In the late 1960's and early 1970's importation of both animals and frozen semen of a large number of continental breeds to North America resulted in breeders having a variety of breeds from which to choose. With the initiation of new blood into the North American population a renewed interest in crossbreeding resulted. Subsequently, considerable emphasis has been placed on developing crossbreeding systems which involve dairy and/or exotic breeds to meet the producer's goal of more efficient beef production.

Effects of Selection and Crossbreeding

Crossbreeding is used in commercial production for two reasons: 1) to take advantage of heterosis or hybrid vigor and 2) through breed combinations which complement each other, to create characteristics not available in any single breed (Warwick and Legates, 1979). Frahm et al (1980) observed that over half of the improvement in production efficiency of beef cattle results from utilizing crossbred cows. There is evidence that more heterosis is observed in growth performance when crossbred cows are mated to a third breed than backcrossed to one of the dam breeds (Allen and Southgate, 1977).

Gregory and Cundiff (1980) stated that the basic objective of beef cattle crossbreeding systems is to simultaneously optimize the use of both nonadditive (heterosis) and additive (breed differences) effects of genes. Cartwright (1970) suggested that making use of breed complementarity appears to be the most effective method of utilizing selection. Breed complementarity refers to a method of choosing a sire breed strong in some desirable characteristic to mate to a breed of dam desirable in some other trait but not as strong in the sire's desirable trait. When breeding in this manner, it would be expected that the offspring would inherit good qualities for both traits.

It is recognized that hybrid vigor is a one-time proposition. However, by selecting in both the purebred and crossbred populations the chances of additional improvement are greater. Consequently, effects of selection and relative breed merit would be fundamental to crossbreeding decisions. Warwick and Cartwright (1955) emphasized that in order to be profitable, beef cattle must have the inherent ability to grow and gain. Biodini et al (1968) asserted that selection for growth rate should be effective not only in modifying growth rate itself, but also should change another important character, carcass composition due to high phenotypic and genetic correlations. He cites various authors who observed that whether animals became fatter or leaner was dependent on the specific criterion for selection. Koch et al (1982) noted that carcass attributes are important in determining the potential value of alternative germ plasm resources for profitable beef production.

Young (1968) rationalized that total efficiency of beef production can be improved by use of combinations of available germ plasm resources that are optimally matched with specific environmental and management conditions. Willham (1970) pointed out that the amount of hybrid vigor depends on 1) gene frequency differences and 2) degree of dominance. Cundiff (1970) observed that the average performance of the breeds would indicate that there are marked differences between breeds in the frequency of genes affecting growth rate and carcass composition and grade. Therefore, it would be a reasonable assumption that heterosis is a greater force when highly divergent breeds are crossed.

Mass Selection - Yearling Weight

Lasley (1972) indicated that yearling weight is of value for selection of both bull and heifer replacements in the breeding herd. Yearling weight is a complex characteristic composed of weaning weight and the rate of gain postweaning. To complicate matters, McPeake (1977) pointed out that weaning weight reflects not only the growth ability of the calf but also the maternal environment created by its dam. The complication arises due to the desire to predict yearling weight of the offspring given data from the two parents. Christian et al (1965) stated that the influence of weaning weight on economic characters expressed at older ages could be due to a carry-over effect of maternal or other environmental factors or the influence of the same genes which acted prior to weaning. Results indicate that final

weight should be the single most important trait in a selection program at improving the production and carcass traits of beef cattle (Dinkel and Busch, 1973).

Shelby et al (1963) asserted mass selection should be effective for growth traits. They found that final weight was a slightly superior criterion for selection than average daily gain. Dunn et al (1970) surmised that estimates of the correlation between a sire's genetic ability to produce straightbred and crossbred progeny were high, indicating that mass selection in purebred populations contributing germ plasm to crossbred populations would be approximately as effective in improving commercial straightbred performance. Miquel and Cartwright (1963) indicated that selection would be equally effective in crossbreds and purebreds.

Koch et al (1974a) examined the selection response in Hereford cattle selected for 1) weaning weight, 2) yearling weight and 3) an index of yearling weight and muscling score. They found the average estimated response per generation was: weaning weight, 0.23, 0.17 and 0.15 and yearling weight, 0.36, 0.43 and 0.33, respectively. Responses were reported in standard deviations. Their conclusion was that selection for yearling weight may increase weaning weight or weight gain more than direct selection for these traits.

In the same study, Koch et al (1974a) looked at the average sire selection differential per generation when selection was based on each of the three criterion. The sire differentials were 1.51, 1.18, 0.86 standard deviations for weaning weight and 1.42, 1.79, 1.22 for yearling weight for each of the selection criteria, respectively. They

defined selection differential as the difference in mean performance of selected parents and the unselected group from which they came. In a separate paper (Koch et al, 1974b) they noted that selection for yearling weight may increase weaning gain or weight more than direct selection for these traits.

Swiger et al (1965) showed a loss of 2% in final weight when selecting strictly on yearling weight versus an index for weaning weight and daily gain.

Biondini et al (1968) selected mice over 10 generations for rapid growth rate. They saw conclusive evidence of changes in gain on test and efficiency resulting from this criterion of selection. This would suggest that selection for yearling weight in beef cattle would result in increased performance in growth traits and the efficiency related to those traits.

Chenette et al (1981) observed the response in Hereford bulls to selection for 1) weaning weight and 2) yearling weight. They found that the two traits generally followed similar patterns of response. In the group selected for yearling weight they observed a direct response of 3.27 lb/year, with a correlated response of 1.5 lb/year weaning weight. In addition, they reported that all correlated measures of response in conformation and condition were quite small, with more positive change occurring in the degree of muscling rather than fatness. Dinkel and Busch (1973) concluded that genes contributing to rapid growth tend to lower trimmable fat.

Cundiff et al (1964) obtained genetic correlations which indicated that selection for growth rate would be effective and would lead

to increased muscular development, improved carcass grade and a slight increase in carcass fatness. His analysis is in direct contrast to Chenette et al (1981) and Dinkel and Busch (1973) which report negative correlations for growth rate and carcass fatness. These results imply that selection for growth rate would be compatible with the production of desirable carcasses.

Cundiff et al (1971) evaluated the expected effect of selection for growth rate on the composition and quality of beef carcasses. They compared these results to the results for direct selection of carcass attributes. Their conclusion was that selection for growth rate could be more intense and implemented at less cost using yearling weight of live animals than direct selection for carcass retail product. Blackwell et al (1962) concurred when they found evidence that carcass grade could be improved by selection for slaughter grade. It was discovered that graders can account for 20-25% of the variation in carcass traits (Gregory et al, 1962). Gregory et al (1962) concluded that more precise estimates of carcass grades were needed for selection of breeding cattle.

In 1969, Cundiff et al observed that single trait selection would be much more effective for growth of retail product than for proportion or yield of retail product at any level of selection intensity because heritability is higher and phenotypic variation is significantly greater. In addition, they asserted that selection for growth would improve overall efficiency of production if the maintenance requirements of breeding animals was not increased a proportionate amount by correlated changes associated with their increased

mature body size. Likewise, there is a strong relationship between the ability to make rapid gains and the ability to make efficient gains in the feedlot (Lasley, 1972).

In recent years, it has been of major concern to cattle breeders to increase yearling weight while keeping birth weight constant. However, due to a positive genetic correlation between the traits, we have witnessed a proportional increase in birth weights when selection is for yearling weight. Dickerson et al (1974) suggest that this does not have to be the case. They advocate that it is biologically feasible to increase yearling weight with very little change in birth weight because the genetic correlation is far from perfect (they estimate it to be .54). Nevertheless, evidence has generally supported an increase in birth weight.

In a crossbreeding study at Michigan State University, McPeake (1977) found that selection for yearling weight was the primary factor responsible for the increase in dollar return to a beef herd over out-of-pocket costs. His results indicated that selection accounted for 11.4% increase in actual weaning weight. Wilson et al (1976) suggested that selecting for rapid growth should improve both rate and efficiency of gain due to moderate heritability of growth rate and the favorable correlation with feed conversion. Smith and Cundiff (1976) presented results indicating that selection for early growth rate may be more appropriate for maternal stocks than for terminal sire breeds. However, they noted that the apparent negative pressure that would be placed on birth weight would have some merit for sire breeds.

Swiger et al (1965) showed that selecting for final weight alone

would be 90% as efficient in improving total net merit, where net merit is defined as net profit, as selecting for an index involving weaning weight, postweaning daily gain, feed consumption and fat. They hypothesized that selecting for final weight should lead to increased net merit through the production of enough extra retail product to overcome the cost of producing extra fat. In addition, it is far simpler and less expensive to select for final weight.

Vinson et al (1969) conducted a study with mice to compare predicted responses of different crossbred selection methods when selection of future parents was confined to purebred individuals. The three selection methods were 1) mass selection based on individual purebred performance, 2) half-sib family selection based on purebred performance and 3) reciprocal recurrent selection based on crossbred performance. Traits studied included birth weight, weaning weight, postweaning gain and litter size. Their results indicated that mass selection would be expected to yield the largest genetic improvement for all traits except weaning weight or litter size.

Many cattlemen have contended that it is possible to select the faster gaining and more efficient animals by paying attention to conformation. Several studies, however, show rather clearly that this is not the case and selection for performance on the basis of conformation is ineffective (Lasley, 1972). Taylor (1982) asserted that selection for beef type may have been detrimental to selection for growth rate. He quoted Hammond (1980) in defining selection of beef type as selecting those cattle with shorter bones and thicker muscles.

Crossbreeding - Feedlot Performance

Numerous studies have been conducted in the southern United States examining the merits of crossing Brahman cattle with various other breeds. However, due to the scope of the present study, only those investigations involving breeds common to the Midwest will be presented.

Adams et al (1973) studied the performance of crosses from Hereford dams bred to six imported sire breeds and Angus and Hereford bulls. They found that Simmental crosses excelled Limousin and Angus by Hereford crosses in 200-day weight ratio and postweaning average daily gain. In the same study, Charolais, Simmental, Maine-Anjou, Brown Swiss and Limousin crosses were shown to exhibit the least amount of fat cover as compared to Angus, Hereford and Lincoln Red crosses. The Angus by Hereford crossbreds were by far the fattest. In addition, the Simmental and Limousin crosses had a significantly greater muscle development score.

Alenda et al (1980b) conducted an experiment to estimate the genetic effects of postweaning daily gain, ribeye area and fat cover. He then utilized these estimates to assess the effectiveness of crossbreeding systems employing Angus, Hereford and Charolais breeds. Their results indicated that the sum of the additive effects of the three breeds differed ($P < .10$) implying that differences among breed means were associated with additive differences. No significant individual heterotic effect was observed in any Charolais cross. The Angus by Hereford cross produced 3% individual heterosis for

postweaning daily gain.

Allen and Southgate (1977) noted that the heavier the sire breed, the more rapid the growth of its offspring and the higher the weight at which they are slaughtered. They also indicated that there is greater heterosis for growth performance when crossbred cows are mated to a third sire breed than backcrossed to one of the dam breeds. For 200-day weight they ranked four beef breeds in the following order: Charolais, Simmental, Hereford and Angus.

Anderson et al (1978) examined postweaning data on 33 crossbred calves sired by Angus, Holstein and Chianina bulls. Those calves sired by Angus bulls gained slower in the feedlot and were lighter at slaughter ($P < .05$). They indicated that when fed to choice grade, efficiency among sire groups was not different.

Barton (1971) compared the growth characteristics of Angus, Beef Shorthorn, Milking Shorthorn and Friesian steers. They demonstrated that the dairy steers grew faster than the beef breeds.

In a comparative feedlot experiment with 53 Hereford and 53 Angus steers, Butler et al (1962) discovered Hereford steers had higher gains (440 lbs vs 419 lbs) with somewhat better feed efficiency (952 lb feed/cwt gain vs 1035 lb feed/cwt gain) ($P < .05$).

Cundiff (1970) expressed the opinion that even though Herefords excell over Angus and Shorthorns in growth, their below average maternal ability makes them no better in total net merit. He also observed that heterosis for postweaning data tended to decrease with increasing age after approximately one year. Gregory et al (1966) also noted a decrease in heterosis with increasing age.

Cundiff et al (1981) studied postweaning growth and feed efficiency for 798 steers representing Hereford (H) and Angus (A) straightbreds, Hereford-Angus reciprocal crosses (HA,AH), Red Poll-Hereford (RH) and Red Poll-Angus (RA) crosses, Brown Swiss-Angus (BA) and Brown Swiss-Hereford (BH) crosses, Gelbvieh-Hereford (GH) and Gelbvieh-Angus (GA) crosses, Maine-Anjou-Hereford (MH) and Maine-Anjou-Angus (MA) crosses and Chianina-Angus (CA) and Chianina-Hereford (CH) breed crosses. The Brown Swiss crosses, Gelbvieh crosses and Maine-Anjou crosses exhibited the most rapid growth rates and heaviest weights at 424 days. Contrary to previous reports, they found that the Hereford-Angus crosses did not gain significantly faster than the Hereford and Angus straightbreds during the postweaning period. Table 1 presents the breed means for growth traits.

Deutscher and Slyter (1978) determined breed of sire to be significant for most feedlot traits. They suggested that Charolais sired three-breed cross calves were heavier at birth and weaning, gained faster in the feedlot and had heavier final feedlot and carcass weights than either Angus or Hereford sired calves. Table 2 gives the least-squares means they found for the various feedlot traits.

Frahm et al (1980) examined three-breed calves sired by Charolais and Limousin bulls. Although the Charolais calves were significantly heavier at birth, the differences in feedlot performance were not significant between the sire breeds.

Gregory and Cundiff (1980) noted that, in general, three-breed rotational crosses showed a higher level of heterosis for most postweaning characters than the two-breed rotational crosses. They

Table 1. Breed Group Means for Live Weights and Growth Rates^a.

Trait	Breed	Breed Group ^b							Avg	SD ^c
		HH AA	AH HA	RH RA	BH BA	GH GA	MH MA	CH CA		
No. of animals	H	43	57	44	53	44	46	56	343	
	A	60	67	67	68	67	63	63	455	
200-day weight, kg	H	179.2	188.7	189.1	198.1	195.8	194.4	198.9	192.0	
	A	192.8	196.3	196.1	209.9	215.9	213.9	214.9	205.7	
	Avg	186.0 ^d	192.5 ^e	192.6 ^e	204.0 ^f	205.8 ^f	204.2 ^f	206.9 ^f	198.9	21.1
Initial weight, kg	H	205.4	217.6	213.5	221.9	224.0	225.4	227.8	219.4	
	A	221.1	227.2	220.9	239.8	247.6	250.3	245.9	236.1	
	Avg	213.2 ^d	222.4 ^e	217.2 ^e	230.8 ^f	235.8 ^{fg}	237.8 ^{fg}	236.8 ^{fg}	227.7	23.4
ADG, kg	H	1.046	1.074	.986	1.099	1.134	1.162	1.094	1.085	
	A	1.007	1.019	.921	1.068	1.098	1.158	1.080	1.050	
	Avg	1.026	1.047 ^d	.954 ^e	1.084 ^{fg}	1.116 ^g	1.160 ^h	1.087 ^g	1.067	.150
SE coefficients	H	.1836	.1530	.1763	.1703	.1875	.1738	.1603	.0699	
	A	.1522	.1500	.1482	.1540	.1549	.1493	.1531	.0658	
	Avg	.1074	.0972	.1234	.1300	.1385	.1243	.1180	.0553	

^a Cundiff *et al.* (1981).^b H = Hereford; A = Angus; R = Red Poll; B = Brown Swiss; G = Gelbvieh; M = Marine Anjou; Ci = Chianina. First letter denotes sire breed and second letter denotes dam breed.^c SD is square root of mean square for sires within breed. Standard error of least-squares mean can be determined by multiplying the SE coefficient x SD of a trait.^d Effect of heterosis in Hereford-Angus crosses ($P < .05$).^{e,f,g,h} Means for F₁ crosses in the same row with no common superscripts differ ($P < .05$).

Table 2. Least-Squares Means of Feedlot Traits^a

Trait	Breed of Sire		
	Angus	Hereford	Charolais
No. of calves	77	83	64
Adj. Final Feedlot wt., kg	372	380	420
Feedlot ADG, kg/day	.84	.88	1.00

^aDeutscher and Slyter (1978)

estimated that a three-breed rotation should give a 20% increase in weight weaned per cow exposed as compared to purebreds, and 4.5% more than in a two-breed rotational mating system.

In an experiment comparing Hereford, Angus, Shorthorn and all reciprocal crosses, Gregory et al (1966) found that differences in growth rate and feed efficiency among sires within breed were significant indicating a large amount of additive genetic variation. In the same study, they found that calves sired by Hereford bulls were superior to the other two breeds in growth rate and feed efficiency. The mean average daily gain of the Hereford sired calves was consistently higher in all phases of the trial as demonstrated in Table 3.

Table 3. Least Squares Means for Growth by Breeding Group^a

Trait	Breed of Sire		
	Hereford	Angus	Shorthorn
ADG, weaning to 284 days	0.688	0.680	0.678
ADG, 284 to 368 days	1.018	0.947	0.933
ADG, 368 to 452 days	0.890	0.811	0.814

^aGregory et al (1966)

Klosterman (1972) pointed out that when cattle are fed to a similar degree of finish or grade, numerous experiments have shown little if any difference in efficiency of feed use among the cattle of various types and sizes. In contrast, when they are fed to a similar

weight, the larger cattle are leaner, grade lower and are more efficient. Finally, when beef steers are fed to the same time, the faster gaining cattle are fatter at slaughter.

Knapp et al (1980) evaluated three breed crosses of Hereford, Charolais, Angus and Brown Swiss breeds on preweaning and weaning traits. They found that cattle with Hereford dams always had higher means than those from Hereford sires. In contrast, Charolais sired calves had greater preweaning means than those from Charolais dams.

Koch et al (1982) analyzed the genetic, environmental and phenotypic relationships among four growth and 12 carcass traits of 2453 crossbred steers representing 16 different sire breeds. The sire breeds in the project were Angus, Hereford, Jersey, South Devon, Simmental, Limousin, Charolais, Red Poll, Brown Swiss, Gelbvieh, Maine-Anjou, Chianina, Sahiwal, Brahman, Pinzgauer and Tarentaise. They suggested that selection for increased growth rate resulted in later maturing lean types. Their results indicated that selection criteria, except gain to weaning, that increased retail product percentage also decreased marbling, but the decline was generally small.

Kempster et al (1976) asserted that lean distribution can be ignored in breed comparisons. In contrast, Swiger et al (1965) asserted differences in growth rate of lean was much more important than differences in quality grade when considering a selection index. Ziegler et al (1971) noted the amount of lean was of utmost importance because of the simple economics involved in feed conversion during production and the ultimate retail value.

In a study to evaluate heterosis and management effects in post-

weaning growth of Angus, Hereford and reciprocal cross cattle, Long and Gregory (1975) observed that the crossbreds exceeded the purebreds by 5 to 6% for postweaning gain and weight.

Mason (1966) concluded that in crosses composed of British breeds there is a small but consistent amount of hybrid vigor (1-10%) for most characters of size and growth. He found no greater hybrid vigor for a Charolais by British cross than when two British breeds were crossed. However, there was an advantage in size and growth rate of 10% or more when Brahman crosses with British cattle.

No significant breed differences were found for birth weight, weaning weight or slaughter age when McAllister et al (1976) compared the Polled Hereford, Charolais, Limousin and Simmental breeds as sires of crossbred calves. In addition, they found the Polled Herefords averaged less for slaughter weight per day of age and more for fat thickness.

In an investigation comparing crossbred calves sired by South Devon, Maine-Anjou and Simmental bulls, Newman et al (1974) observed that calves from the Maine-Anjou sires were heavier when starting on test (262 kg as compared to 238 and 258 kg by the South Devon and Simmental sired calves, respectively) and gained 1.42 kg per day while on test as compared to 1.18 kg by the South Devon sired calves and 1.26 kg by calves from Simmental sires.

Olson et al (1978a) conducted an experiment involving the Angus, Hereford and Shorthorn breeds. They observed three-breed cross steers from crossbred dams were 5.2% heavier ($P < .01$) at the beginning but had no advantage in postweaning gain over two-breed cross steers from

straightbred dams in a 224-day postweaning test. All steers were slaughtered at the end of the postweaning feeding period in which the three-breed steers averaged 8.3 days older at slaughter. There was also an indication of increased fat in steers from F_1 dams over those from straightbred dams. In another study using the same cattle, Olson et al (1978c) found crossbreds slightly more efficient in postweaning gain than the straightbreds. He noted their advantage in rate of growth was enough to offset their higher maintenance requirements.

Shreffler and Touchberry (1959) found the general effect of crossbreeding on skeletal growth in dairy cattle (Guernsey by Holstein) was too small to be of practical or statistical significance. They found heterosis to be of importance in rapid growth up to 2 years of age.

Smith et al (1976) crossed Hereford and Angus dams with Hereford, Angus, Jersey, South Devon, Limousin, Charolais and Simmental sires. In their study, Charolais and Simmental crosses were the largest, fastest gaining breed groups.

Vogt et al (1967) examined postweaning performance to slaughter in Angus, Hereford, Shorthorn and all reciprocal cross calves. The two-breed crosses averaged 40 gm more in yearling daily gain than purebreds. They found no difference in two- and three-breed crosses, but the backcross was significantly below the two-breed cross. Feedlot daily gain was not different for any of the groups.

Warwick (1968) stated that in 12 of 13 crossbreeding experiments, it was shown the crossbreds had a 2-4% advantage in postweaning rate of gain with a slight advantage in efficiency.

Feedlot performance of progeny of Hereford, Hereford X Holstein and Holstein cows were evaluated by Wyatt et al (1977). They observed as Holstein breeding increased 1) initial weight increased (30 to 55 kg), 2) slaughter weight increased (49 to 104 kg) and 3) number of days to reach choice increased.

Crossbreeding - Carcass Characteristics

In specific details there is lack of agreement as to what constitutes desirability in beef carcasses. However, there is general agreement on the essentials - namely, that carcasses should have 1) a maximum of lean combined with tenderness and other maximum palatability and 2) a minimum of excess fat (Warwick and Legates, 1979). Of course, due to the nature of carcass characteristics, an animal must be selected on the performance of its sib or progeny test.

Deutscher and Slyter (1978) found breed of sire significant for most feedlot traits. In an experiment involving 77 Angus, 83 Hereford and 64 Charolais sired crossbred calves the least-squares means for various carcass characteristics were: carcass weight (kg), 224, 225, 262; dressing percent (%), 61.7, 61.6, 62.3; marbling score, 4.9, 4.49, 4.77; carcass grade, 18.6, 18.0, 18.4; fat thickness (cm), 1.14, 1.17, 0.94; ribeye area (cm²), 64.5, 65.8, 74.2; kidney fat (%), 2.9, 2.6, 3.0; cutability (%), 50.2, 50.4, 51.0; and yield grade, 2.93, 2.85, 2.60 for Angus, Hereford and Charolais sired calves, respectively. For carcass grade, 18 represents high good and 19 is low choice with the scale increasing by 1 for each 1/3 of a grade. The

marbling score is based on 4 being slight and 5 small with an increase of 1 for each step up in marbling. Therefore, it appears the rank of the sires for carcass grade based on leanness and muscling would be 1) Charolais, 2) Hereford and 3) Angus. Cundiff et al (1971) conducted a trial in which carcass weight adjusted for age was used as the measure of growth rate. They observed the association between cutability and carcass weight was more environmental than genetic. The analysis of genetic variation within breed of sire - breed of dam groups indicated that selection for rate of growth would be effective and that associated changes in carcass composition and marbling would be greatly influenced by age or weight at slaughter. Brackelsberg et al (1971) showed that carcass weight was a significant source of variation for all carcass traits except marbling and final carcass grade. Data collected by Adams et al (1977) suggested that carcass weight would be of value as a predictor of carcass fatness within breed group but not in a population comprised of several breeds.

In a trial designed to evaluate traits in the U.S.D.A. yield grade equation for predicting beef carcass cutability in breed groups differing in type, Crouse et al (1975) concluded carcass weight was a good predictor within a breed group, but poor over all steers. They surmised fat thickness was the most useful predictor and longissimus area the worst.

Koch et al (1982) explored the wholesale cut composition of 642 carcasses obtained from steers that were from matings of Hereford and Angus cows to Hereford, Angus, Tarentaise, Pinzgauer, Brahman and Sahiwal sires. They observed that increases in weight associated with

continued feed intake resulted in greater fat to lean ratio than from increased genetic growth potential. Their conclusion was that most of the variation in wholesale cut percentages and composition of cuts was associated with differences in total lean and fat yield among sire breed groups. They also noted that as side weight increased, percentage of retail product and bone-in cuts decreased whereas fat trim increased in all cuts.

Clyburn et al (1961) studied the effects of breed and cross on carcass characteristics of beef steers. They observed Angus, Polled Hereford, Santa Gertrudis and all two and three-way cross steers. Their major observation was that Angus had the largest loin eye per 100 pounds of carcass (1.95 cm^2) and the Santa Gertrudis the smallest (1.54 cm^2).

Butler et al (1962) compared carcass merit of 106 Hereford and Angus steers. The analysis favored the carcasses from the Angus steers in marbling score and showed a 2/3 grade advantage in final carcass grade. However, it was observed that the Angus cattle had a higher percent in forequarter while the Herefords were significantly higher in hindquarter.

Beef- and dairy-type cattle were compared for cutability and eatability (Branaman et al, 1962). They noted the dairy-type averaged 3% less in dressing percent; however, they equalled the beef cattle in percentage of high-priced cuts. They did observe a more desirable average quality grade in the beef steers (C^0) as compared to the dairy (St^+). The only palatability attributes that appeared to be associated with type were the intensity of lean flavor and juiciness.

Therefore, they concluded there was little advantage for beef-type from the standpoint of carcass cut-out.

Bass et al (1981) compared calves from Angus dams sired by Simmental, Blonde d'Aquitane, Charolais, Maine-Anjou, Friesian, Jersey, Hereford and Angus bulls. He concluded dairy breeds had the heaviest internal fat. The remaining results were compatible with previously reported studies.

Alenda et al (1980b) attempted to estimate genetic effects on ribeye area and fat cover and to utilize these estimates to assess effectiveness of crossbreeding systems. They observed cattle of Angus, Charolais and Hereford parentage. In analyzing ribeye area, they noted that the Charolais additive effects were 26% greater than either Hereford or Angus, where the additive effect of the i^{th} breed was calculated as

$$\varepsilon_i = \frac{(n-1)B_{iii} - \sum_{j=1}^n (B_{jjj} + B_{jii} - B_{ijj})}{n}, \quad j \neq i$$

where, n is the number of breeds and B_{ijk} is the least square mean for the breed class having breed i as the sire, breed j as the maternal grand sire and breed k as the maternal grand dam. Individual heterosis (calculated as the sum of the dominance effect and one-half the additive X additive effect) was 3% for the Angus by Charolais crosses and 2% for the Hereford by Charolais crosses. The Charolais by Hereford had no significant heterotic effects. Maternal heterosis was large and negative for all crosses, indicating crossbred dams produce calves with smaller ribeyes. Angus and Hereford additive effects were more than 1.0 cm greater than Charolais for fat cover. Any cross

containing Charolais did not produce individual heterosis effects. For future ribeye area of the various crosses they predicted 0.1, -0.9 and -1.9 cm² deviations from the mean of the three purebreds for the Angus X Hereford and Charolais X Hereford crosses, respectively. They suggested that the decrease was due to large negative maternal effects. No cross was expected to out-perform the purebred Charolais for ribeye area.

Koch et al (1976) examined the carcass composition, quality and palatability of various crossbreds. Breed of sire (Hereford, Angus, Jersey, South Devon, Limousin, Charolais and Simmental) was highly significant for all traits. Charolais-sired calves had the heaviest carcass weights and Jersey-sired calves were the lightest. Dressing percent did not differ among sire breeds, with the Charolais and Simmental calves carrying less fat than the other breeds.

Kempster et al (1982) examined dissection data for 753 steer carcasses comprising 17 breed-type X feeding system groups. Breed types included Ayrshire, Friesian, Friesian X Ayrshire and crosses out of Friesians by Angus, Charolais, Hereford, Limousin, Simmental and South Devon sires. They advised that when cattle are slaughtered at equal fatness, differences between breeds in the longissimus area is closely related to differences in carcass weight.

Eighteen hundred purebred and crossbred calves produced from 1966 through 1970 were included in a study by Helphinstine and Elings (1971). Data collected in 1966 involved only straightbred Hereford calves. In 1967, the first reciprocal crosses between Angus and Hereford were produced. Brown Swiss sires were used initially in the

1967 breeding season resulting in mostly crossbred calves for the 1968, 1969 and 1970 calf crops. They noted differences in dressing percent, ribeye area and percent major trimmed cuts due to the increase in the number of crossbred calves.

Hedrick et al (1970) found crossbreds about 7% superior in ribeye area in an experiment involving Angus, Hereford and Charolais straightbred and crossbred cattle. No sire differences were detected, which they attributed to the fact that the bulls were sampled from the best of each breed.

In a later study involving the same three breeds, Hedrick et al (1975) concluded Charolais could be used with advantage as males in combination with Hereford females. He found carcasses from Charolais sired calves outweighed Herefords, which in turn outweighed Angus. However, he noted the Angus and Hereford sired calves had significantly fatter carcasses than those from Charolais sires, with the Angus sires producing calves with the highest quality grade. The steers sired by the Charolais bulls were consistently larger in loin eye area.

Gregory et al (1966) ranked the Hereford, Angus and Shorthorn in that order for net merit of carcass traits. They found that the Hereford breed contributed more than either Angus or Shorthorn breed to the average heterosis effects.

Data were analyzed on slaughtered weight, hot carcass weight, U.S.D.A. quality grade, adjusted fat thickness at the 12th rib, estimated kidney and pelvic fat, longissimus area and estimated cutability adjusted to an age-constant basis of 453.2 days on 537 carcasses in a

four-breed diallel cross design including the Red Poll, Brown Swiss, Hereford and Angus breeds to estimate heterosis and breed transmitted effects on major economic traits of beef cattle (Gregory et al , 1962). Brown Swiss ranked first and Red Poll last in breed transmitted effects for carcass traits associated with weight. When carcass traits were adjusted to a constant carcass weight (270.9 kg) heterosis effects were not important. For the age-constant analysis, heterosis was significant for slaughter weight, carcass weight, adjusted fat thickness and estimated cutability. The least-squares means by breed of sire are presented in Table 4 and Table 5 on an age constant and weight constant basis, respectively.

Gerlaugh et al (1951) examined the carcass merit of Angus, Hereford and their reciprocal crosses. They found the crossbreds heavier with a higher dressing percent than either of the purebreds. In a similar experiment, Gaines et al (1967) examined the heterosis effects from crosses among Angus, Hereford and Shorthorns. They observed the adjusted carcass weight average was 9.1 kg heavier than straightbreds, an increase of 3.1%. The adjusted loin eye area was 2.5 cm² larger than the mean of straightbreds (3.6% increase). There appeared to be no heterosis for carcass grade, marbling score or carcass conformation.

In a study to examine the differences in carcass traits of Charolais and Limousin sired three-breed cross calves, Frahm et al (1980) found dressing percent the only trait which differed between breeds. They observed a slight advantage for the Limousins.

Ziegler et al (1971) compared certain carcass traits of several

Table 4. Least-Squares Means for Carcass Traits -- Age Constant Basis^a.

Trait	Breed of Sire				Mean
	Red Poll	Brown Swiss	Hereford	Angus	
U.S.D.A. Quality Grade ^b	8.7	8.9	8.6	9.5	8.9 $\pm$.10
Adj. Fat Thickness (cm)	1.04	.83	1.22	1.29	1.10 $\pm$.02
Est. Kidney & Pelvic (%)	4.4	3.7	3.3	3.7	3.8 $\pm$.05
Longissimus Area (cm ²)	66.6	74.4	66.2	68.4	68.9 $\pm$.45
Estimated Cutability (%)	54.8	57.3	55.1	54.2	55.3 $\pm$.14

^a Gregory *et al.* (1962).

^b 8 = average good; 9 = high good; 10 = low choice; 11 = average choice.

Table 5. Least-Squares Means for Carcass Traits -- Weight Constant Basis^a

Trait	Breed of Sire				Mean
	Red Poll	Brown Swiss	Hereford	Angus	
U.S.D.A. Quality Grade ^b	8.8	8.4	8.6	9.6	8.8 $\pm$.10
Adj. Fat Thickness (cm)	1.05	.79	1.18	1.26	1.07 $\pm$.02
Est. Kidney and Pelvic Fat (%)	4.4	3.6	3.3	3.7	3.7 $\pm$.05
Longissimus Area (cm ²)	67.2	71.2	66.0	67.2	67.9 $\pm$.43
Estimated Cutability (%)	54.7	57.4	55.3	54.3	55.4 $\pm$.15

^a Gregory et al. (1962).

^b 8 = average good; 9 = high good; 10 = low choice; 11 = average choice.

breeds and crosses. Their results indicated the Charolais and Holstein steer groups had a significantly greater ($P < .01$) cutability than any other breed group (Charolais (C), Hereford (He), Holstein (Ho), Shorthorn, Angus (A), A by A-Ho, He by A-Ho, Polled He by A-Ho). In addition, the Angus and Shorthorn steers had significantly greater marbling scores than the other breed groups. The Charolais, Holstein and Polled He by A-Ho steer groups were lower in total acceptability.

Young et al (1978) attempted to characterize various types of three-breed cross cattle for carcass traits. Their trial included 282 steers with carcass data collected on 275 produced by artificially inseminating yearling heifers of 12 crossbred groups (Hereford-Angus reciprocal crosses plus F_1 crosses produced by mating Jersey, South Devon, Simmental, Limousin and Charolais sires to Hereford and Angus cows) to Hereford, Angus, Brahman, South Devon and Holstein bulls. When age was held constant breed of sire was significant for all traits except loin eye area and maturity. Breed of sire of cow was a significant source of variation for fat thickness, longissimus area, estimated percentage kidney, heart and pelvic fat, yield grade and conformation. Breed of dam of cow was not significant for any slaughter trait. Holstein sired steers had the least amount of fat over the longissimus, which resulted in the best yield grade for any sire breed. When weight was held constant, breed of sire was significant for the same traits as when age was constant. In addition, breed of sire of cow was significant for all carcass traits except slaughter weight, maturity and quality grade.

Wyatt et al (1977) analyzed the carcass traits of progeny from

Hereford, Hereford X Holstein and Holstein cows bred to Charolais bulls. As percent Holstein breeding increased: 1) Carcass weight increased, 2) ribeye area was larger, 3) cutability decreased and 4) conformation scores were lower.

In a study to appraise genetic parameters of carcass characteristics from progeny of Polled Hereford sires and Holstein-Angus cows, Wilson et al (1976) found the faster growing cattle tended to have lower marbling scores. Marbling score only accounted for 7.3% of the variance in shear score.

Warwick (1968) failed to find any heterotic effects. Although the three-breed British cross never exceeded the purebreds in a single trait, in total net merit crosses usually exceeded the best purebred. They showed Charolais sired calves were superior in leanness of carcass, but were 1/3 to 2/3 lower in carcass grade than British sired calves at the same weight.

Temple et al (1960) contrasted the carcass quality of crossbred steers sired by six breeds of bulls. They ranked the breeds: Short-horn, Hereford, Angus, Brahman, Brangus and Charolais. However, the range of grades was only from low good to low choice indicating small differences in quality due to sire breed. In the study, they found the Charolais sired calves had the largest ribeye area of the six breeds.

In an investigation of the carcass characteristics and meat quality of Hereford and Friesian steers, Taylor (1982) found a definite advantage for the breed in dressing percent ($P < .01$), although there were no differences in live weight. As implied by the larger

dressing percent, the Hereford steers were fatter, denoting their early maturing characteristic. However, he was unable to show any differences in tenderness, juiciness or flavor.

Olson et al (1978b) observed maternal heterosis was nonsignificant for carcass traits of steers when slaughter age was included as linear and quadratic covariables. Lasley et al (1971) concurred when they, too, indicated that heterosis may not be important for carcass traits.

Newman et al (1974) compared production traits of steers by South Devon, Maine-Anjou and Simmental sires. They found the breed of sire differences in slaughter age, loin eye area and carcass weight were not significant. They did find that the South Devon breed was fatter per 100 kg of carcass resulting in a more desirable marbling score.

Carcass quality and fat, lean and bone distribution were analyzed from British and Continental sired (P. Hereford, Charolais, Limousin and Simmental) crossbred steers. The Polled Hereford calves averaged less for slaughter weight, loin eye area and percent trimmed loin per day of age. Although the Charolais and Limousin sired calves had heavier ($P < .01$) carcass weights, the Simmental calves had a greater ($P < .05$) percent hindquarter.

Long and Gregory (1975) contrasted the carcass traits of Angus, Hereford and reciprocal cross cattle with hot carcass weight as a covariate. They concluded cattle with Angus sires or dams produced heavier carcasses with higher dressing percentages, conformation scores, marbling scores and final grades. Nevertheless, they were

fatter with lower cutability. The authors observed heterosis effects for loin eye area and fat thickness.

Phenotypic and Genetic Parameters

Genetic change through selection is dependent on the genetic variability found in the population. Shelby et al. (1963) noted the phenotypic and genetic relationships existing between and within various traits used as criteria for selection must be known to maximize the rate of progress in a selection program. It has been shown in swine that the amount of variation explained by genetics is different from one breed to the next (Blunn and Baker, 1947).

Alenda et al. (1980a) suggested that having estimates of the genetic and maternal effects, the magnitude of both mean and variance can be predicted and/or controlled by selection of breeds entering into or by changing the order of breeds in the rotation.

Heritability - General

Selection is based on the phenotypic value of breeding animals and at times on those of their relatives. These phenotypic values are used to obtain an expected breeding value as an initial step in the selection process. The relative agreement between phenotype and breeding value is measured by the coefficient of heritability or simply heritability (h^2).

Lush (1945) pointed out the importance of heritability and empha-

sized its role in predicting the breeding value of an animal. Lush (1940) defined heritability in the "narrow sense" as the proportion of the total variance in a trait that is attributed to the average or additive effects of genes.

$$h_N^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2}$$

Because only additive genetic effects in a population contribute to the permanent gain from selection, an estimate of heritability in the narrow sense is more desirable for predicting the results from selection procedures (Lush, 1945).

Dickerson (1958) discussed the advantages and disadvantages of various estimates of heritability. He suggested the regression of offspring on midparent (b_{op}) is the most nearly unbiased estimate of effective heritability. However, it is subject to bias from environmental correlation between parent and offspring and by selection of parents if the regression is nonlinear.

Another estimate suggested was the doubled regression of offspring on dam ($2b_{od}$). It is usually computed within sire progenies to avoid effects of any assortative mating or environmental correlations (Lush, 1940). Dickerson points out that when compared to h_{op}^2 it overestimates heritability by $(.5\sigma_m^2 + \sigma_{mg}^2) * (1/\sigma_p^2)$ where σ_m^2 is the variance attributable to maternal factors. σ_p^2 is the phenotypic variance and σ_{mg}^2 is the covariance between the maternal and genetic portion of variation. A similar estimate is the doubled regression of offspring on sire ($2b_{os}$), however it tends to underestimate the true heritability.

Three additional methods were presented by Dickerson: 1) from the sire component (h_{4s}^2), 2) from the dam component (h_{4d}^2) or 3) from the full-sib correlation (h_{d+s}^2). The first method is identical with the quadrupled correlation between paternal half-sibs ($4r_{pp}$). The magnitude of the bias of the estimate depends on the gene-environment interaction.

Heritability - Feedlot Traits

Swiger et al. (1963) evaluated the postweaning gain in beef cattle. They discovered that heritability increased as age of calf increased. Heritability of 550-day weight was estimated as .37. Urick et al. (1957) found similar results with heritabilities of postweaning gain varying from .09 to .43. They concluded that varying amounts of progress for rapid gaining ability could be made based on selection at differing points in the postweaning gain.

Carter and Kincaid (1959) estimated feedlot daily gain heritability by various methods. Their estimates were: paternal half-sib, .38; regression of progeny average on sire, .21; and intra-sire regression of offspring on dam, .40.

Some of the published estimates of heritability for feedlot traits are presented in Table 6. As can be seen, the feedlot traits tend to be moderately to highly heritable indicating that selection for those traits should be successful.

Table 6. Heritability Estimates of Feedlot Traits in Beef Cattle.

Author	Postweaning daily gain	Final weight	Yearling weight
Benyshek (1981)	.52	.52	---
Blackwell <u>et al.</u> (1962)	.76	.70	.10
Buchanan <u>et al.</u> (1982a)	.42	---	.30
Busch & Dinkel (1967)	.55	.85	---
Chenette <u>et al.</u> (1981)	---	---	.14
Christians <u>et al.</u> (1962)	.88	1.00	---
Dickerson <u>et al.</u> (1974)	.26	.48	---
Dinkel & Busch (1973)	.55	.85	---
Dunn <u>et al.</u> (1970)	---	.56	---
Knapp & Clark (1950)	.65	.86	---
Knapp & Nordskog (1946a)	.46	.69	---
Koch (1978)	.92	---	.69
Koch & Clark (1955a)	.39	---	.47
Koch & Clark (1955b)	.18	---	.43
Koch <u>et al.</u> (1974b)	---	---	(.19,.46) ^a
Laskey (1972)	.57	---	---
Newman <u>et al.</u> (1973)	---	0	.45
Shelby <u>et al.</u> (1955)	.60	.84	---
Shelby <u>et al.</u> (1963)	.48	.64	---
Warwick & Legates (1979)	.45-.50	---	.50-.60

^a The first estimate was based on bulls and the second on heifers.

Heritability - Carcass Traits

Blackwell et al. (1962) presented evidence that variable pretest conditions could materially affect estimates of genetic parameters.

Knapp and Nordskog (1946b) determined in an experiment to estimate heritabilities of carcass traits that dressing percent is controlled more by individual environmental influences than genetic. However, Christians et al. (1962) found evidence to the contrary (see Table 7).

A summary of heritability estimates for carcass traits is given in Table 7. These heritabilities also tend to be reasonably high. However, selection for carcass traits is not possible. Therefore, correlations between feedlot traits and carcass traits would be desirable in order to predict the amount of indirect progress made in carcass traits while selecting for a growth trait.

Phenotypic and Genetic Correlations

Warwick and Legates (1979) defined the genetic correlation as the correlation between the additive breeding values for two traits (g_1, g_2) or between the sum of additive effects of the genes influencing these two traits. These correlations result from primarily pleiotropy, a situation where a gene influences both traits. In addition, linkage may play a small transitory part. However, even with a genetic correlation of -0.45, a large proportion of the additive genetic effects for the two traits are independent. When the

Table 7. Heritability Estimates of Carcass Traits in Beef Cattle.

Author	Hot carcass weight	Dressing percent	Rib-eye area	Fat thickness	Cutability	Marbling	Carcass grade	Yield grade
Benyshek (1981)	.48	.31	.40	.52	.49	.47	---	---
Blackwell <i>et al.</i> (1962)	.92	.25	---	---	---	---	---	---
Brackelsberg <i>et al.</i> (1971)	---	---	.40	.43	---	.73	.74	---
Busch and Dinkel (1967)	---	---	.25	.57	---	.31	---	---
Carter and Kincaid (1959)	---	---	---	---	---	---	.20	---
Christians <i>et al.</i> (1962)	.96	.74	.76	.38	---	---	.78	---
Cundiff <i>et al.</i> (1964)	.39 ^a	---	.73	.43	---	---	.62	.36
Cundiff <i>et al.</i> (1971) ^b	.56	---	.41	.50	.28	.31	---	---
Cundiff <i>et al.</i> (1971) ^c	---	---	.32	.53	.35	.33	---	---
Cundiff <i>et al.</i> (1971) ^d	---	---	.32	.51	.35	.30	---	---
Dinkel and Busch (1973)	---	.15	.25	.57	.66	.31	.34	---
Dunn <i>et al.</i> (1970)	---	---	.02	.94	.65	-.15	.08	---
Knapp and Clark (1950)	---	---	.68	---	---	---	.33	---
Knapp and Nordskog (1946)	---	---	.69	---	---	---	.84	.01
Koch (1978)	.68	---	.28	.68	---	.34	---	---
Laskey (1972) ^e	.46	---	.70	.38	---	---	.48	---
Shelby <i>et al.</i> (1955)	.73	---	.72	.38	---	---	.16	---
Swiger <i>et al.</i> (1965)	---	---	---	.50	---	---	.32	---
Wilson <i>et al.</i> (1976)	---	---	.42	.41	.44	.33	---	---
Wilson <i>et al.</i> (1971)	.32 ^a	---	.47	.18	---	.09	---	---

^a Carcass wt/day of age.^b Age constant.^c Weight constant.^d Age and weight constant.^e Average of 1 to 5 studies.

genetic correlations between two traits approach 1.0 or -1.0, less and less independent additively genetic effects would be available for selection.

Hazel et al (1943) first demonstrated the extension of variance component analysis to estimation of correlations. An expression for the genetic correlation is:

$$r_{g1g2} = \hat{\sigma}_{g1g2}^2 / (\hat{\sigma}_{g1} \hat{\sigma}_{g2})$$

where, the numerator is the covariance between the additive breeding values for traits X_1 and X_2 and $\hat{\sigma}_{g1}$ and $\hat{\sigma}_{g2}$ are the genetic standard deviations of the two traits.

Phenotypic correlations are the gross correlations that include both the environmental and the genetic portions of the covariances (Lasley, 1972). An expression for computing the phenotypic correlation is:

$$r_{X1X2} = \hat{\sigma}_{X1X2}^2 / (\hat{\sigma}_{X1} \hat{\sigma}_{X2})$$

where, the numerator is the covariance between the phenotypic values for the two traits and $\hat{\sigma}_{X1}$ and $\hat{\sigma}_{X2}$ are the phenotypic standard deviations of the two traits.

Thus, we are introduced to the concept of correlated selection response. A correlated response is one in which selection is primarily for one trait, but due to a genetic correlation a change occurs in a second trait (Warwick and Legates, 1979).

The direct response to selection, in populations where animals are selected on their own performance, can be represented as

$$G_D = h^2_i \sigma_{p1} = h^2_i \sigma_{g1}$$

where, i is the selection differential in standard deviation units.

Likewise, the correlated response can be expressed

$$G_c = r_{g_1 g_2} h_2 \frac{\sigma_{g_1}}{\sigma_{p_2}} i \sigma_{p_2} = r_{g_1 g_2} h_2 i \sigma_{g_1}$$

From the above expressions, it is apparent that if $r_{g_1 g_2} = 1.0$ and $h_1 h_2$ then the direct and correlated responses would be equal. Warwick and Legates (1979) summarized the relationships between selected beef production characteristics and carcass traits:

- 1) There are positive genetic relationships between all measures of size and growth. Thus, selection for weight at any age or for rate of growth at any life stage would be expected to have indirect effects at other ages.
- 2) There is a high positive genetic correlation between rate of postweaning gain and gain per unit of feed consumed when tests are for gain through a prescribed weight period such as 225 to 405 kg or for fixed periods of time. The correlation is much smaller and may be near zero if feeding is to a constant degree of fatness.
- 3) Growth rates and weights at specific ages are negatively related to all measures of carcass fatness when slaughter is at a standard weight. The relationships are much lower if slaughter is at a standard age.
- 4) Per cent of mature weight attained at any age tends to be negatively related to mature weight. This means that cattle heavy at maturity tend to mature more slowly.

Table 8 gives estimates of phenotypic and genetic correlations between yearling weight and other beef production characteristics of interest. Although there are numerous studies giving correlations between final weight and other beef characteristics, there are few which look at yearling weight. Carter and Kincaid (1959) observed a high positive correlation between gain from birth to weaning and feedlot gain (.69).

Table 8. Phenotypic (P) and Genetic (G) Correlations Between Yearling Weight and Various Beef Cattle Production Traits.

Author		Final weight	Weight gain	Carcass weight	Dressing percent	Carcass grade	Fat thickness	Marbling	Rib-eye area
Blackwell <u>et al.</u> (1962)	P	.53	.22	>1	>1	.92	---	---	---
	G	.48	.24	.54	.14	.11	---	---	---
Dickerson <u>et al.</u> (1974)	P	---	.84	---	---	---	.29	.15	---
	G	---	.96	---	---	---	.11	-.16	---
Koch (1978)	P	---	.80	.94	---	---	.33	.13	.35
	G	---	.87	.96	---	---	.86	-.57	.01
Koch and Clark (1955a)	P	---	.76	---	---	---	---	---	---
	G	---	.83	---	---	---	---	---	---

MATERIALS AND METHODS

Base Population

Henry and Edsel Ford donated a herd of Hereford cows to Michigan State University in 1966. Two hundred cows were then selected to represent the base of a breeding project at the Lake City Experiment Station. These cows were divided into age groups and randomly assorted into four groups of 50 cows each.

The first matings of the project were made in 1967 with the F_1 dams producing their first calves in 1970.

Breeding Program

Four breeding groups of 50 females each were involved in the base breeding herd. The breeding groups were: 1)unselected control; 2)selection on yearling weight using Hereford bulls; 3)yearling weight selection and crossbreeding using Angus, Charolais, Hereford and Simmental bulls; and 4)selection based on yearling weight, and rotational crossbreeding using Angus, Holstein-Friesian, Hereford and Simmental sires. The number of steers in the experiment is shown in Table 9. This study focuses on the effect of the various breeding strategies on feedlot and carcass traits after adjustment for certain nutritional and management practices.

Table 9. Number of Steers Within Breed Group.

Breeding group	Selection	Mating System	n
1	None	Random using hereford bulls	66
2	Yearling weight	Straightbred using hereford bulls	64
3	Yearling weight	Crossbred using Angus, Charolais, Hereford, and Simmental	61
4	Yearling weight	Crossbred using Angus, Holstein-Friesian, Hereford, and Simmental	66

Group 1 was an unselected group of straightbred females used as a control. Each female was mated to one of four bulls unselected for yearling weight. Replacement heifers were taken from within the line and were retained according to birth date. The ten oldest heifers were saved each year in an attempt to avoid unintentional selection for yearling weight. Similarly, the first male calf born to each sire within group 1 was retained to be used as a sire the following year. These bulls were used as clean-up bulls their first year of service. Following the first breeding season, semen was collected and frozen from each young sire and used to inseminate cows the following year.

Each spring, up to fifteen heifers were saved in groups 2, 3 and 4 based on their actual yearling weight. In the fall, this number was reduced to 10 based primarily on the pregnancy test and secondarily on yearling weight. Bulls in these groups were selected from breeders that were selecting within their herds on yearling weight. The Holstein-Friesian bulls were selected on the basis of their estimated genetic ability for yearling weight. The dairy sires were obtained from Select Sires where Clint Meadows of M.A.B.C. (Michigan Animal Breeding Co-op) estimated their expected breeding values.

Management

Cows

Cows were weighed each year at weaning and once again at the beginning of pasture season in mid to late May. All cows were kept together except for the last 45 days of the breeding season which began around the middle of April and lasted for 90 days. The cows

were bred artificially for the first 45 days of the breeding season and then assigned by breeding group to designated clean-up bulls on pasture for the final 45 days.

Prior to calving, each cow was given an annual Vitamin A and D injection. At the same time, they were inoculated for leptospirosis and vibriosis and wormed. In the fall, when the cows were pregnancy checked, they were treated for lice and grubs and, when appropriate, tested for brucellosis.

Replacement Heifers

The replacement heifers were grouped and fed together at weaning. They were fed corn silage and enough grain to facilitate reproductive efficiency.

All heifers were given booster immunizations against infectious bovine rhinotracheitis (IBR), bovine virus diarrhea (BVD) and parainfluenza (PI₃) prior to the breeding season.

Following the first 45 days of the breeding season during which they were all bred by artificial insemination (A-I), the heifers were grouped with the cows and turned into pasture with clean-up bulls corresponding to their respective breeding groups.

Calves

Shortly after birth, each calf was tattooed, ear-tagged, weighed and given vitamin shots of A, D and selenium-tecopherol. All male calves were castrated with the exception of the four calves maintained as sires in group 1. In addition, all horned calves were dehorned. Prior to pasture season, the calves were vaccinated against blackleg

and malignant edema.

At weaning, the calves were weighed and given immunization shots for IBR, BVD and PI₃. At this time, the steer calves were moved to the Beef Cattle Research Center (BCRC) of Michigan State University in East Lansing, approximately 150 miles away.

Steers

Upon arrival at East Lansing, the steers were weighed and sorted into eight pens, two pens corresponding to each breeding group. Weights were recorded approximately every 28 days while the steers were on test.

While the steers were at the Beef Cattle Research Center, they were involved in numerous nutritional and management trials. This involved differences in ration and/or hormonal implants. Therefore, a treatment factor was included in the model to remove any effect due to management or treatment. Treatments were randomized in each breeding group to insure a balanced design.

From 1978 to 1980 the steers were slaughtered when a committee of judges estimated that 80% of the steers would reach U.S.D.A. choice grade. In 1981, the cattle were slaughtered when they were determined to reach choice grade, which resulted in three distinct slaughter groups.

All cattle were taken to a commercial packing plant where they were slaughtered. Hot carcass weights were obtained and the carcasses were chilled for 24 hours. A government grader collected quality and yield grade data, while Michigan State personnel assisted in obtaining loin eye area and external fat measures (12th rib). Numbers of steers

by sire breed group and by year are presented in Table 10. The primary traits of interest were feedlot daily gain (lb), carcass weight (lb), adjusted yearling weight (lb), marbling, quality grade, internal fat (KPH), fat thickness (in), yield grade and loin eye area (cm²).

Statistical Analysis

A total of 267 records on Lake City steers were collected from 1978 to 1981. However, due to the small number of calves produced by Angus, Charolais and Holstein sires, the steers sired by these breeds were dropped from the analysis.

A preliminary analysis was conducted to determine variables of importance in estimation and testing procedures for the dependent variables of interest.

The following preliminary model was examined:

$$Y_{ijklmn} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \tau_{(i)k} + \gamma_l + S_{(l)m} + E_{ijklmn}$$

where,

Y_{ijklmn} is the nth observation of the particular trait of interest; the nine traits of interest are feedlot daily gain (lb), carcass weight (lb), adjusted yearling weight (lb), marbling, quality grade, internal fat (KPH), fat thickness (in), yield grade and loin eye area (cm²);

μ is a constant common to all observations;

α_i is the fixed effect of the ith year, with $i=1,2,3,4$ which represents the four years 1978, 1979, 1980 and 1981, respectively.

β_j is the fixed effect of the jth breed group, $j=1,2,3,4$ which represents the four breeding groups as previously described;

Table 10. Number of Steers by Year and Sire Breed Group.

Year	Sire Breed	Number
1978	Angus	3
	Charolais	0
	Holstein	0
	Simmental	41
	Hereford	45
		86
1979	Angus	0
	Charolais	0
	Holstein	0
	Simmental	29
	Hereford	35
		64
1980	Angus	0
	Charolais	1
	Holstein	0
	Simmental	28
	Hereford	34
		62
1981	Angus	3
	Charolais	0
	Holstein	1
	Simmental	25
	Hereford	30
		55

- $(\alpha\beta)_{ij}$ is the fixed interaction effect of the i th year and j th breed group;
- $\tau_{(i)k}$ is the fixed effect of the k th treatment nested within year, $k=1,2,3,4$;
- γ_l is the fixed effect of the l th breed of sire, with $l=1,2$ where 1 corresponds to Hereford and 2 to Simmental;
- $S_{(1)m}$ is the random effect of the m th sire nested within the l th breed of sire, $m=1,2,\dots,7$;
- E_{ijklmn} is the random residual effect associated with the n th observation, $n=1,2,\dots,267$.

Season was not included in the equation since all calves were born in the fall. The equation can be rewritten in matrix form:

$$y = Xb + Zu + e$$

where,

- y is the observation vector of length of 267 when considering feedlot traits and 257 when carcass traits are under consideration;
- X is a 267×43 matrix corresponding to b . It contains 0's and 1's corresponding to an observation's presence or absence in each class. The column corresponding to μ contains all 1's;
- b is an unknown vector of length 43 containing the constants of the fixed effects, i.e. 4 years, 4 breeding groups, 16 treatment within year rows, 16 year by breeding group rows, 2 breed of sires and one row for μ ;
- Z is a $267(257) \times 49$ incidence matrix containing 1's and 0's corresponding to the presence or absence of observations within each sire;
- u is an unknown vector of length 49 containing the random effects for sires;
- e is an unknown vector of random residual effects of length 267 or 257;

Assumptions for the model were:

- 1) $E(y) = Xb$ and $Var(y) = V = ZGZ' + R$
- 2) $Var(s) = G = I_{49}\sigma_s^2$; this assumption will be relaxed in the final analysis; this implies independent sampling of

sires with mean 0 and variance σ_s^2 ;

- 3) The sires are normally distributed;
- 4) $\text{Var}(e) = R = I_{267} \sigma_e^2$ which further implies the errors are independently drawn from the same population with mean 0 and variance σ_e^2 ;
- 5) It is further assumed that the residuals are normally distributed;
- 6) $\text{Cov}(u, e) = 0$;
- 7) All interactions other than year by breeding group are trivial.

The variance-covariance matrix for the random factors is:

$$\text{Var} \begin{bmatrix} \tilde{y} \\ \tilde{u} \\ \tilde{e} \end{bmatrix} = \begin{bmatrix} V_{\tilde{267}} & Z & I_{\tilde{267}} \sigma_e^2 \\ & I \sigma_s^2 & 0 \\ \text{symmetric} & & I_{\tilde{267}} \sigma_s^2 \end{bmatrix}$$

The mixed model equations are:

$$\begin{bmatrix} \tilde{X}'\tilde{X} & \tilde{X}'\tilde{Z} \\ \tilde{Z}'\tilde{X} & \tilde{Z}'\tilde{Z} \end{bmatrix} \begin{bmatrix} \tilde{b} \\ \tilde{s} \end{bmatrix} = \begin{bmatrix} \tilde{X}'\tilde{y} \\ \tilde{Z}'\tilde{y} \end{bmatrix}$$

which are equivalent to the normal equation of Generalized Least Squares for the fixed effects (Mao, 1981). All fixed effects were tested using the usual F-ratio.

The full model analysis indicated the year by breeding group interaction was not important ($P > .01$) for any of the nine traits. Therefore, this factor was dropped from the model and the remainder of the analyses were performed using the given model with the interaction term removed.

Bartlett's Test of Homogeneity

Close inspection of the data raised the question concerning the

equality of variances between breeds of sire. Bartlett's test of homogeneity as described by Gill (1978) was used to test the hypothesis, $\sigma_1^2 = \sigma_2^2$.

The test statistic is calculated as follows:

$$q = \left\{ \sum_{i=1}^t (\sum v_i) \ln \left(\frac{\sum ss_i}{\sum v_i} \right) - \sum_{i=1}^t (v_i \ln s_i) \right\} / g$$

where,

v_i = the degrees of freedom for the i th breed

ss_i = the sum of squares for the i th breed

s_i = the standard deviation of the i th breed

t = the number of breeds

$$g = \left\{ 1 + \left\{ \sum_{i=1}^t (1/v_i) - (1/\sum v_i) \right\} / 3(t-1) \right\}$$

This statistic is then compared to the table value of $\chi^2_{\alpha, t-1}$. All tests were performed at $\alpha=.2$ to insure the detection of heterogeneity. When results indicated heterogeneous variances the subsequent analyses were performed within breed.

Variance Component Estimation

Until recent years variance components have been estimated using the traditional ANOVA method of equating the calculated mean squares to their expectations. In 1953, Henderson devised three methods of estimating variance components from unbalanced data. Each method was specific to a particular kind of model and each utilized ANOVA techniques but did not require an underlying distribution. The normal equations were invoked, treating every effect as if it were fixed.

In 1967, Hartley and Rao presented the method of maximum likelihood (ML)

assuming a multivariate normal distribution. The ML method possesses certain properties which makes it more advantageous than Henderson methods 1, 2 and 3. These estimates are always non-negative and are asymptotically normal and efficient being functions of the minimal sufficient statistics. However, the ML estimates are biased due to simultaneous estimation of the fixed factors which make them undesirable for animal breeding research.

The restricted maximum likelihood (REML) procedure was obtained by maximizing the random portion of the likelihood which is invariant to the fixed effects in the model. Patterson and Thompson (1971) generalized the REML method of estimating variance components, which has become widely used in dairy research.

Some of the more desirable properties of REML are: 1) non-negativity is guaranteed within the parameter space, 2) REML techniques lend themselves to iterative procedures due to the various parameter dependencies and 3) in addition, REML is easier to implement in terms of computation. However, because of the iterative procedure, no mathematical methods are available for determination of the biasedness property of the estimators. In addition, the iteration process can also be a big disadvantage due to the large number of iterations required.

Due to the method of choosing sires for group one some genetic relationships existed among the sires of that breed (Hereford). Therefore, a relationship matrix was incorporated into the mixed model equations for the Hereford analysis. These relationships are shown in Table 11.

Table 11. Relationship Matrix (A^{-1})
for Hereford Sires in Group 1

	123	130	131	132	133	134	135	136	137	139	140	141	143	144	145	146
123	1															
130	0	1.125														
131	0	0	1													
132	0	0.078	0	1												
133	0	0	0	0	1											
134	0	0.078	0	0.250	0	1										
135	0.500	0	0	0	0	0	1									
136	0	0	0	0	0	0	0	1								
137	0	0	0	0	0	0	0	0	1							
139	0	0	0.0625	0	0	0	0	0	0	1						
140	0.125	0	0	0	0	0	0.0625	0	0	0	1					
141	0	0	0	0	0	0	0	0	0	0	0	1				
143	0.125	0	0	0	0	0	0.0625	0	0	0	0.250	0	1			
144	0	0.500	0	0.500	0	0.125	0	0	0	0	0	0	0	1		
145	0	0	0.500	0	0	0	0	0	0	0.03125	0	0	0	0	1	
146	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

SYMMETRIC

Mixed Model Equation

In generalities, the mixed model equations (MME) with t random factors are

$$\left[\begin{array}{c|cccc} \tilde{X}'\tilde{R}^{-1}\tilde{X} & \tilde{X}'\tilde{R}^{-1}\tilde{Z}_1 & \tilde{X}'\tilde{R}^{-1}\tilde{Z}_2 & \dots & \tilde{X}'\tilde{R}^{-1}\tilde{Z}_t \\ \hline & \tilde{Z}_1'\tilde{R}^{-1}\tilde{Z}_1 + G^{11} & \tilde{Z}_1'\tilde{R}^{-1}\tilde{Z}_2 + G^{12} & \dots & \tilde{Z}_1'\tilde{R}^{-1}\tilde{Z}_t + G^{1t} \\ & & \tilde{Z}_2'\tilde{R}^{-1}\tilde{Z}_2 + G^{22} & \dots & \tilde{Z}_2'\tilde{R}^{-1}\tilde{Z}_t + G^{2t} \\ & & & \ddots & \vdots \\ & & & & \tilde{Z}_t'\tilde{R}^{-1}\tilde{Z}_t + G^{tt} \end{array} \right] \begin{bmatrix} \tilde{b} \\ \tilde{u}_1 \\ \tilde{u}_2 \\ \vdots \\ \tilde{u}_t \end{bmatrix} = \begin{bmatrix} \tilde{X}'\tilde{R}^{-1}\tilde{y} \\ \tilde{Z}_1'\tilde{R}^{-1}\tilde{y} \\ \tilde{Z}_2'\tilde{R}^{-1}\tilde{y} \\ \vdots \\ \tilde{Z}_t'\tilde{R}^{-1}\tilde{y} \end{bmatrix}$$

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where, $\text{Var}(\tilde{e}) = \tilde{R}$ and

$$\text{Var}(\tilde{u}) = \tilde{G} = \begin{bmatrix} G_{11} & G_{12} & \dots & G_{1t} \\ & G_{22} & \dots & G_{2t} \\ & & \ddots & \vdots \\ \text{symmetric} & & & G_{tt} \end{bmatrix} \quad \tilde{G}^{-1} = \begin{bmatrix} G^{11} & G^{12} & \dots & G^{1t} \\ & G^{22} & \dots & G^{2t} \\ & & \ddots & \vdots \\ \text{symmetric} & & & G^{tt} \end{bmatrix}$$

For this particular application, the assumption was made that $\tilde{R} = \tilde{I}_n \sigma_e^2$.

For the Simmental analysis, the additional assumption was made that

$$\tilde{G} = \tilde{I}_t \sigma_s^2.$$

The simplest mixed model equation then becomes

$$\left[\begin{array}{c|cccc} \tilde{X}'\tilde{X}/\sigma^2 & \tilde{X}'\tilde{Z}_1/\sigma^2 & \tilde{X}'\tilde{Z}_2/\sigma^2 & \dots & \tilde{X}'\tilde{Z}_t/\sigma^2 \\ \hline & \tilde{Z}_1'\tilde{Z}_1/\sigma^2 + \tilde{I}\rho^2 & \tilde{Z}_1'\tilde{Z}_2/\sigma^2 & \dots & \tilde{Z}_1'\tilde{Z}_t/\sigma^2 \\ & & \tilde{Z}_2'\tilde{Z}_2/\sigma^2 + \tilde{I}/\sigma^2 & \dots & \tilde{Z}_2'\tilde{Z}_t/\sigma^2 \\ & & & \ddots & \vdots \\ & & & & \tilde{Z}_t'\tilde{Z}_t/\sigma^2 + \tilde{I}\rho^2 \end{array} \right] \begin{bmatrix} \tilde{b} \\ \tilde{u}_1 \\ \tilde{u}_2 \\ \vdots \\ \tilde{u}_t \end{bmatrix} = \begin{bmatrix} \tilde{X}'\tilde{y}/\sigma^2 \\ \tilde{Z}_1'\tilde{y}/\sigma^2 \\ \tilde{Z}_2'\tilde{y}/\sigma^2 \\ \vdots \\ \tilde{Z}_t'\tilde{y}/\sigma^2 \end{bmatrix}$$

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Multiplying both sides of the equation by σ^2 , the equation becomes

$$\begin{bmatrix} \tilde{X}'\tilde{X} & \tilde{X}'\tilde{z}_1 & \tilde{X}'\tilde{z}_2 & \cdots & \tilde{X}'\tilde{z}_t \\ \hline & \tilde{z}'_1\tilde{z}_1 + I\tilde{k}_1 & \tilde{z}'_1\tilde{z}_2 & \cdots & \tilde{z}'_1\tilde{z}_t \\ & & \tilde{z}'_2\tilde{z}_2 + I\tilde{k}_2 & \cdots & \tilde{z}'_2\tilde{z}_t \\ & & & \ddots & \vdots \\ & & & & \tilde{z}'_t\tilde{z}_t + I\tilde{k}_t \end{bmatrix} \begin{bmatrix} \tilde{b} \\ \tilde{u}_1 \\ \tilde{u}_2 \\ \vdots \\ \tilde{u}_t \end{bmatrix} = \begin{bmatrix} \tilde{X}'\tilde{y} \\ \tilde{z}'_1\tilde{y} \\ \tilde{z}'_2\tilde{y} \\ \vdots \\ \tilde{z}'_t\tilde{y} \end{bmatrix}$$

SYMMETRIC

where $\tilde{k}_i = \sigma^2\sigma_i^2$.

However, when the analysis was duplicated for the Hereford sires a complication arose due to their relationships. These relationships were accounted for by substituting the $\tilde{k}_i$ in the MME by $\tilde{A}_i^{-1}\tilde{k}_i$, where the off-diagonal elements in $\tilde{A}$ are additive genetic relationship coefficients between individuals and diagonals are one plus the inbreeding coefficient of the individual. The MME then becomes

$$\begin{bmatrix} \tilde{X}'\tilde{X} & \tilde{X}'\tilde{z}_1 & \tilde{X}'\tilde{z}_2 & \cdots & \tilde{X}'\tilde{z}_t \\ \hline & \tilde{z}'_1\tilde{z}_1 + \tilde{A}^{11}\tilde{k}_1 & \tilde{z}'_1\tilde{z}_2 + \tilde{A}^{12}\tilde{k}_2 & \cdots & \tilde{z}'_1\tilde{z}_t + \tilde{A}^{1t}\tilde{k}_t \\ & & \tilde{z}'_2\tilde{z}_2 + \tilde{A}^{22}\tilde{k}_2 & \cdots & \tilde{z}'_2\tilde{z}_t + \tilde{A}^{2t}\tilde{k}_t \\ & & & \ddots & \vdots \\ & & & & \tilde{z}'_t\tilde{z}_t + \tilde{A}^{tt}\tilde{k}_t \end{bmatrix} \begin{bmatrix} \tilde{b} \\ \tilde{u}_1 \\ \tilde{u}_2 \\ \vdots \\ \tilde{u}_t \end{bmatrix} = \begin{bmatrix} \tilde{X}'\tilde{y} \\ \tilde{z}'_1\tilde{y} \\ \tilde{z}'_2\tilde{y} \\ \vdots \\ \tilde{z}'_t\tilde{y} \end{bmatrix}$$

SYMMETRIC

It has been shown that biases due to selection of sires can be eliminated by inclusion of the relationship matrix. It also aids in comparison of bulls which could otherwise not be compared due to disconnectedness (Mao, 1981).

Solutions to the MME are generated by multiplying the right hand side of the equation by the generalized inverse of the coefficient matrix. Let $\tilde{C}$ represent the inverse of the coefficient matrix.

In this case, only one random factor (sires) was included in the model. Therefore, $\tilde{C}$ can be represented as

$$\tilde{C} = \begin{bmatrix} \tilde{X}'\tilde{X} & \tilde{X}'\tilde{Z} \\ \tilde{Z}'\tilde{X} & \tilde{Z}'\tilde{Z} + A^{-1}k \end{bmatrix}^{-1} = \begin{bmatrix} \tilde{C}_{X'X} & \tilde{C}_{X'S} \\ \tilde{C}_{S'X} & \tilde{C}_{S'S} \end{bmatrix}$$

Then, the REML estimators are:

$$\begin{aligned} \hat{\sigma}_e^2 &= (\tilde{y}'\tilde{y} - \tilde{b}'\tilde{X}'\tilde{y} - \tilde{u}'\tilde{Z}'\tilde{y}) / \{n - r(\tilde{X})\} \\ \hat{\sigma}_s^2 &= \{\tilde{u}'A^{-2}\tilde{u}_s + \sigma_e^2 \text{tr}(\tilde{C}_{S'S}A^{-1})\} / q_s \end{aligned}$$

where $r(\tilde{X})$ is the rank of the fixed portion of the incidence matrix and q_s is the number of sires. In the Simmental analysis, where the sires were unrelated, the estimator for the sire component was

$$\hat{\sigma}_s^2 = \{\tilde{u}'_s\tilde{u}_s + \sigma_e^2 \text{tr}(\tilde{C}_{S'S})\} / q_s$$

The procedure was then iterated by estimating new variance and covariance solutions from each new set of estimated components. The iteration can be performed due to the dependence of $\tilde{b}$ and $\hat{u}$ on k ; the dependence of $\hat{u}$, $\tilde{b}$ and k ; and the dependence of k on σ_e^2 and σ_s^2 . Therefore, the iterations should continue until there are no longer any changes in any of these estimates.

To speed up the convergence, a boosting factor was included in each iteration, as suggested by Mao (1982). The difference between two successive iterations was multiplied by a factor whose magnitude was arbitrary depending on the characteristics of the variable under consideration.

To begin the iterative process, an a priori value of k had to be introduced. This value was obtained by using previous estimates of

heritability and the formula from the paternal half-sib correlation:

$$\hat{h}^2 = 4/(1+k)$$

The a priori values used in this analysis are presented in Table 12.

Heritabilities and Genotypic and Phenotypic Correlations

The heritability estimates were calculated using the paternal half-sib correlation method with the REML estimates of σ_s^2 and σ_e^2 . The formula for this estimation is:

$$\hat{h}^2 = 4\hat{\sigma}_s^2/(\hat{\sigma}_s^2 + \hat{\sigma}_e^2)$$

Dickerson (1969) observed that biases occur in this estimate whenever 1) the covariance between genetic and environmental effects is not equal to zero, 2) the maternal effect is greater than zero or 3) the covariance between maternal and genetic effects is not zero. Kempthorne (1966) presented a formula for calculating the approximate standard error of a heritability estimate:

$$\hat{\sigma}_h^2 = (4/\hat{\sigma}_p^2)\{V(\hat{\sigma}_s^2)\}^{1/2}$$

where, the variance component estimates obtained in the final iteration of the REML procedure were used for $\hat{\sigma}_s^2$ and $\hat{\sigma}_p^2 = \hat{\sigma}_s^2 + \hat{\sigma}_e^2$.

Kempthorne (1969) presented the methods for estimating the variances of the respective components. These equations are presented below:

$$V(\hat{\sigma}_s^2) = (4/q_e)\{((MS_s)^2/q_s) + (\hat{\sigma}_e^4/q_e)\}$$

$$V(\hat{\sigma}_e^2) = (2\hat{\sigma}_e^4)/q_e$$

where, MS_s is the mean square of the sire effect. The equations are exact only when σ_e^2 is known.

Due to the fact that selection was to be made based on yearling

Table 12. A priori Values of Heritabilities
and k Values Used in the REML Analysis

Trait	h^2	k
Yearling Weight	.378	9.58
Average Daily Gain	.580	5.90
Loin Eye Area	.460	7.70
Fat Thickness	.494	7.10
Marbling	.310	11.90
Carcass Grade	.444	8.01
Yield Grade	.185	20.62
Final Weight	.730	4.48
Internal Fat (KPH)	.210	18.05

weight, and the traits of interest were feedlot and carcass traits, it was imperative the phenotypic and genetic correlations for the traits with yearling weight to be investigated.

Genetic Progress through Selection and Crossbreeding

Hereford

Due to the disconnectedness exhibited between groups 1 and 2, direct statistical comparisons were not possible. However, the least squares means for each group were plotted and means were discussed.

Simmental

The effects of breeding groups 3 and 4 were compared using estimable functions as described by Mao (1982). In addition, the least squares means for each group were plotted and differences were noted.

Hereford vs Simmental

Because of the distinct sires used within each breed (disconnected data), no statistical tests were performed to determine differences between the two sire breeds. However, the means were again plotted and obvious differences were observed.

RESULTS AND DISCUSSION

Phenotypic Correlations

Hereford

Estimates of phenotypic correlations of two feedlot traits and six carcass traits with yearling weight are presented in Table 13. All eight of the observed traits in the Hereford breed were moderately to highly positively correlated with yearling weight, the selection variable, with the exception of marbling and carcass grade. However, this would be expected due to the method of determining time of slaughter. The small positive correlations that are exhibited by the two variables may indicate some stronger relationship between yearling weight and those variables when time of slaughter is at a constant time rather than a constant live grade.

These estimates are somewhat higher than previously reported correlations. Similar correlations were reported for marbling by Dickerson et al (1978) and Koch (1978). In this study, average daily gain had a stronger relationship to yearling weight than Blackwell found in 1962. However, Dickerson et al (1974) and Koch (1978) reported comparable correlations (.84 and .80, respectively).

All correlations were determined to be different from zero, indicating that on the average heavier Hereford cattle at 365 days were fatter and had more muscling at slaughter than Hereford cattle that were lighter at a year of age.

Table 13. Phenotypic Correlations of
Feedlot and Carcass Traits with Yearling Weight
by Breed of Sire

Trait	Breed of Sire	
	Hereford	Simmental
Marbling	.19 [*]	-.02
Yield Grade	.52 ^{**}	-.01
Average Daily Gain	.89 ^{**}	.53 ^{**}
Loin Eye Area	.50 ^{**}	.31 ^{**}
Internal Fat (KPH)	.49 ^{**}	-.03
Carcass Grade	.17 [*]	.03
Fat Thickness	.99 ^{**}	-.05
Final Weight	.88 ^{**}	.77 ^{**}

^{*}P<.05

^{**}P<.01

Simmentals

Contradictory results were found when the same eight traits were investigated in the Simmental breed. The correlations for Simmental-sired calves are presented in Table 13. The only phenotypic correlations which differed from zero ($P < .05$) were loin eye area, final weight and average daily gain.

The reported statistic for loin eye area agrees with the reported correlation by Koch (1978). However, the correlation found between final weight and yearling weight was stronger than the one reported by Blackwell et al (1962). The coefficient for average daily gain was not as large as others reported in the literature.

The differences found in the Simmentals and Herefords can be explained by the differing characteristics of the two breeds. Simmentals can be characterized as a medium to tall breed of cattle with moderate to heavy muscling, whereas the Herefords are smaller framed with lighter muscle. The heavier muscled, taller framed breeds, in general, grow faster and put on less fat during the same period as their smaller, lighter muscled contemporaries.

Consequently, a negative correlation would be expected for a growth trait with a fat-related trait in the larger Continental breed. But, in contrast, the smaller Hereford would be expected to reach maturity sooner and then begin putting on fat which would be revealed in the positive correlations seen in the Hereford breed.

Genetic Correlations

Herefords

All genetic correlations between feedlot and carcass traits with yearling weight in the Hereford breed were different from 0 other than internal fat. However, the genetic correlations revealed some interesting relationships that were not seen when observing the phenotypic correlations. These correlations are shown in Table 14.

Marbling score exhibited a strong negative correlation genetically with yearling weight. This agrees with Koch (1978) who reported a genetic relationship of $-.57$. This would indicate that selection for yearling weight will simultaneously decrease the amount of intramuscular fat, which in turn would likely decrease carcass grade. The observed negative genetic correlation between carcass grade and yearling weight supports this hypothesis.

The large negative genetic correlation found between final weight and yearling weight is contradictory to reported literature (Blackwell et al, 1962) and biological "sense". Biologically, we know that final weight should explain a large portion of the total variation seen in yearling weight and, therefore, should exhibit a positive, if not strong positive, genetic correlation.

Simmentals

The results in Table 14 indicate fat thickness, yield grade and average daily gain are all genetically correlated to yearling weight. The coefficients indicate that selection for heavier yearling weight simultaneously selects against the fat-related characteristics, i.e.

Table 14. Genetic Correlations of
Feedlot and Carcass Traits with Yearling Weight
by Breed of Sire

Trait	Breed of Sire	
	Hereford	Simmental
Marbling	-.86**	-.28
Yield Grade	.67**	-.62**
Average Daily Gain	.58**	.49*
Loin Eye Area	.72**	.10
Internal Fat (KPH)	-.32	-.38
Carcass Grade	-.48**	.00
Fat Thickness	.92**	-.89**
Final Weight	-.71**	-.04

*
P<.05

**
P<.01

fat thickness, marbling and internal fat, in the Simmental breed.

There was a negative correlation between yield grade and yearling weight. This, too, would be expected since the single, most important factor affecting yield grade is fat.

Agreeable results were found in the Simmental and Hereford genetic correlations for most characteristics. Discrepancies occurred in the relationship between yearling weight and yield grade and yearling weight and fat thickness. These differences again can be explained by the inherent differences in the breeds.

Heritabilities

Hereford

Table 15 presents the sire and error variance components estimated from 144 Hereford steers using the restricted maximum likelihood (REML) method of analysis. Every estimate required at least thirty "equivalent" rounds of iteration and some as many as 2000.

Heritabilities and approximate standard errors were calculated using these estimates and are shown in the same table. The heritabilities observed from these data are generally smaller than those reported in previous literature. However, all the estimates had high standard errors, a reflection on the small sample size used to obtain the estimates.

The heritability of fat thickness agreed closely with results reported by Lasley (1972) and Shelby et al (1955).

The heritability of yearling weight is considerably below estimates reported in the literature, however its standard error is three times the point estimate. These results would indicate that selection on

Table 15. Sire and Error Variance Components and Heritabilities
for Feedlot and Carcass Traits in the Hereford Breed

Trait	$\hat{\sigma}_s^2$	$\hat{\sigma}_e^2$	$\hat{h}^2$
Marbling	1.48± 0.09	6.04± 0.36	.79±.40
Yield Grade	0.02± 0.01	0.46± 0.10	.19±.83
Average Daily Gain	0.00± 0.00	0.04± 0.03	.02±1.59
Loin Eye Area	0.00± 0.02	1.10± 0.15	.01±.68
Internal Fat (KPH)	0.00± 0.00	0.15± 0.06	.04±1.12
Carcass Grade	0.10± 0.03	1.82± 0.20	.22±.59
Fat Thickness	0.00± 0.00	0.03± 0.02	.36±1.62
Final Weight	439.29±73.12	4858.21±10.17	.33±.03
Yearling Weight	26.03±61.41	4081.57± 9.35	.03±.09

yearling weight would be futile. However, Warwick and Legates (1979), Koch (1978) and Newman et al (1973) reported estimates which ranged from .45 to .69.

Simmental

The REML estimates for sire and error variances in the Simmental breed are reported in Table 16. The estimates were based on 123 records from the Lake City herd. The convergence took anywhere from 25 to 200 iterations, considerably less than those required for the estimates within the Hereford breed. A boosting factor of 5 was used to speed convergence.

The resulting heritability estimates are shown in Table 16. Once again, the standard errors tend to be large for most of the traits. In addition, there were two estimates which fell outside the parameter space of heritability, i.e. 0 to 1. However, their standard errors indicate that the problem could be in sampling and not the method of estimation.

The reported heritability for yearling weight would indicate that it would be a desirable variable for selection, and the genetic correlation indicates that when selecting for this variable, progress should be observed in feedlot average daily gain with additional progress observed in loin eye area.

The heritability estimate of .62 for yearling weight concurs with estimates made by Koch (1978) and Warwick and Legates (1979). Other reported estimates were lower, ranging from .10 to .47. However, all estimates suggest that yearling weight would be a responsive trait on which to select.

Table 16. Sire and Error Variance Components and Heritabilities
for Feedlot and Carcass Traits in the Simmental Breed

Trait	$\hat{\sigma}_s^2$	$\hat{\sigma}_e^2$	$\hat{h}^2$
Marbling	2.15±0.08	4.39±0.30	1.32±.41
Yield Grade	0.05±0.06	0.38±0.09	.49±.85
Average Daily Gain	0.00±0.00	0.05±0.03	.30±1.37
Loin Eye Area	0.16±0.02	1.49±0.17	.38±.60
Internal Fat (KPH)	0.11±0.00	0.22±0.07	1.38±.87
Carcass Grade	0.45±0.02	1.13±0.15	1.14±.58
Fat Thickness	0.00±0.00	0.02±0.02	.20±1.73
Final Weight	204.19±81.42	6102.40±10.73	.13±.08
Yearling Weight	825.82±61.00	4503.30±9.22	.62±.08

The observed heritability for final weight is noticeably smaller than those reported in the literature (see Table 16). Newman et al (1973) obtained a heritability of 0 which is in disagreement with this and other investigations. The heritability for average daily gain is in agreement with Dickerson et al (1974) and Koch and Clark (1955a), but tends to be lower than other reported heritabilities for this trait.

Internal fat (KPH), marbling and carcass grade had heritabilities of greater than one. Several explanations exist for this outcome. As indicated in previous discussion, the sample size would be expected to cause unfavorable results for estimation of parameters. However, marbling and carcass grade are both discrete variables, and the properties for REML with discrete data are not fully explored. Gianola (1979) observed that considerable amounts of nonadditive variance are present when the distribution of responses by category is very uneven in categorical data. He indicates that when this occurs, the likelihood of epistatic biases in heritability estimates becomes a greater possibility.

Additionally, Gianola (1979) asserts the assumption of independence between the random variables, u , and the error, e , in the observed scales is not tenable and since the genetic variance depends on the main incidence, it would be necessary to use a different variance-covariance matrix for each subpopulation defined in the model.

The heritability estimate for yield grade is larger than those reported in the literature. Knapp and Nordskog (1946) estimated this heritability at .01.

The estimates for loin eye area and fat thickness are a little smaller than estimates in the literature. Once again, the standard

errors are quite large.

Sample Size

Due to the large discrepancies observed in the data, Pirchner's (1969) method of determining number of observations needed for minimal sampling variance was used to determine a desirable sample size. These estimates are presented in Table 17. As can be seen, the total number of animals needed is largely dependent on the average number within a family. The only two variables in which these minimums are obtained in this study are final weight and average daily gain in the Simmental breed. From observation of the data, yield grade and internal fat should be the most inaccurate of the heritability estimates.

Response to Selection

Due to the disconnectedness of the unselected and selected Hereford data, no statistical tests were performed. However, means were plotted and trends were observed. Figures 1 to 9 present the means of the unselected and selected Herefords. These were the estimated means from the MME solutions.

In Figure 8 it can be observed that selection for greater yearling weights within group two has consistently produced calves with higher means than those produced by the unselected Herefords over the four years of this study. Both groups increased in yearling weight during the first three years, but they both decreased in the fourth year, 1981. This observation could probably be attributed to nutritional and/or management differences from year to year.

Table 17. Estimated Sample Size Needed
for Minimal Sampling Variance of Heritability

Trait	h^2 ^a	t ^b	n ^c	T ^d	
				Simmental	Hereford
Marbling	.31	.08	13.0	221	416
Yield Grade	.185	.05	21.7	369	694.4
Average Daily Gain	.54	.13	7.4	125.8	236.8
Loin Eye Area	.46	.11	8.7	147.9	278.4
Internal Fat (KPH)	.28	.07	14.3	242.8	457.6
Carcass Grade	.44	.11	9.0	153	288
Fat Thickness	.49	.12	8.1	137.7	259.2
Final Weight	.73	.18	5.5	93.5	176
Yearling Weight	.38	.09	10.6	180	339.2

^aHeritability estimates from literature

^bIntraclass Correlation, $t=h^2/4$

^cNumber of samples within a family, $n=1/t$

^dTotal number of steers required, $T=nN$ where N is the number of families

Figure 1. Means of Marbling Scores of
Unselected and Selected Herefords, 1978-1981

Figure 1.

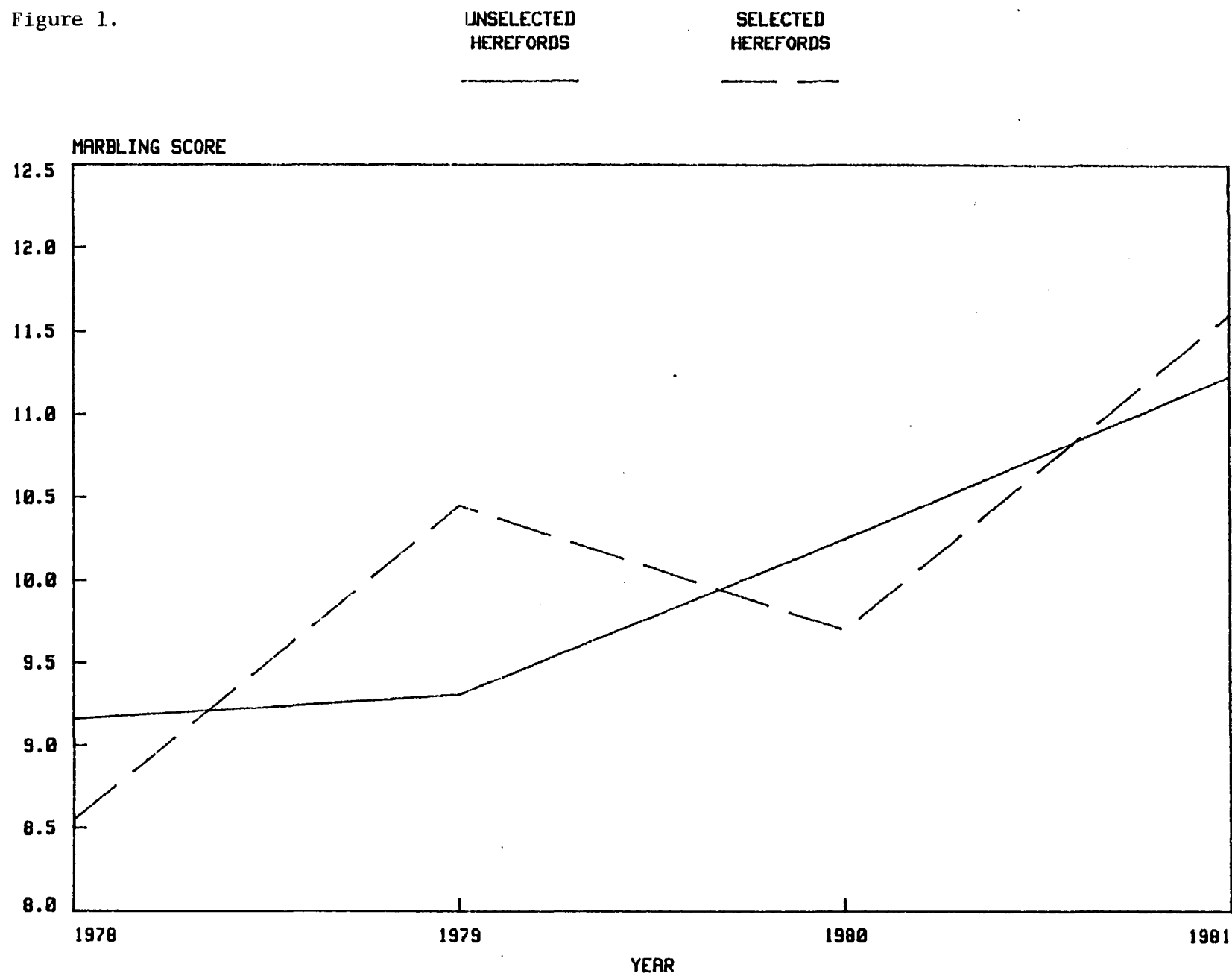


Figure 2. Means of Yield Grades of
Unselected and Selected Herefords, 1978-1981

Figure 2.

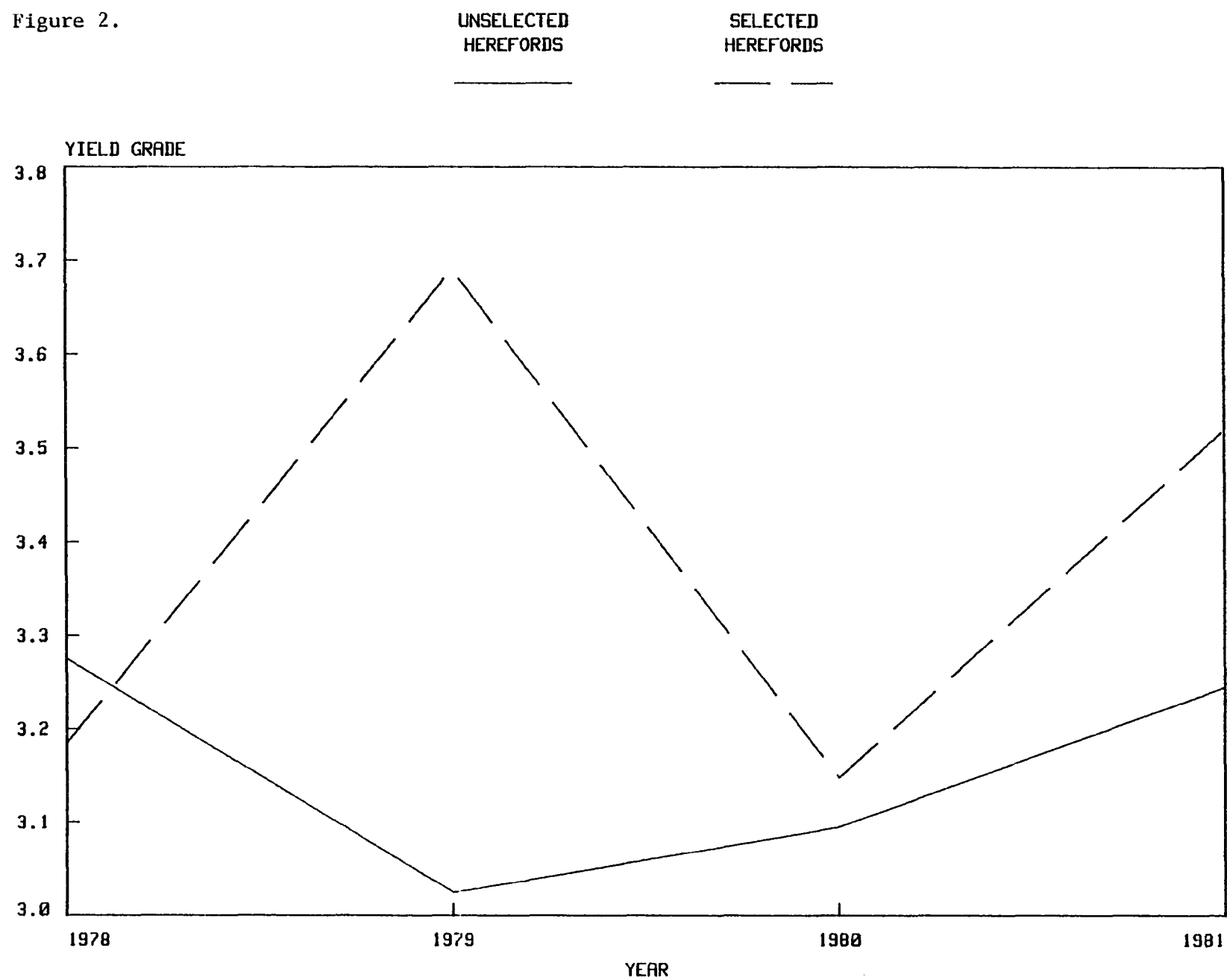


Figure 3. Means of Average Daily Gain of
Unselected and Selected Herefords, 1978-1981

Figure 3.

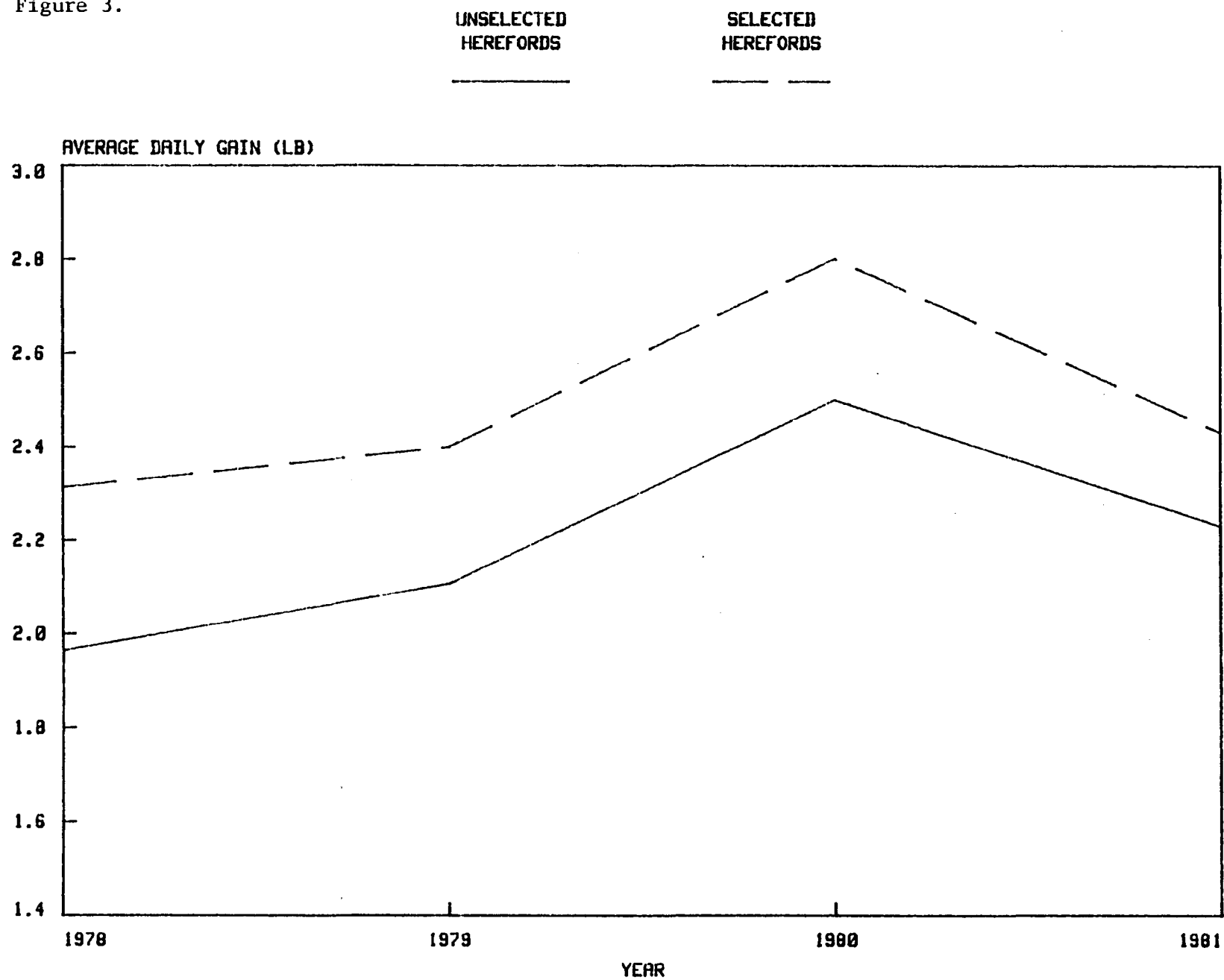


Figure 4. Means of Loin Eye Areas of
Unselected and Selected Herefords, 1978-1981

Figure 4.

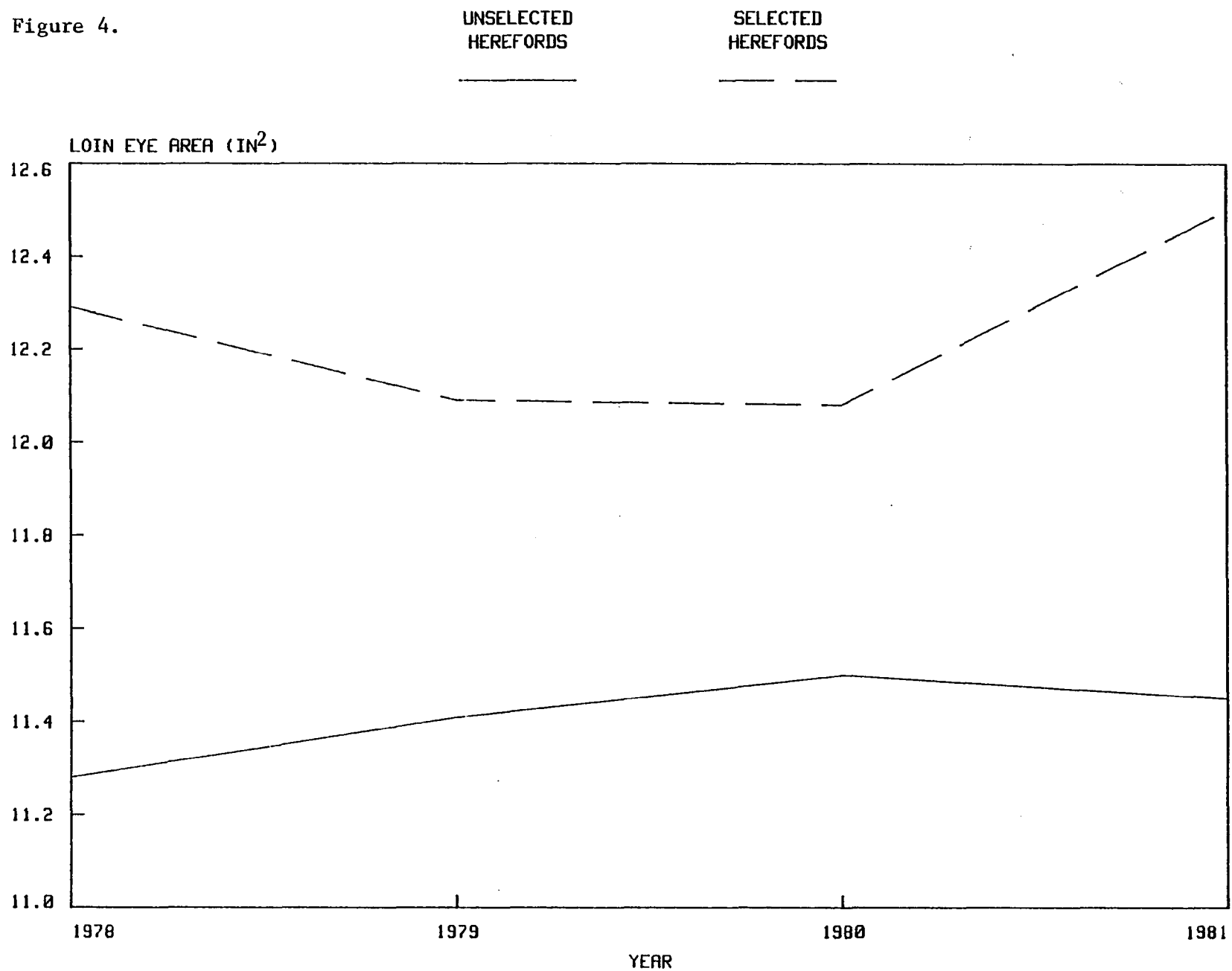


Figure 5. Means of Internal Fat of
Unselected and Selected Herefords, 1978-1981

Figure 5.

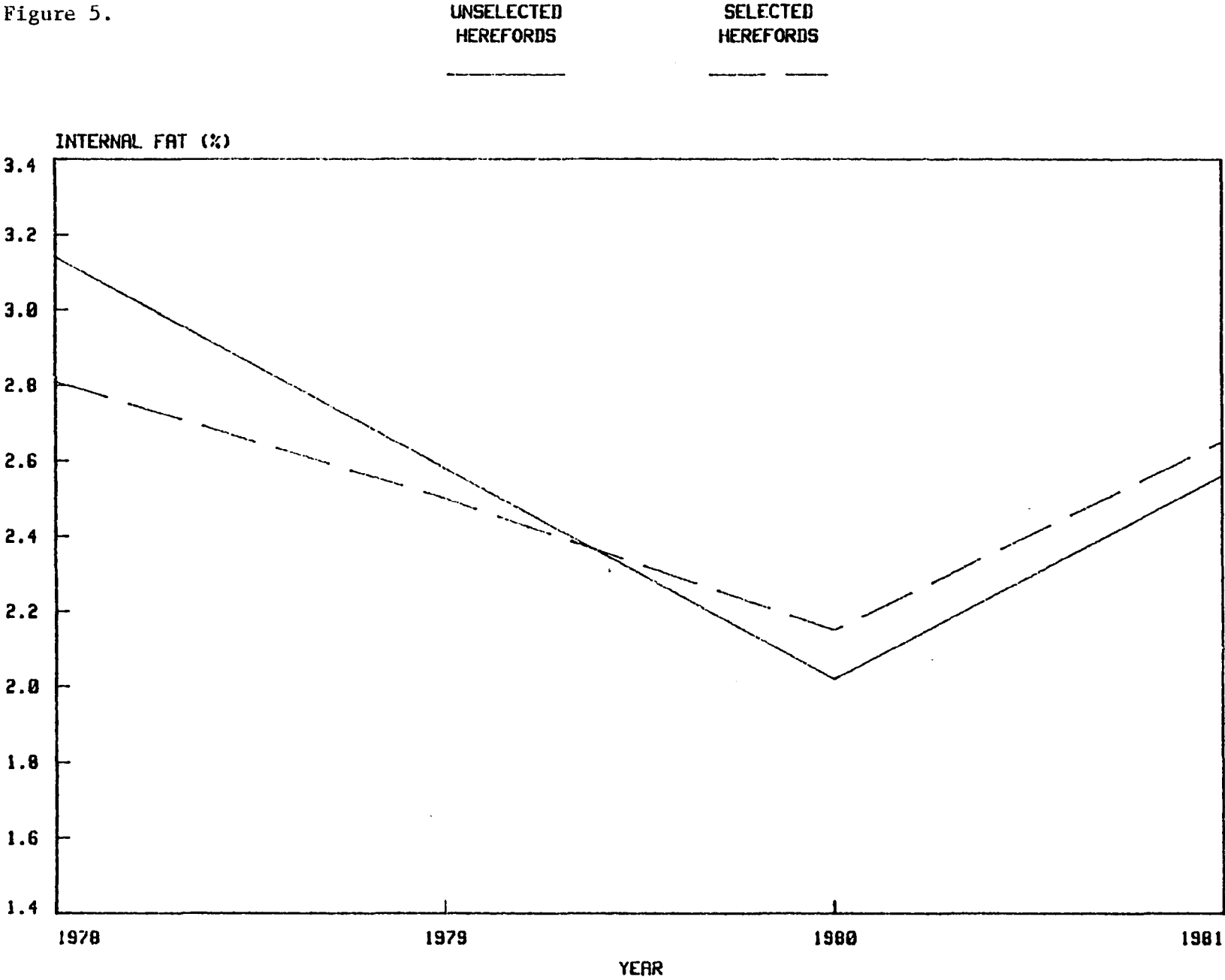


Figure 6. Means of Carcass Grades of
Unselected and Selected Herefords, 1978-1981

Figure 6.

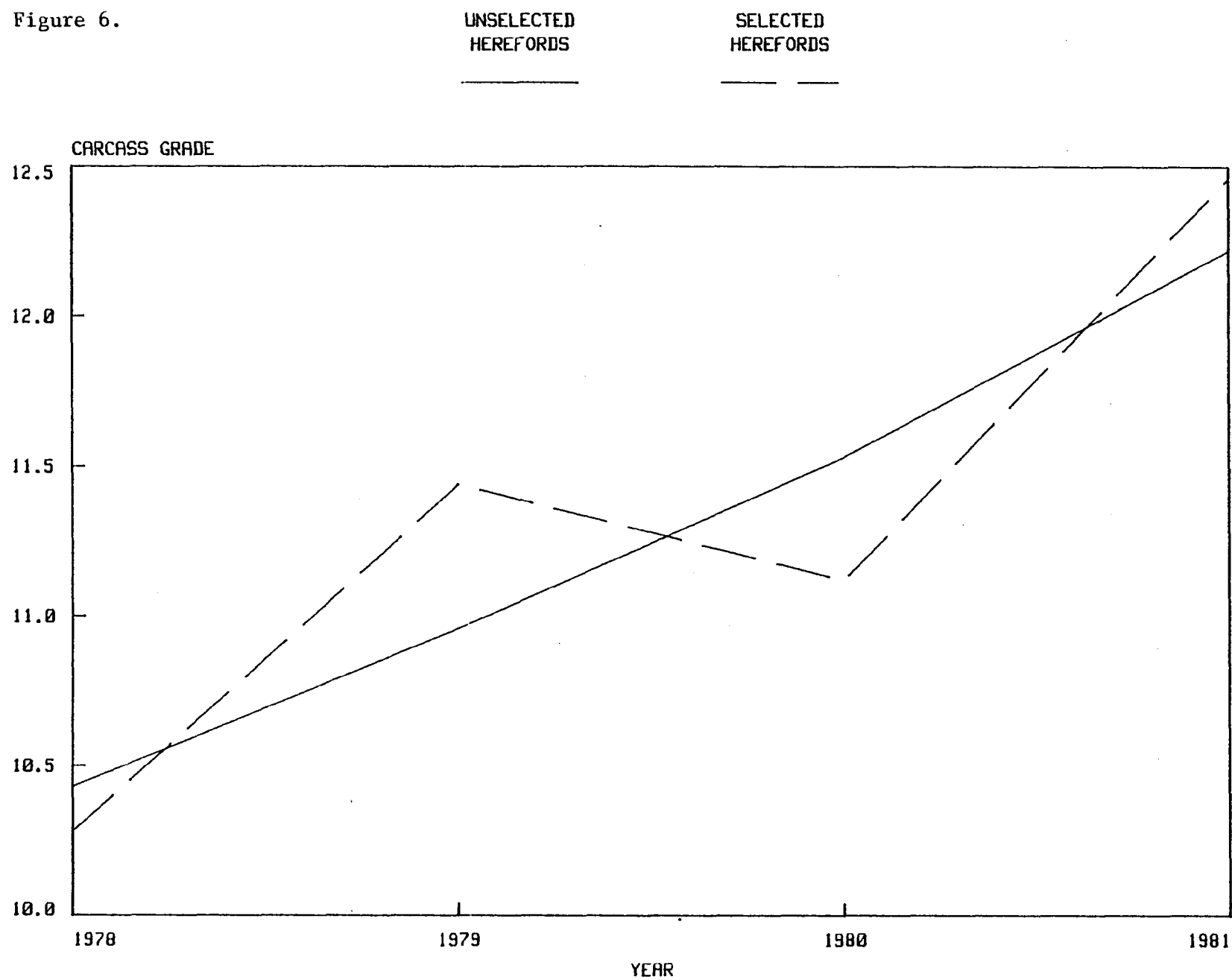


Figure 7. Means of Fat Thickness of
Unselected and Selected Herefords, 1979-1981

Figure 7.

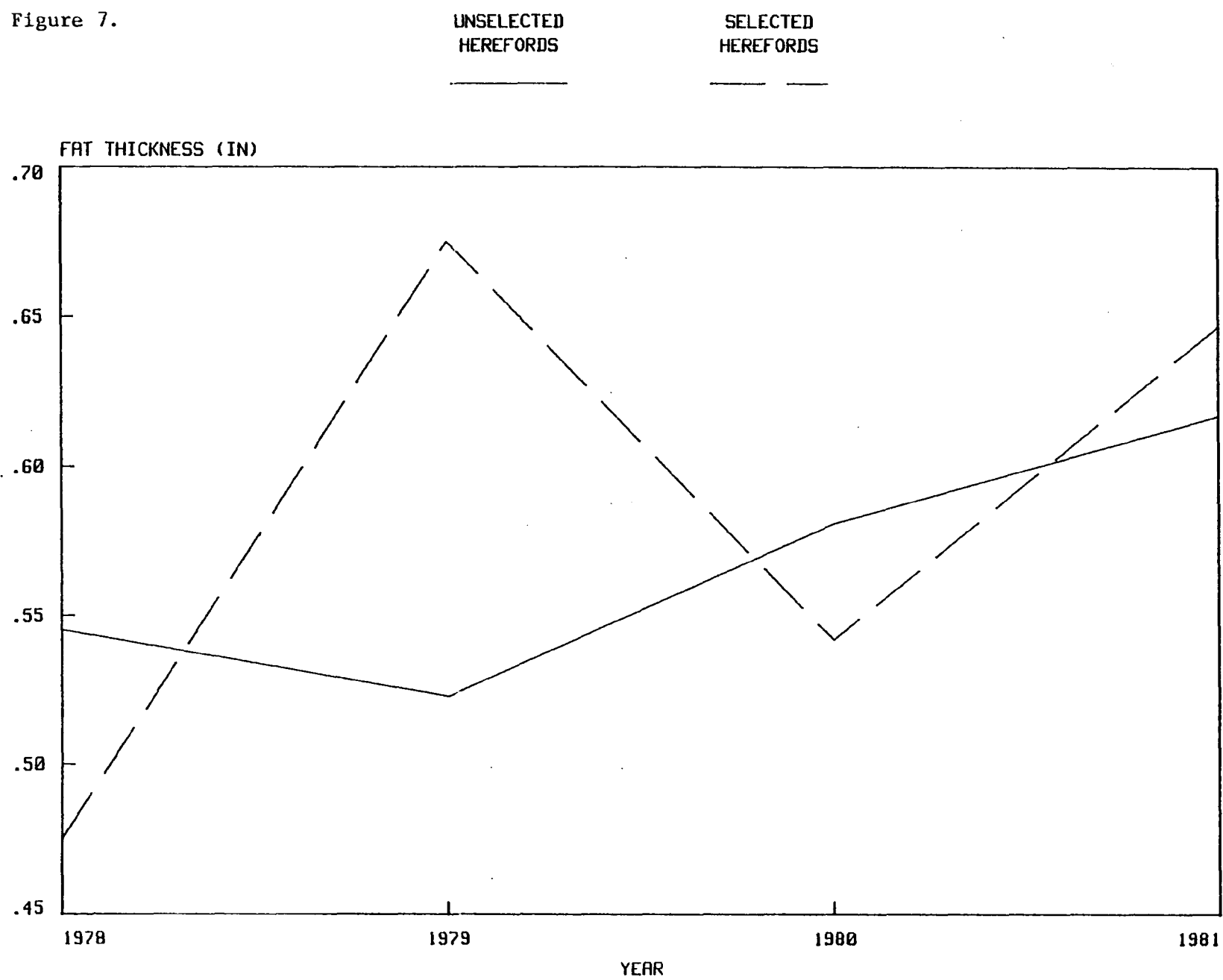


Figure 8. Means of Final Weight of
Unselected and Selected Herefords, 1978-1981

Figure 8.

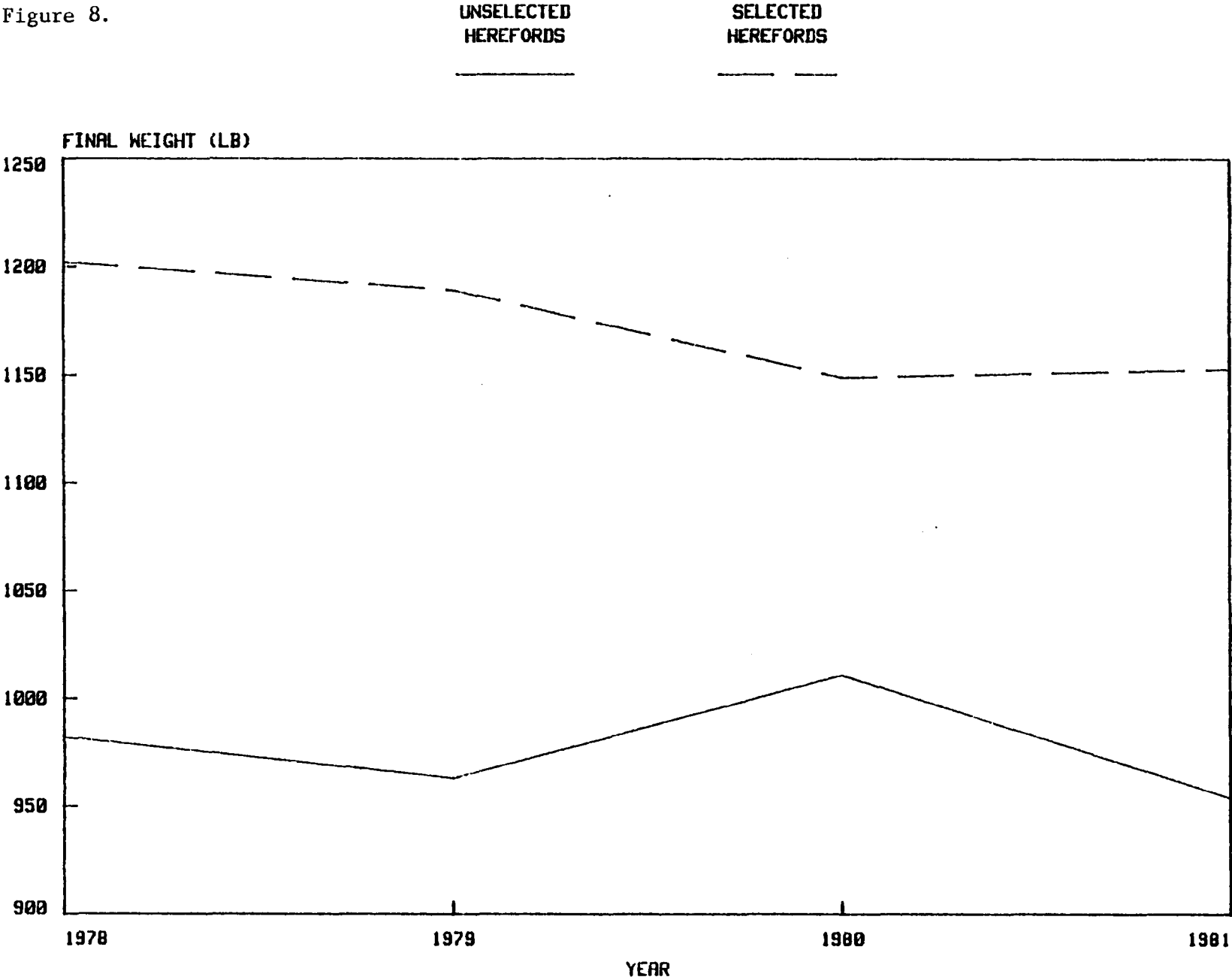
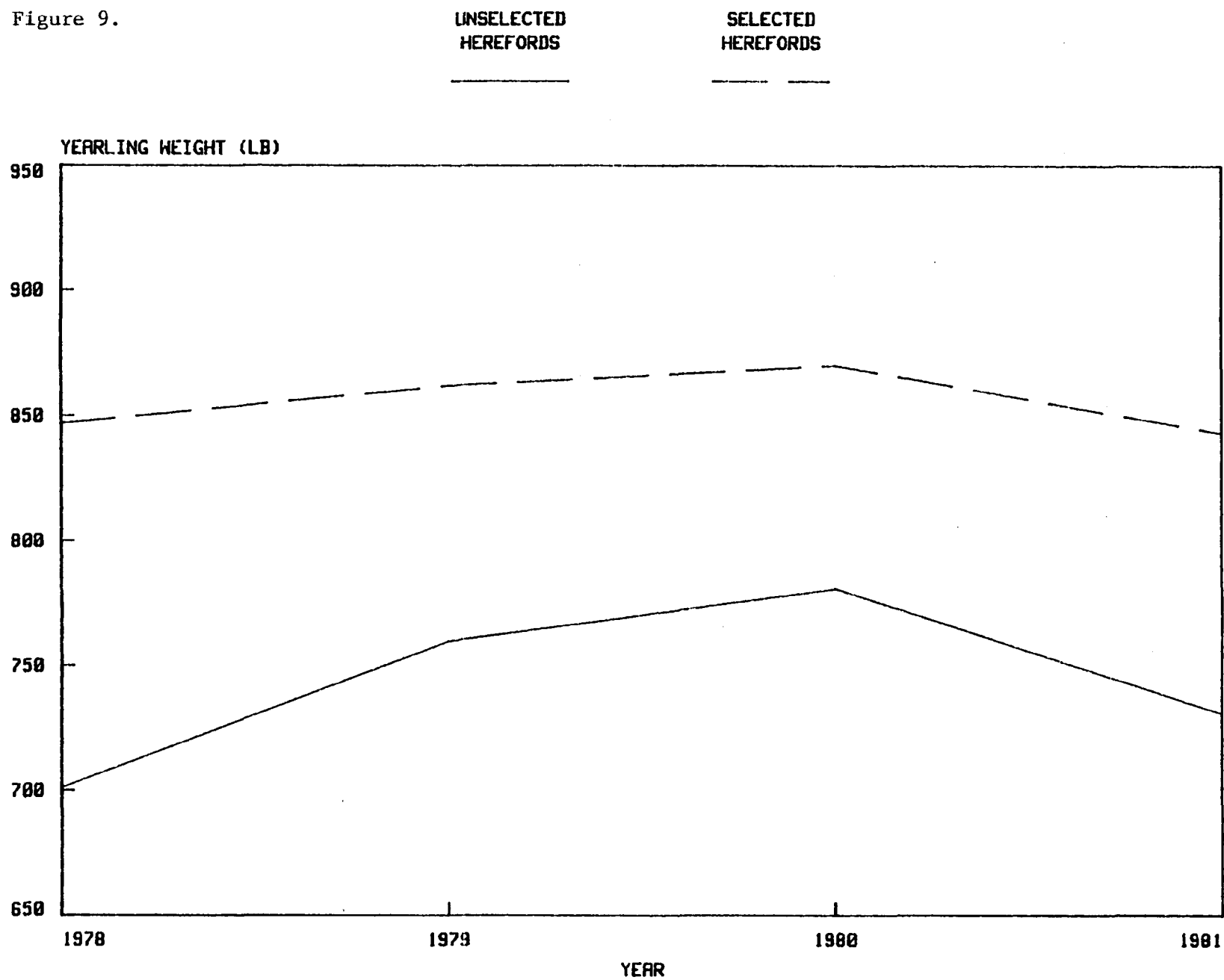


Figure 9. Adjusted Yearling Weight Means of
Unselected and Selected Herefords, 1978-1981

Figure 9.



By observing the remaining figures, it can be seen that the selected Herefords were consistently heavier at slaughter and gained faster in the feedlot.

Observation of the other traits reveals consistently more muscle and varying differences in fat indicators. It appears that the two groups responded differently to varying management regimes. However, this interaction was not significant ($P > .05$) in the preliminary analysis indicating the discrepancies must be due to sampling within the years.

Dairy Cross Dam vs Beef Cross Dam

All steers included in this analysis from groups three and four were sired by Simmental bulls. However, the cows in group 3 were crosses of Angus, Hereford, Simmental and Charolais breeds, while those in group 4 were Angus, Hereford, Simmental and Holstein-Friesian crosses. Therefore, the effect contrasting the two breeds would be comparing the steers from a dairy cross dam with the steers from a Charolais cross dam.

Table 18 presents the contrast effect for each trait. The results indicate that the dairy cross steers out-weighed the group 3 steers at 365 days of age and again at final weight. However, the group 3 steers gained faster while in the feedlot. In addition, the steers from dairy crossed dams were more desirable in their marbling which resulted in a higher carcass grade.

Table 18. Contrast Effects of Feedlot
and Carcass Traits Between Group 3 and Group 4

Trait	Effect
Final Weight	-35.4 ^{**}
Average Daily Gain	.0606 ^{**}
Yearling Weight	-60.52 ^{**}
Internal Fat	.0048
Yield Grade	-.0694
Loin Eye Are	-.1030
Marbling	-.4380 [*]
Fat Thickness	.0020
Carcass Grade	-.3129 ^{**}

* P<.05

** P<.01

Note: Degrees of freedom for carcass traits is 98; degrees of freedom
for feedlot traits is 106

Crossbreeding Effects

Comparisons were desired contrasting the performance of the crossbred cattle with the selected Hereford steers. However, this particular effect was not estimable due to the disconnected data. Figures 10 to 18 illustrate the trends of the three groups from 1978 to 1981. However, the observed differences can be attributed to breed of sire as well as differences in the crossbred status of the steers.

The crossbred steers were more desirable in growth traits and amount of muscling. In addition, they exhibited less 12th rib fat with group 4 averaging considerably less fat in 1981 than either of the other groups.

Carcass grades did not appear to be much different in crossbreds than in the straightbred Herefords. However, groups 3 and 4 were more desirable in yield grade, which would be a reflection of their overall leanness in comparison to the Herefords.

Contrast effects comparing the steers in group 2 to the crossbred Herford-sired steers in groups 3 and 4 are presented in Table 19. The significance of the contrast was investigated utilizing Bonferonni's t statistic. The group 4 steers out-performed the selected straightbred Herefords in all growth traits, i.e. final weight, average daily gain and yearling weight. In addition, they were leaner over the 12th rib and exhibited more muscle as indicated by their average loin eye area.

Group 3 steers differed from the selected Herefords in final weight and yearling weight ($P < .05$ and $P < .01$, respectively). These results indicate favorable feedlot performance of the crossbred steer when the crossbred dam contains some dairy genes.

Figure 10. Means of Marbling Scores of
Groups 2, 3 and 4, 1978-1981

Figure 10.

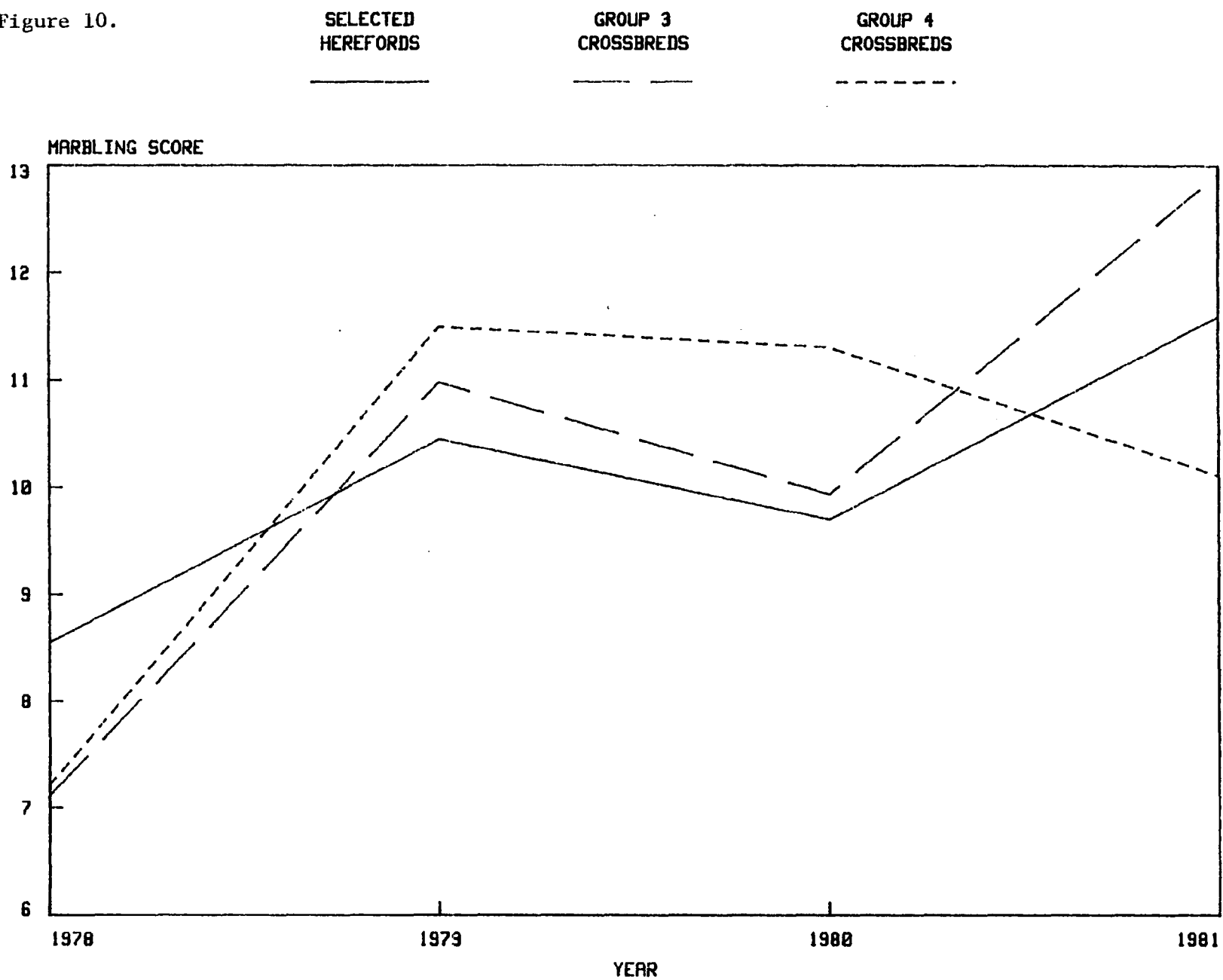


Figure 11. Means of Yield Grades of
Groups 2, 3 and 4, 1978-1981

Figure 11.

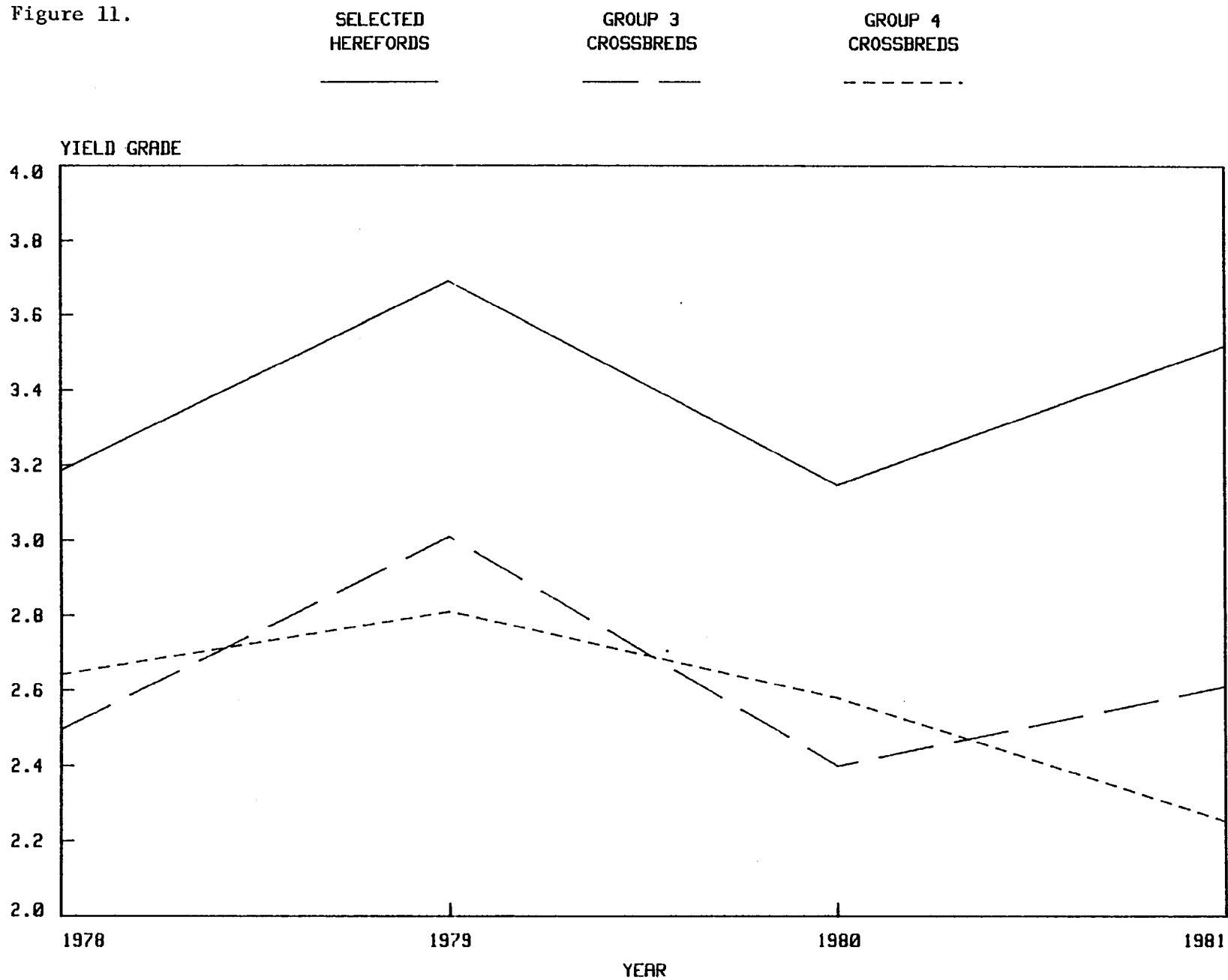


Figure 12. Means of Average Daily Gains of
Groups 2, 3 and 4, 1978-1981

Figure 12.

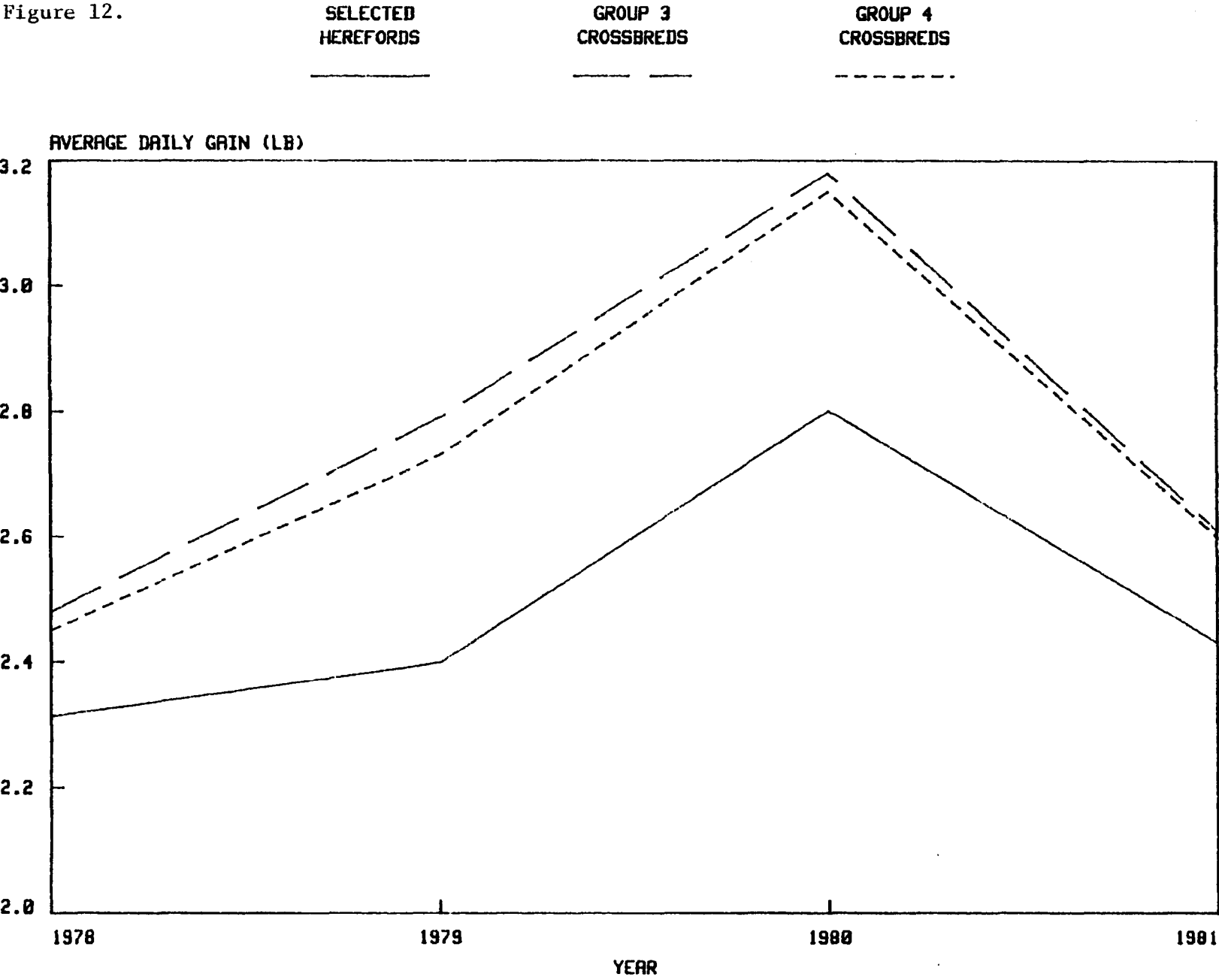


Figure 13. Means of Loin Eye Areas of
Groups 2, 3 and 4, 1978-1981

Figure 13.

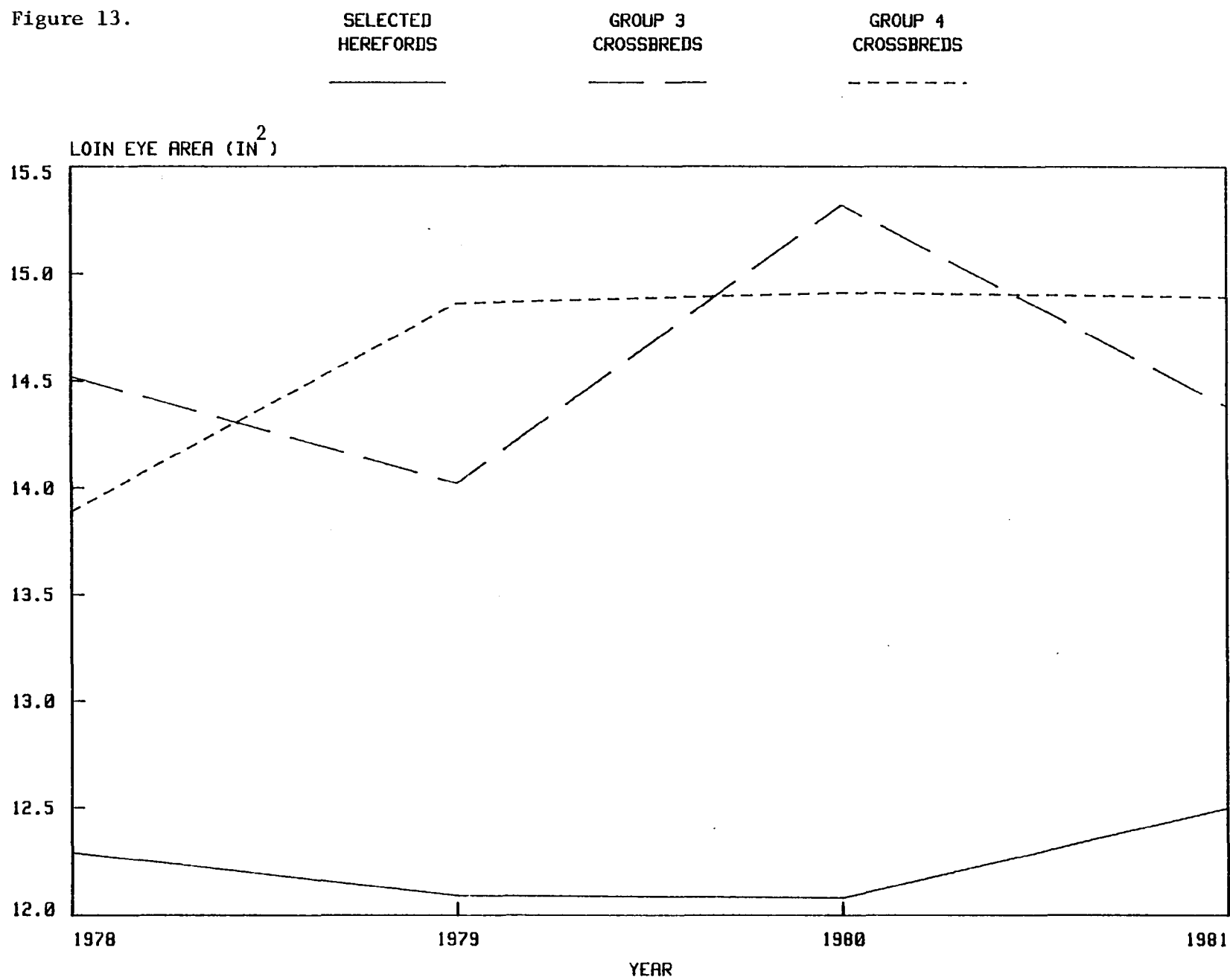


Figure 14. Means of Internal Fat of
Groups 2, 3 and 4, 1978-1981

Figure 14.

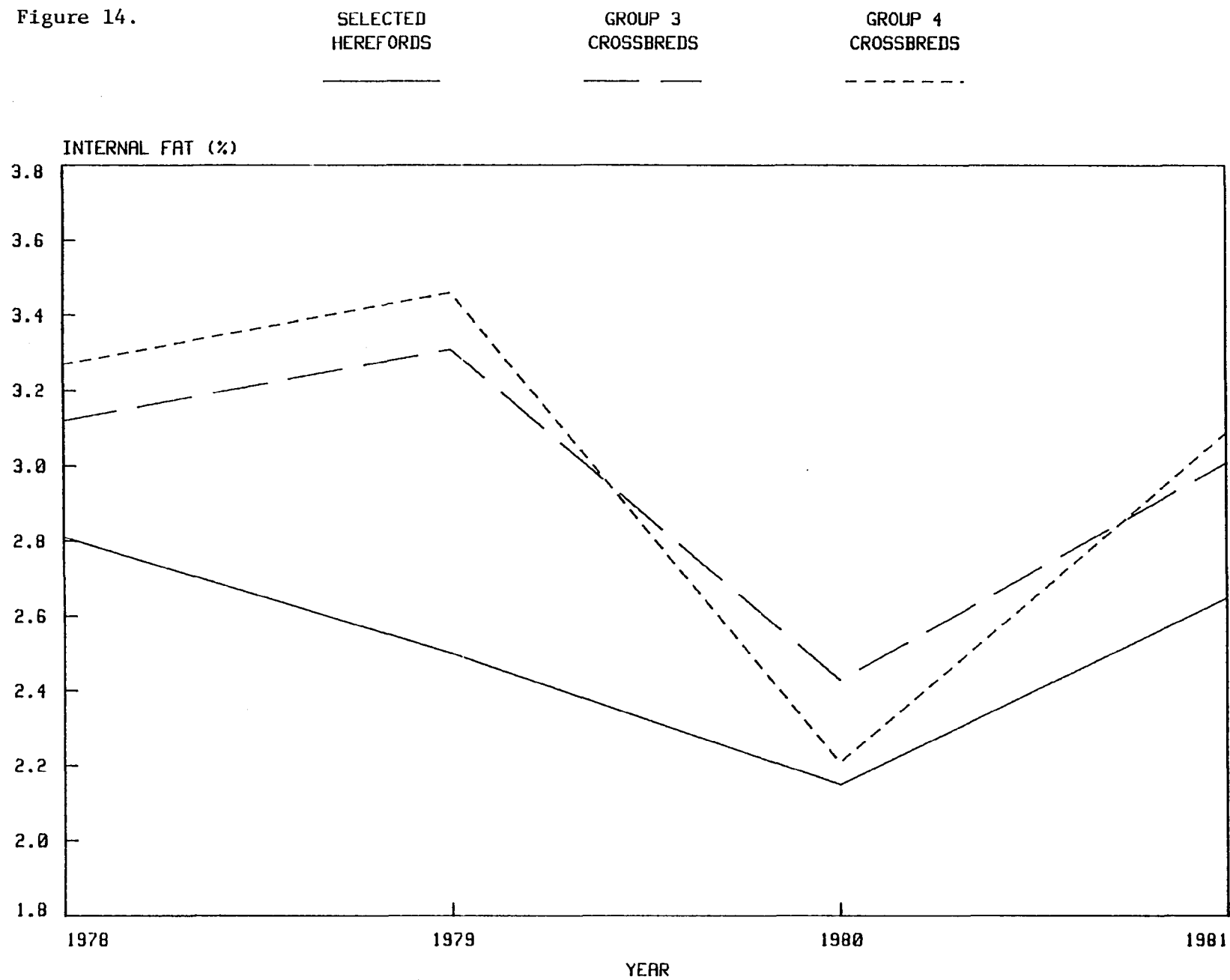


Figure 15. Means of Carcass Grades of
Groups 2, 3 and 4, 1978-1981

Figure 15.

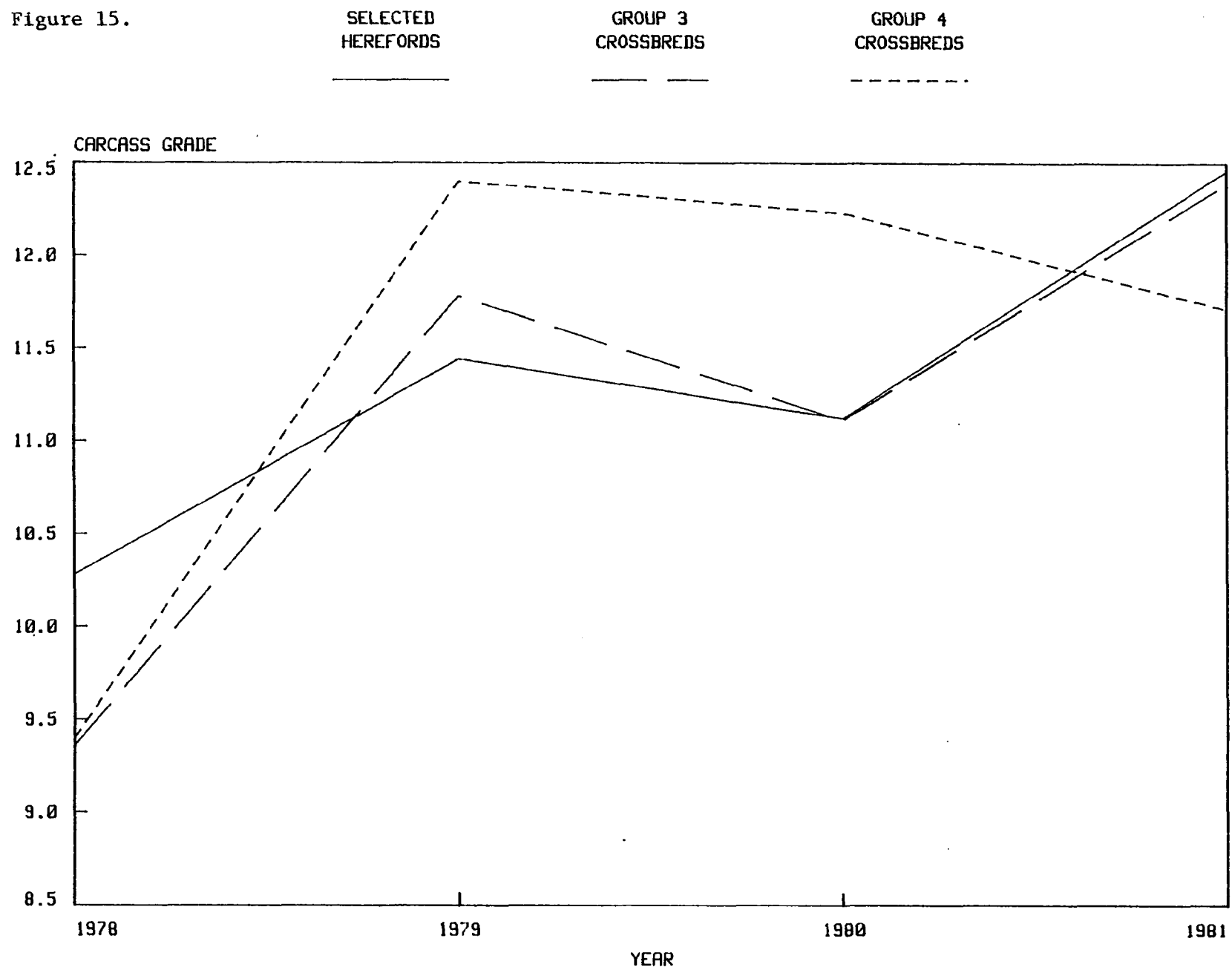


Figure 16. Means of Fat Thickness of
Groups 2, 3 and 4, 1978-1981

Figure 16.

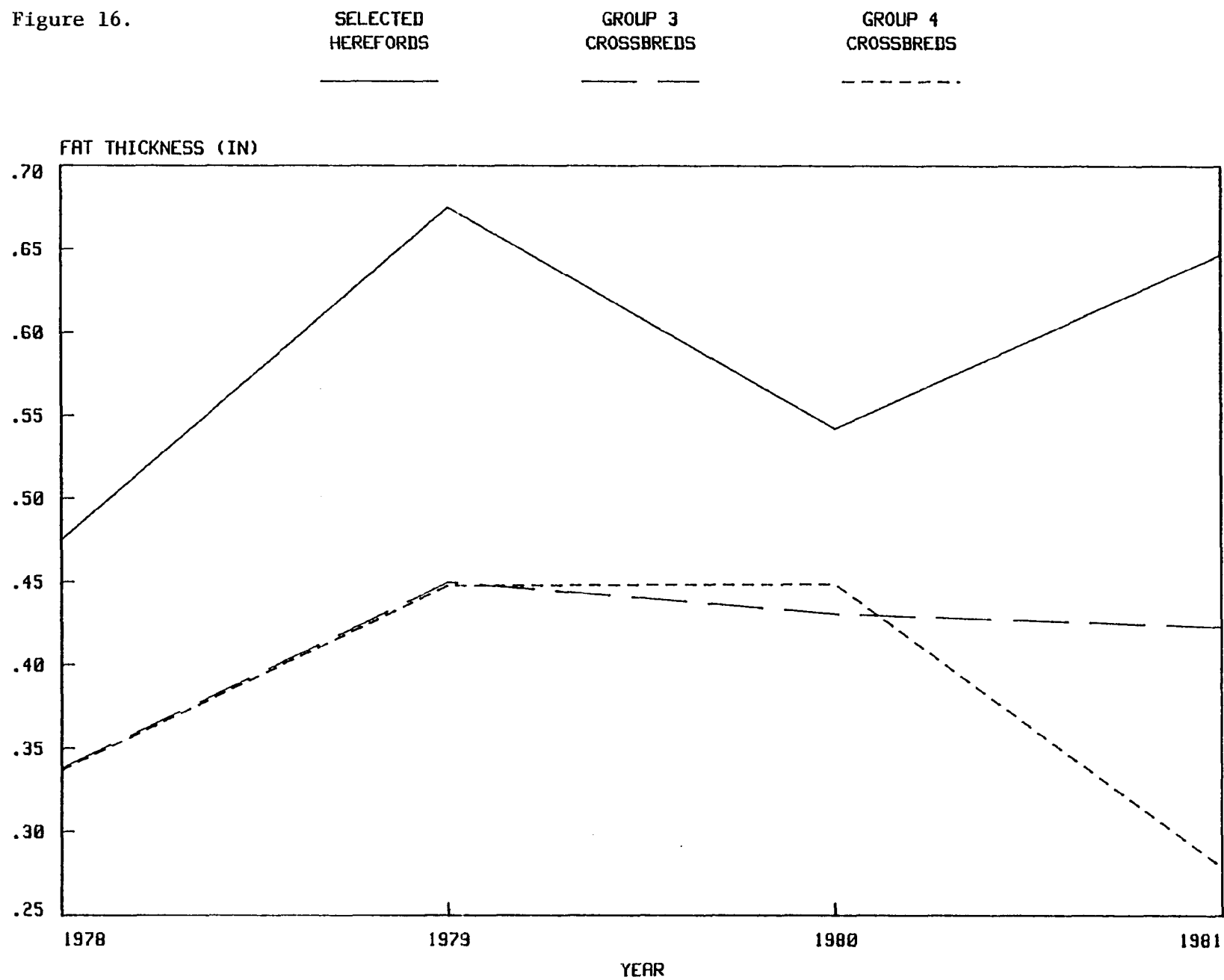


Figure 17. Means of Final Weight of
Groups 2, 3 and 4, 1978-1981

Figure 17.

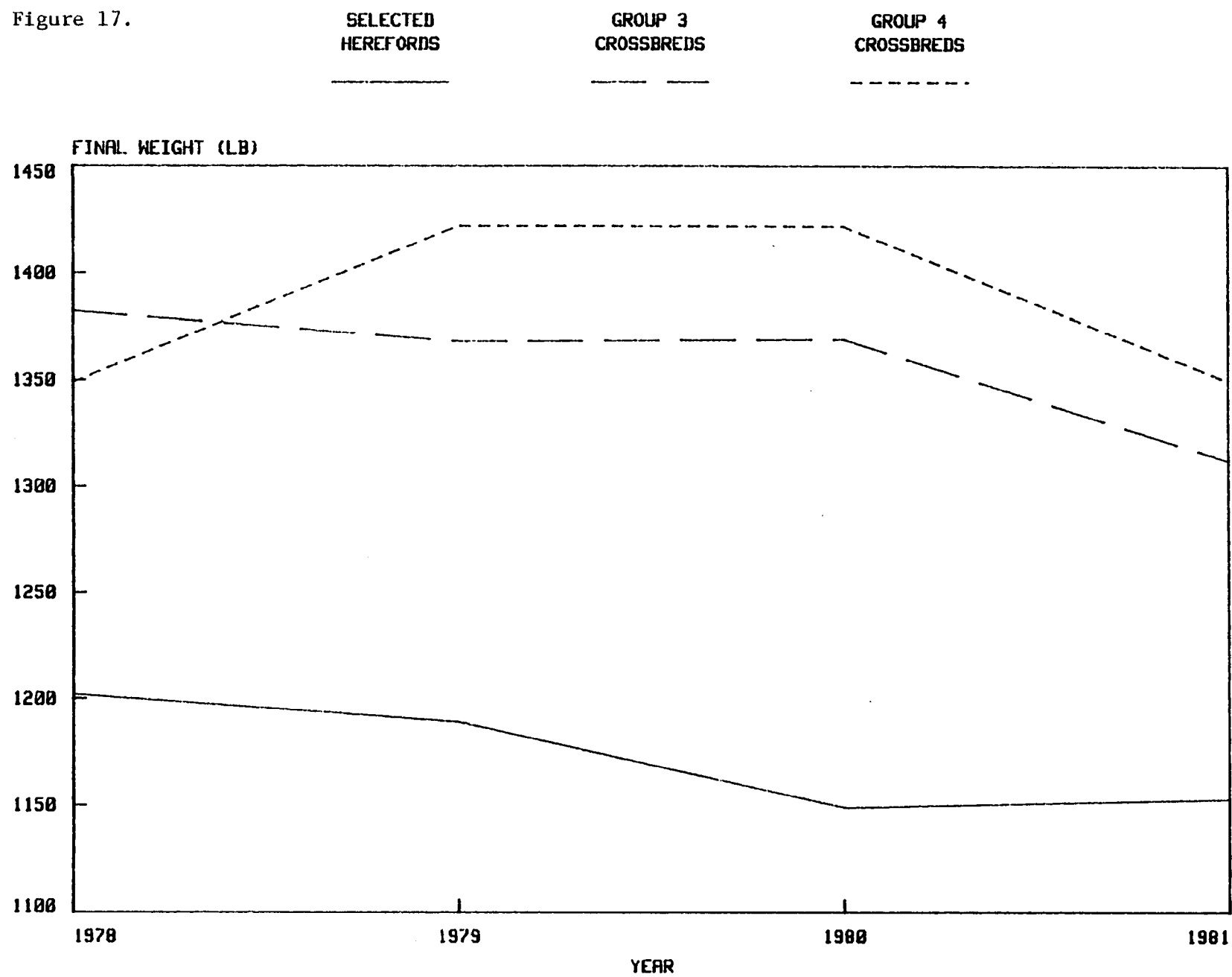


Figure 18. Adjusted Yearling Weight Means of
Groups 2, 3 and 4, 1978-1981

Figure 18.

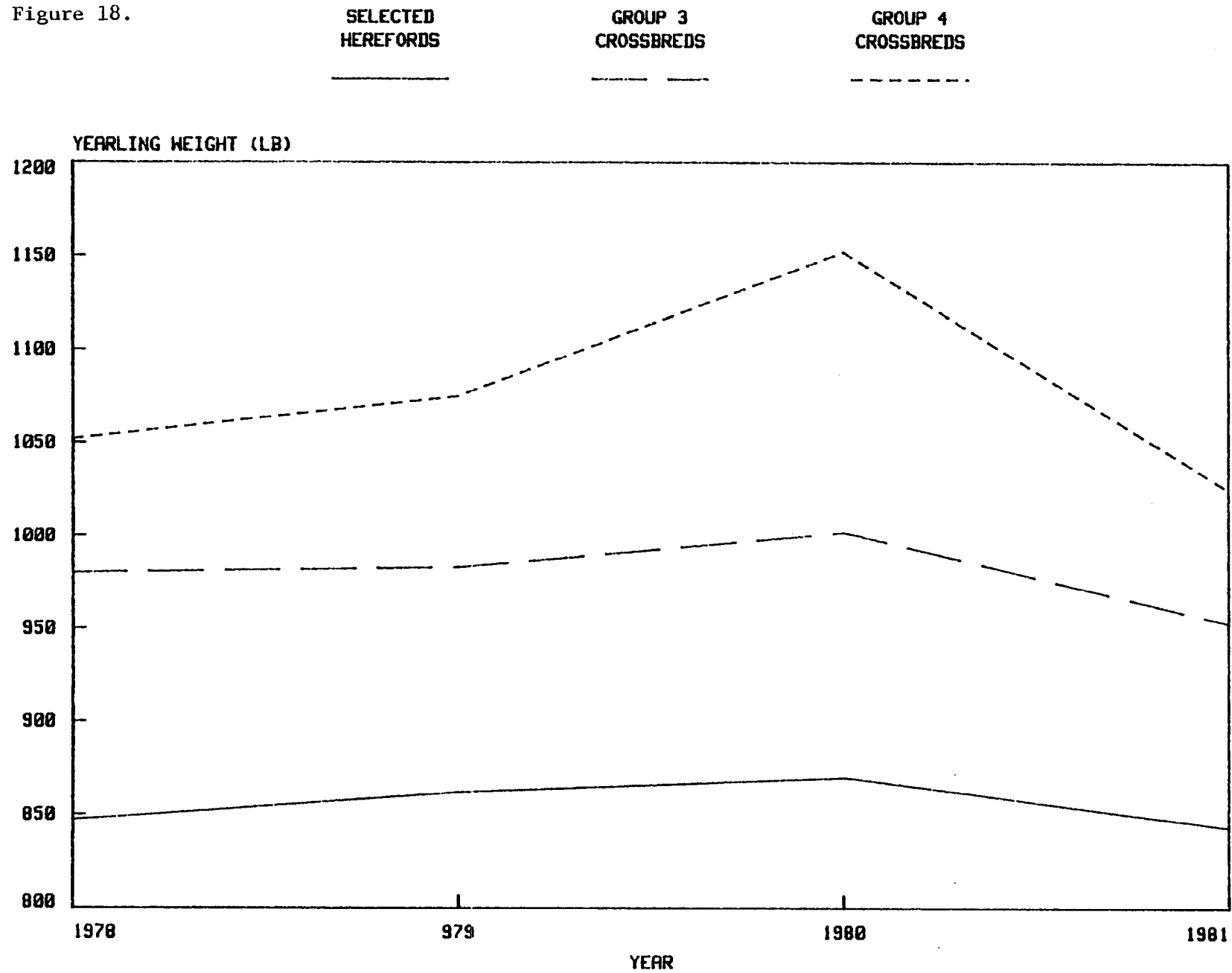


Table 19. Contrast Effects of Feedlot
and Carcass Traits in Crossbred Steers

Trait	Group 2 vs Group 3	Group 2 vs Group 4
Final Weight	-80.0 [*]	-173.5 ^{**}
Carcass Grade	.249	.851
Fat Thickness	.03139	.21428 [*]
Yield Grade	.1959	.6351
Marbling	-.1605	.5897
Internal Fat (KPH)	-.0989	-.2696
Loin Eye Area	-.385	-1.448 [*]
Average Daily Gain	-.0908	-.2921 [*]
Yearling Weight	-129.09 ^{**}	-219.4 ^{**}

^{*}P<.05

^{**}P<.01

SUMMARY AND CONCLUSIONS

Commercial beef cattle producers currently attempt to breed cattle in a manner that will insure the fastest growing cattle on as an efficient a diet as possible. In addition, they expect these fast growing calves to have carcasses with the greatest amount of edible beef per unit of weight.

For several years producers have been using crossbreeding and selection as tools to achieve their final goals. In order for them to utilize these tools as effectively as possible, it is desirable for them to know the heritabilities and correlations of the traits they are actively selecting for and the related traits that they hope to influence.

In addition, because of the tremendous need to breed the best sire breed to the best dam breed, it is necessary for them to know how a particular cross compares to a well-established purebred.

The purposes of this study were: 1) to determine the effect of selection for yearling weight, 2) to compare the performance of crossbred steers to the performance of straightbred Hereford steers, 3) to estimate heritabilities and correlations of selected feedlot and carcass traits in beef cattle selected for yearling weight and 4) to compare estimates of heritability obtained using REML techniques to previously reported estimates.

Two hundred sixty-seven records on Lake City steers were collected from 1978 to 1981. The final analysis indicated that the Herefords selected on yearling weight gained more in the feedlot and were considerably

heavier at slaughter than their unselected counterparts. In addition, the selected Herefords had consistently more muscling than the unselected Herefords.

When dairy crossed steers were compared to beef steers, the steers from the dairy cross dams outweighed the beef steers at 365 days of age and again at final weight. In addition, the dairy cross steers were more desirable in their marbling. However, the beef steers consistently gained faster while in the feedlot.

When the crossbred steers were compared to the Herefords the crossbreds were more desirable in growth traits and total amount of muscling. The two crossbred groups also exhibited less 12th rib fat than the straightbred steers and, consequently, produced more desirable yield grades. No differences were observed in carcass grades between the two groups.

Phenotypic correlations of the eight observed traits with yearling weight were similar to previously reported correlations. Differences in correlations were observed between the Simmental-sired steers and the Hereford-sired steers as could be expected due to the distinct breed differences.

Unexplainable negative genetic correlations were observed between final weight and yearling weight. The only apparent explanation for such a "non-biological" result is the small sample size used for estimation.

Heritability estimates were, in general, different from previously reported heritabilities. However, many of these differences could be explained by the distinct population of cattle at the Lake City Experiment Station. In addition, a small sample size contributed to a few of the estimates being outside of the parameter space.

In conclusion, it appears that selection for yearling weight combined with crossbreeding will produce cattle that gain faster in the feedlot and produce more desirable carcasses with more edible meat per unit of carcass weight.

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LITERATURE CITED

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