DIRECT AND CORRELATED RESPONSES TO SELECTION FOR INCREASED WEANING AND YEARLING WEIGHTS IN HEREFORD CATTLE

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WEIGHTS IN HEREFORD CATTLE

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CHAPTER I

INTRODUCTION

Selection, a primary force for changing gene frequency, is the process of permitting certain kinds of individuals to reproduce at a higher rate or leave more offspring than others. Although genes are the units of inheritance that selection acts upon, the whole animal, not just a few genes, is what is selected or rejected. The producer may evaluate individual traits of each animal and these traits may involve many genes, but whether that animal becomes a herd bull, enters the cow herd or is sent to market depends upon all of his or her characteristics. The producer's decision, weighing all strengths and weaknesses in comparison with other animals, ultimately decides sires and dams of future calf crops. Thus, it is the net effect of selection, considering many traits and economic evaluation, that should finally be appraised.

The alterations which selection produces in the genetic structure of a population are difficult to see or measure directly, but whatever changes are made through selection are cumulative over generations. Changes from selection are difficult to evaluate because they have often been coupled with the impact of improved management practices as well as large environmental variation from year to year which greatly influences actual performance levels.

Improvement of the genetic composition of a cattle herd can essentially only be achieved through selection of individuals genetically superior for economically important traits. Most producers today put considerable emphasis on growth rate of cattle. We need fast growing, efficient cattle from birth to slaughter; cattle that will produce heavy weaning weights for the cow-calf producers; efficient gains for the stocker operators and feedlots; heavy, lean, high yielding carcasses for the packer; and tasty, tender products for the consumer.

Numerous selection experiments have been conducted in laboratory species demonstrating that selection can be effective in increasing growth rate; however, very few studies have been designed to evaluate the effectiveness of selection for growth rate in our livestock populations, especially cattle. Information is needed to quantify how rapidly improvement can be obtained in certain traits along with correlated responses in other traits, in other words, net merit realized from selection.

This study was undertaken in the early sixties to: (1) quantify selection pressure achieved in a long term study of beef cattle, (2) to estimate direct response to selection for weaning and yearling weights, and (3) to estimate correlated responses in other economically important traits in two lines of Hereford cattle. Hopefully, information gained from this study will aid the industry in developing selection programs aimed at choosing cattle genetically superior for economically important traits.

CHAPTER II

REVIEW OF LITERATURE

Selection Theory

Two methods may be employed by livestock breeders to cause changes in the genetic structure of a population. One is the use of various mating systems or controlling the way in which animals are mated. This would include inbreeding, linebreeding, outcrossing and crossbreeding. The other method to alter genetic structure of a population is through selection. Selection means allowing some animals with more desirable genotypes to become parents and leave more offspring than others. While mating systems affect the genotypic frequencies in a population, selection is a directional force to change gene frequency which therefore also changes genotypic frequency.

The brief summary to follow concerning basic selection theory is based on information presented in texts by Lush (1945), Falconer (1960) and Pirchner (1969). Selection theory had its foundations in the early portion of this century through development of quantitative genetic theory by such great minds as R. A. Fisher, J. B. S. Haldane and S. Wright. The initial application of this theory to animal breeding and the development of animal breeding principles can mainly be attributed to J. L. Lush and his students.

The primary genetic effect of selection is to permanently change gene frequency and the magnitude of the effect of selection depends upon how much change occurs in these gene frequencies (Lush, 1945). The changes of gene frequency can rarely be seen or measured directly since it is not possible to determine how many loci actually influence a particular quantitative trait (Falconer, 1960). If, in fact, superior individuals are chosen, the progeny generation should have a higher frequency of more desirable genes and mean progeny performance for the selected trait should be higher than the mean performance of the prior generation. If environmental influences, dominance and epistasis are negligible, the mean performance of the progeny is expected to be the average breeding value of the selected parents (Pirchner, 1969). Due to errors in estimating breeding values of both parents and offspring, mean of offspring usually does not equal the average breeding value of the selected parents. Because environmental, dominance and epistatic effects do exist, means, variances and covariances are often used to describe the effects of selection since they are determinable quantities (Falconer, 1960).

The desirable goal of selection is to change the population mean for some particular character; therefore the major response of interest to selection is the difference of mean performance of offspring from selected parents and average performance of the parental generation before selection. Consequently, effectiveness of selection, in part, depends upon the selection differential or difference of average phenotypic value of selected animals and that of the contemporary herd (Falconer, 1960). The degree to which differences in phenotypes are inherited also influences response to selection; thus, genetic gain (ΔG) expected in one generation of selection is given by heritability (h^2) times selection differential (Falconer, 1960 and Pirchner, 1969).

Heritability is the proportion of total phenotypic variation that is attributed to additive genetic effects (Lush, 1945 and others). It provides a measure of the extent that differences among phenotypes are reflected by differences in genotypes and how well these differences will be passed on to the next generation. Heritability, and thus, response to selection, is influenced by the magnitude of environmental, non-additive and additive genetic variation for the trait under consideration (Falconer, 1960 and others.) Highly heritable traits (those with a large proportion of their phenotypic variation caused by additive genetic variation) would be expected to respond quite favorably to selection, while notable responses to selection for lowly heritable traits would take a much longer time. Often realized heritabilities are calculated from selection studies by response from selection dived by selection differential (Pirchner, 1969).

Size of the selection differential is dependent upon two factors, selection intensity (the proportion of the herd selected to be parents) and the phenotypic variation of the character in question (Falconer, 1960). Since more extreme phenotypes will occur and be selected for a trait with considerable variation, the selection differential is expected to be larger than for a trait with little phenotypic variance (Falconer, 1960).

The other factor influencing selection differential, selection intensity, cannot be completely controlled by the breeder as he must maintain a somewhat constant herd size. The smaller the proportion of animals saved for breeding, the higher the selection intensity and thus, the larger the selection differential (Lush, 1945). In livestock populations, generally far fewer males are kept for breeding purposes than females, so the selection differential for males will usually be much larger for males than females (Falconer, 1960). Also, selection differentials can be markedly increased through artificial insemination and embryo transfer.

Most breeders are interested in genetic gain per year, not per generation. This is obtained by dividing genetic response per generation by generation interval. Generation interval is defined as the average age of parents when offspring are born that will becom e parents of the next generation, so the shorter the generation interval, the more gain realized from selection per year (Falconer, 1960).

Also of interest are correlated responses to selection or indirect selection for traits that are influenced by some of the same genes that affect the trait under direct selection. The generalized formula for correlated response is given by:

$CRy = r_g \sigma_{a_y} h_x i_x$ (Falconer, 1960)

where: CRy = correlated response on trait y when selecting for trait x

r_g = genetic correlation of traits x and y

σ_{a_y} = additive standard deviation of trait y

h_x = square root of the heritability of trait x

i_x = selection intensity of trait x

Correlated responses to selection can thus be predicted if genetic correlations, heritability, additive variance and selection intensity are known; or conversely, if the correlated response is measured, realized genetic correlations can be estimated if other parameters and selection intensity is known.

Some traits of interest are difficult to measure or occur later in an animal's life and are thus difficult to directly select for. If there are favorable genetic correlations with traits that are easier to measure, then selection on those traits may be an effective way for improving some economically important traits in our livestock populations not so easily measured (Falconer, 1960 and Pirchner, 1969).

Results of Selection Experiments in Species Other Than Beef Cattle

Mice

Numerous experiments conducted with laboratory species concerning selection for growth traits analogous to those that are economically important in beef cattle have been reported. Although these results may be less applicable than those from cattle experiments, they can give additional insight to selection studies due to much greater number of generations and greater precision in experimental techniques. Chapman (1951) reviewed the effectiveness of selection in laboratory animals and concluded that no obvious inconsistencies between experimental work and genetic theory were evident. Chapman also summarized many studies and arrived at these generalizations: (1) major changes in traits selected for occur in the first generations with alternating periods of little or no change, (2) relative variation within selected lines remained fairly constant throughout generations of selection, (3) noted correlated changes do occur in traits for which no conscious selection was practiced and (4) reduction of heritability in later generations of selection.

Another review by Roberts (1965) concerning contributions of the laboratory mouse to animal breeding research, summarizes the literature relative to selection for body weight and other measures of growth. Roberts found the following generalizations to be applicable to livestock populations in regard to selection for body weight: (1) selection is primarily cummulative in nature, (2) selection is uncomplicated by interactions, genetic or environmental, (3) it is effective in bringing about marked changes in weight, (4) limits are not reached for 20 or more generations, (5) selection schemes based on individual performance such as performance testing rather than progeny tests may be more effective for weight traits and (6) marked correlated changes may occur and they may not always be favorable.

A summary of numerous reports on selection studies involving body weight in mice and a few with rats are presented in Table I. Some of these studies merit further mention. In a long term selection experiment involving 84 generations of selection for increased 60 day weight in mice, Wilson et al. (1971) reported a very distinctive leveling response with no appreciable response the last 49 generations. This experiment was first reported by Goodale (1938) and the object of the study was to determine limits of change that could be made by selection. Goodale and co-workers set out to breed the largest, heaviest mice possible from a line of big albino mice with four males and 11 females as foundation stock. Results of this study suggest there is a point of exhaustion of genetic variation in a population, but prior to this exhaustion major changes can occur in the trait selected (72% increase in 60 day weight). This experiment also points out the value of experiments with laboratory animals, as a similar study involving cattle would take 378 years if the generation interval was 4.5 years.

Falconer (1973) also reported a leveling effect of response to selection for increased six week weight after 23 generations Many studies (Falconer, 1953; Falconer, 1955; Lang and Legates, 1969; McLellan and Frahm, 1973; and Baker and Chapman, 1975) report asymmetry in response to selection for the same trait in opposite directions with greater response

TABLE I

RESULTS OF SELECTION EXPERIMENTS IN MICE OR RATS

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Baker and Chapman (1975)	± 3-9 wk gain	13	3-9 wk gain		.25	0 #young raised to 9 wks 0 fertility	Study done with rats; control line used; Significantly greater response (23%) downward than upward.
Baker *et al.* (1975b)	± 3-9 wk	13	± 3-9 wk gain	+ 3 wk wt		+ litter size at birth + litter size at birth	Same study as above; rats control lines; 2 wk litter wt (measure of lactation) was greater in positive selection lines than negative lines.
Bakker *et al.* (1976)	6 wk wt	36	3 wk wt 6 wk wt 3-6 wk gain	+22% +33% +46%			Control lines used.
	3-6 wk gain	36	3 wk wt 6 wk wt 3-6 wk gain	+28% +50% +70%			
Bradford (1971)	+ 3-6 wk gain	24	3 wk wt 6 wk wt 3-6 wk gain	+30% +54% +76%	.20 ± .01	+ ovulation rate 0 parental loss 0 litter size	Proportion of fertile mating declined in later generations.
Carter (1972)	+ 3 wk wt	21	3 wk wt 6 wk wt	+20% +15%			In 3 wk wt line, little response in 6 wk wt after 6th generation;
	+ 3-6 wk gain	21	3 wk wt 6 wk wt	+20% +33%			In 6 wk wt line, response in 3 wk wt up to 25% in 6th generation, then declines;
	+ 6 wk wt	21	3 wk wt	+ 7%			In 6 wk wt line, response in 3 wk wt up to 25% in 6th generation, then declines; In 6 wk wt line, showed greater response in gain than gain line; 4 lines, 8 pairs per generation.

TABLE I (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Dalton (1967)	Full feed +3-6 wk gain	13	3-6 wk gain		.23	+ mature wt	6 lines, selected for high and low growth within litters on full nutritional diluted diet with control lines on each diet.
	Full feed -3-6 wk gain	13	3-6 wk gain		.21	+ mature wt	
	Diluted diet +3-6 wk gain	13	3-6 wk gain		.30	+ mature wt	
	Diluted diet -3-6 wk gain	13	3-6 wk gain		.22	+ mature wt	
Falconer (1953)	+6 wk wt	11	6 wk wt 3 wk wt	+17% 0	.22	+ 12 day wt (milk production) +fertility + fertility 0 birth interval - activity	6 pair mated each generation in each line from 6 families; No plateau observed in either line.
	-6 wk wt	11	6 wk wt	-33%	.49	+ 12 day wt (milk production) + fertility - birth interval - activity	
Falconer (1955)	-6 wk wt	30	6 wk wt		(to gen. 21) .175	Small +6 wk wt of dam with 3 wk wt of offspring	15 gm differential between the 2 lines at level of limit of selection;
	-6 wk wt	24	6 wk wt		(to gen. 19) .518	+ 6 wk wt of dam with 3 wk wt of offspring	Selection for increased size less effective than for decreased size.
Falconer (1973)	+6 wk wt	23	6 wk wt 3 wk wt 3-6 wk gain	+45% +38% +29%	(10 gen.) .40	- litter size - fertile matings - natural fitness	Assymmetry of response between lines selected in opposite directions; after 23 gen., large lines approaching limits; reproductive failure problems after 10 gen.; used control line.
	-6 wk wt	23	6 wk wt 3 wk wt 3-6 wk gain	-38% 0% -23%	(10 gen.) .33	+ litter size + fertile matings + natural fitness	

TABLE I (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Frahm and Brown (1975) and Brown and Frahm (1975)	+3 wk wt	14	3 wk wt	+31%	.17	+ litter size	Control lines used; replicate lines.
			3-6 wk gain	+17%		+ 12 day litter wt	
			8 wk wt	+19%		+ feed efficicney (21 to 42 days of age)	
	+3-6 wk gain	14	3 wk wt	+21%			
			3-6 wk gain	+53%	.27	+ litter size	
			8 wk wt	+46%		+ 12 day litter wt	
						- feed efficiency (21 to 42 days of age)	
Harvey (1972)	+12-21 day gain and +51 day wt	10	12-21 day gain	+62%	.17 (over lines)		Used control lines.
			51 day wt	+34%	.27 (over lines)		
	+12-21 day gain and -51 day wt	10	12-21 day gain	-19%			
			51 day wt	-26%			
	-12-21 day gain and +51 day wt	10	12-21 day gain	+26%			
			51 day wt	+36%			
	-12-21 day gain and -51 day wt	10	12-21 day gain	-34%			
			51 day wt	-30%			
Hull (1960)	+ 3 wk wt	5	3 wk wt	+	.74		When selecting for increased weight, abdominal fat weight is altered.
			4½ wk wt	+			
			6 wk wt	+			
	+ 4½ wk wt	5	4½ wk wt	+	.44		
			3 wk wt	+			
			4½ wk wt	+			
	+ 6 wk wt	5	6 wk wt	+	.57		
			3 wk wt	+			
			4½ wk wt	+			
Lang and Legates (1969)	+ 6 wk wt	30	6 wk wt	+14%		- maternal ability	Conrol lines used.
			postweaning ADG	+		+ efficiency of growth	
	- 6 wk wt	30	6 wk wt	-26%		- efficiency of growth	
			postweaning ADG	-			

TABLE I (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
LaSalle et al. (1974)	+ 3-6 wk gain	12	3-6 wk gain	+54%	.24	0 litter size	
			42 day wt	+		- reproductive efficiency	
			56 day wt	+		+ 12 day litter wt	
			42-56 day gain	+		(milk production)	
Legates (1969)	+ 6 wk wt	15	6 wk wt		.13	- litter wt	Assymmetry of response between
			growth to 6 wks	+		+ litter size	lines selected in opposite
			6-8 wk gain	-		+ maternal performance	directions; reduced fertility in negative line.
						+ feed efficiency	
	- 6 wk wt	15	6 wk wt		.42	+ litter wt	
			growth to 6 wks	+		+ litter size	
			6-8 wk gain	-		+ maternal performance	
						+ feed efficiency	
MacArthur (1949)	+ 60 day wt	21	60 day wt	-74%		+ litter size	Assymmentry of response between
						- activity	lines selected in opposite
	- 60 day wt	21	60 day wt	-47%		+ litter size	directions; some infertility
						- activity	near end of experiment; many differences in coat colors, temperment and proportion of parts.
McLellan and Frahm (1973)	+ hindleg wt (84 days)	7	hindleg wt (84 d.)	+12%	.24	+ #live offspring/litter	Used control lines;
			3 wk wt	+ 3%			Selection more effective for
			3-6 wk gain	+ 9%		0 maternal performance	decreased hindmuscle weight.
			6 wk wt	+ 8%			
			12 wk wt	+14%		+ % muscle	
	- hindleg wt (84 days)	7	hindleg wt (84d.)	-18%	.70	+ maternal performance	
			3 wk wt	- 9%			
			3-6 wk wt	-24%		+ % muscle	
			6 wk wt	-17%			
			12 wk wt	-11%			
McPhee and Neill (1976)	+ 8 wk wt	25	8 wk wt	+35%			Close symmetry at end of 25 gen.; high line mice became rapidly
	- 8 wk wt	25	8 wk wt	-33%			fatters; control line used.

TABLE I (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Rahnefeld *et al*. (1963)	+ 18-42 day gain	17	18-42 day gain	+58%	.18	+ litter size 0 maternal effect on postweaning growth	Control line used.
Sutherland *et al*. (1970)	+ 4-11 wk gain	21	4-11 wk gain	+89%	.24	+ feed intake + grass efficiency	Control line used.
Wilson (1973)	+ 3-6 wk gain	8	3 wk wt	+ 9%		+ litter size at birth	Control line used.
			6 wk wt	+24%		+ litter size at weaning	
			9 wk wt	+25%			
			3-6 wk gain	+40%	.23		
			6-9 wk gain	+30%			
			3-9 wk gain	+38%			
			3-6 wk gain / 3-9 wk gain	+ 2%			
	+ 3-6 wk gain / 3-9 wk gain	8	3 wk wt	- 1%		+ litter size at birth	
			6 wk wt	- 1%			
			9 wk wt	- 8%		+ litter size at weaning	
			3-6 wk gain	- 2%			
			6-9 wk gain	-51%			
			3-9 wk gain	-13%			
			3-6 wk gain / 3-9 wk gain	+114%	.32		
Wilson *et al*. (1971)	+ 60 day wt	84	60 day wt	+72%	.32	- litter size at birth - litter size at 60 days	Distinct leveling response, no response last 49 generations.
Zucker (1960) (rats)	± 9 wk wt	10	9 wk wt	30%	.40		Symmetry of response curves; observed changes in coat color with more albinos in large lines.

for downward selection. MacArthur (1949) and Falconer (1973) also report assymmentry of response curves, but with greater upward response for 42-day and 60-day weights, respectively. Close symmetry of response to selection for eight week weight was reported by McPhee and Neill (1976) at the end of 25 generations; however, the low line had a more curvilinear response than the high line.

There are many correlated traits of interest reported in these studies. White and Robinson (1973) reported a significant increase in milk yield as the result of 14 generations of selction for postweaning average daily gain. Falconer (1953), Legates (1969), Frahm and Brown (1975) and others report a positive relationship between growth traits and maternal performance. Many studies also report reproductive failures or infertility, especially in the later generations of selection (MacArthur, 1949; Legates, 1969; Bradford, 1971; Falconer, 1973; LaSalle et al., 1947; and others). MacArthur, (1949) reported some physical differences in high and low lines selected for 60-day weight such as coat color and proportion of parts. He also found differences in temperment had developed, with the large lines more docile and less active and low lines wild and very excitable.

Poultry

Many experiments have been reported with chickens and turkeys concerning selection for body weight as increased body weight at a particular age is of great value to the turkey and broiler industries. Table II summarizes a few of these experiments. Just as in many mice selection experiments, selection for high-low lines result in asymmetrical responses (Maloney et al., 1963; Festing and Nordskog, 1967). Yamada

TABLE II

RESULTS OF SELECTION EXPERIMENTS IN CHICKENS OR TURKEYS

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Abplanalp *et al.* (1963) (turkeys)	+ 8 wk wt	7	8 wk wt	+33%	.43		Control line used; fair agreement with expected change.
			24 wk wt	+13%			
	+ 24 wk wt	5	8 wk wt	+21%	.62		
			24 wk wt	+27%			
	index (8 wk wt; 24 wk wt)	7	8 wk wt	+26%			
			24 wk wt	- 4%			
Festingand Nordskog (1967) (chickens)	+ 32 wk wt	8	32 wk wt		.34	+ egg weight - egg production	Control line used; other lines involved selected on egg wight or egg production; deviation of the high-low lines after 8 generations; asymmetrical response.
	- 32 wk wt	8	32 wk wt		.52	+ egg weight + egg production	
Maloney *et al.* (1963) (chickens)	+ 12 wk wt	10	12 wk wt	+51%	.34		Asymmetrical response; more response in high line.
			6 wk wt	+		0 to + egg wt	
	- 12 wk wt	10	12 wk wt	-27%	.07		
			6 wk wt	0		+ egg weight	

et al. (1958) reported a selection plateau was reached after ten years of selection for increased egg production in a closed population of White Leghorns, with most gains occuring the first five years and genetic variance decreasing rapidly during this time. Yamada also noted realized gains from selection were significantly less than predicted.

Sheep

Results of ten years of selection for net merit of inbred lines of range Rambouillets were reported by Terrill (1951). Overall merit of lambs, based on a weanling index increased, but improvement was less than expected from selection. Also, in spite of positive selection differentials for body weight and fleece weight, these two traits decreased slightly over the ten year period. No attempt was made however, to parition environmental and genetic effects.

Terrill (1958) also summarized the literature concerning fifty years of progress in sheep breeding, concluding definite gains had been made through selection and even more gains were possible. He noted an average gain in fleece weight of 1.5 pounds, a 2 to 10 percent increase in lamb survival and an increase in lamb slaughter weights during the first 50 years of this century, but realized some of these gains were partially due to improved feeding and management practices. Terrill also observed commercial producers of lamb and wool often seemed more aware of the importance of selection for production traits than purebred breeders and showring emphasis had played a major role in determining traits for selection with occasional emphasis on economically unimportant traits.

Responses to selection for weight per day of age to 170 days in Rambouillet and Romnelet sheep were reported by Vesely and Peters (1975) over a five year (two generations) period. Two methods were used to evaluate selection response; (1) difference of phenotypic regression and within sire regression to estimate one-half the genetic response and (2) repeat matings to monitor environmental trends. Pooling over breeds and methods, gain in weight per day of age was 8.15 g/generation and correlated responses in weaning weight and postweaning gain were 2 lb/generation and 1.15 lb/generation, respectively. Realized heritabilities for weight per day were .28 and .20 for Rambouillets and Romnelets, respectively.

Osman and Bradford (1965) investigated selection for 120 days weight in two environments on crossbred fine wool x long wool sheep. One environment was quite harsh and the other, favorable. New rams were used each year and over the five year period of selection, realized heritabilities of .18 and .22 were calculated for the harsh and good environments, respectively. Weaning weight means at both locations were very similar each year, but there was greater phenotypic variance for weaning weight in the favorable environment. Positive genetic correlations were reported for 120 day weight and 450 day weight or conformation score, while small, nonsignificant correlations were observed for 120 day weight and fleece traits.

Traits under selection in a study reported by Ebmeier (1977) were 180 day weight and yearling weight in Hampshire sheep. A control line was also maintained for this six year study. Realized heritabilities were .17 and .67 for 180 day weight and 365 day weight, respectively. Realized genetic correlations between yearling weight and birth weight, 70 day weight and 180 day weight were .64, 1.12 and 1.71, respectively, while 180 day weight and birth weight, 70 day weight and 365 day weight correlations were -.19, 1.94 and .64, respectively.

Pattie (1965a,b) investigated positive and negative selection for weaning weight for ten years in Merino sheep. Three flocks (one control line) of 100 ewes and five rams each were maintained. In the line selected for increased weaning weights, realized heritabilities were .18 for rams and .33 for ewes, while estimates in the low weaning weight line were .23 for rams and .22 for ewes. Also, realized heritabilities from divergence of these lines were reported (.19 for males, .31 for females). No significant correlations were observed between weaning weights and reproductive traits. The realized genetic correlation between weaning weight and 17 month weight (.72) indicates that selection for increased 17 month weight could be as effective for increasing weaning weight as direct selection for weaning weight.

Pattie (1965b) also reported milk production estimates on these ewes and correlations with growth traits of lambs. The oxytocin method of obtaining milk was employed, so fat, protein and total solids not fat content of the milk was also reported. Within group correlations were significant for lamb birth weight and milk volume, lamb growth and milk volume, pounds of protein or pounds of solids not fat and lamb weaning weight and milk volume; however, a small nonsignificant correlation was estimated between lamb growth and pounds of fat.

Swine

Craft (1958) summarized fifty years of progress in swine breeding. He noted major points of improvement: (1) hogs reached market weights of 200 to 220 lb two months younger, (2) feed required per 100 lb gain had decreased by 80 to 100 lb, (3) since 1924 there had been an increase of 1.6 pigs per litter at weaning and (4) improvement of hog carcasses with major emphasis on lean cuts. Craft, like Terrill (1958), pointed out that some of these gains were due to improved environment as well as selection.

Fredeen (1958) summarized selection studies done to that time in swine. Considering Danish field records of Landrace and Large White Swine from 1926 to 1956, Fredeen reported trends for increased carcass length, belly thickness and average daily gain and decreases in backfat and feed efficiency (lb feed/lb gain). Although improved environment may account for much of these trends, he noted the positive correlation of belly thickness and fat thickness, but trends increased belly thickness while fat decreased, so selection must have been at work. Fredeen concluded: (1) most selection studies done in swine were in relation to the development of inbred lines; (2) that most populations dealt with were small and selection was only for a short duration; (3) most studies lacked a control line, giving questionable precision to the estimation of genetic gain; and (4) selection was most effective on carcass traits, intermediate responses noted in rate and efficiency of growth and least effective selection for reproductive traits.

Table III presents results of several swine selection studies dealing with various growth traits. In general, most observed responses to selection were less than predicted. Dickerson and Grimes (1947) found selection for rate of gain was nearly as effective to improve feed efficiency as direct selection for feed efficiency and it was much easier to measure. Another interesting conclusion of Dickerson and Grimes was dams transmitting more economic gaining ability, provide poorer nutrition during the suckling period, thus neutralizing superiority for their transmitted influence.

TABLE III

RESULTS OF SELECTION EXPERIMENTS IN SWINE

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Cleveland (1978)	+ Index of ADG (56d to 175 lbs) and backfat	5	Index ADG Backfat	+5.8 units/gen +.031 lb/d/gen -.02 in/gen			Index = 100 + 286.6 ADG - 39.4 BF
Craig et al. (1956)	+ 180 day wt (or 154 day wt)	10	154 day wt birth wt 21 day wt 56 day wt 180 day wt birth wt 21 day wt 56 day wt	+1.5 lb/gen(+13%) 0 + + +2.8 lb/gen(+19%) 0 + +	.17(from divergence) .16(from divergence)		Selection criteria 1939-1941 on 180 day wt, 1942-43 on 150 day wt, 1944-49 on 154 day wt. Selection as effective in later generations as in first; Hampshire swine.
	- 180 day wt (or 154 day wt)	8	154 day wt birth wt 21 day wt 56 day wt 180 day wt birth wt 21 day wt 56 day wt	-5.0 lb/gen(-34%) 0 + + -4.1 lb/gen(-22%) 0 + +			
Dettmers et al. (1965)	- 140 day wt	10	birth weight 56 day wt 140 day wt	-14% -23% -29%	 .11 .41	0 litter size	Minature pigs for research purposes; predicted response over 11 years greater than actual, but last 7 years predicted and actual response similar; no indication of selection plateau.
Dettmers et al. (1971)	-140 day wt	17	140 day wt	-34%(in last 9 generations)	.67	+ litter size	Continuation of above study; produced response greater than actual; decrease in litter size may be attributable to inbreeding.

TABLE III (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Dickerson and Grimes (1974)	+ feed requirements (72d to 225 lb)	5	feed/100 lb gain ADG birth wt 72 day wt	+11.8 lb/gen — — —		+ days on feed	Line selected for decreased feed requirements visiably fatter, more active and excitable; Duroc swine.
	- feed requirements (72d to 225 lb)	5	feed/100 lb gain ADG birth wt 72 day wt	-8.6 lb/gen — — —		+ days on feed	
Fine and Winters (1953)	+154 day wt and + market score	7	154 day wt market score	+ 1% +7.5%	.20 .20		Minn. 1 and Minn. 2 swine; increase in inbreeding of 3.2%/yr; amount of selection not sufficient to affect inbreeding effects.
Freeden (1977)	+ gain birth to 200 lb	9	gain backfat	+1.32 lb/gen - .24 in/gen		- age at 200 lb - fat + index	Lacombe swine; control line used and replicate lines.
	- backfat at 200 lb	9	gain backfat	-3.52 lb/gen - .79 in/gen		- age at 200 lb - index	
	Index (of above 2 traits)	9	gain backfat	.6% -1.8%		- age at 200 lb	
Krider _et al_. (1946)	+ 180 day wt (or +150 day wt)	4	birth wt 21 day wt 56 day wt 150 day wt 180 day wt	+ 9% +16% -10% -13% - 9%	 .16 .19		Hampshire swine; selection on 180 day wt, 1939-1941 and on 150 day wt, 1942-1943; responses less than expected; selection was effective in changing mean level of performance between the lines; yearly effects a big influence.
	- 180 day wt (or -150 day wt)	4	birth wt 21 day wt 56 day wt 150 day wt 180 day wt	+ 1% +11% -26% -27% -25%			

TABLE III (Continued)

Reference	Selection criteria	Number of generations	Growth traits: Trait	Growth traits: Response (direct or correlated)	Realized h^2	Other correlated responses	Comments
Rahnefeld (1971)	+ postweaning ADG (42d to mkt wt)	7	postweaning ADG	+ 9%	.126	+ litter size	Lacombe swine response only 33% of predicted; control line of Yorks; no indication of decreased genetic variance.
Rahnefeld (1973)	+ postweaning ADG	9	weaning wt feed efficiency (lb feed/ 100 lb gain)	.07 lb/gen(+7%) 1.3 lb/gen(-1%)			Lacombe swine; response in weaning wt 3.1% of predicted, in feed efficiency 10% of predicted.
Rahnefeld and Garnett (1976)	+ postweaning ADG	11	postweaning ADG birth wt preweaning ADG weaning wt	.03 lb/d/gen 0 + +	.203		Lacombe swine; response 61% of predicted.
Garnett and Rahnefeld (1976)	+ postweaning ADG	11	postweaning ADG birth weight	+ 0		0 number born 0 number born alive 0 number weaned + preweaning mortality - gestation length	Companion paper of one above.

Results of Selection Experiments in Beef Cattle

There are probably more difficulties in carrying out selection experiments in beef cattle than any other livestock species because of longer generation intervals and the cost of maintaining the large populations necessary to reduce sampling errors and chance deviations in gene frequency. Because of time, land and monetary investment necessary to properly conduct a selection study, few such studies have been carried out in beef cattle. Also, for many years, beef cattle objectives were poorly defined or were constantly changing as dictated by the industry making it difficult to define experimental selection criteria. Consequently, many studies reported in the literature were not specifically designed to evaluate selection; however, in spite of all these problems, there are many reports that supply valuable information documenting changes due to selection. A summary of many of these studies is presented in Table IV.

Many studies investigated selection and inbreeding in combination (Brinks et al., 1961; Armstrong et al., 1965; Hornbeck and Bogart, 1966; Nwalakor et al., 1976; and others). Generally, these studies show that inbreeding has a detrimental effect on progress realized from selection. Nwalakor et al. (1976) estimated phenotypic and genetic trends in weaning weight of Hereford cattle as -.76 and +2.59 lb/yr, respectively, in inbred lines, but when adjusting for inbreeding effects, these trends increased to +.78 and +4.13 lb/yr, respectively. Inbreeding levels in this study ranged from 21.8 to 33.1 percent.

Other reports dealt with multiple trait selection or trends in herds with no particular selection criteria given (Armstrong et al., 1965; Flower et al., 1964; Vanmiddlesworth et al., 1979; and others). Progress

TABLE IV

RESULTS OF SELECTION EXPERIMENTS IN BEEF CATTLE

Reference	Selection criteria	Number of years	Number of calves	Breed[a]	Trait	Response[b]	Correlated responses	Realized h^2	Comments
Anderson et al.(1974)	+ Yrl wt	11		Sh	Yrl wt Yrl wt	+9.81 lb/yr bulls +6.17 lb/yr heifers	+ birth wt + postweaning ADG + wn wt 0 carcass traits	.50 bulls .39 heifers	Used control line; replicated at 2 locations primary genetic change in rate of postweaning gain to increased yrl wt.
Armstrong et al.(1965)	Multiple traits in inbred lines	17	785 inbred 77 control	He	Wn Wt Wn score Final grade Sizeable negative changes in all traits	+ .44 lb/yr + .02 units/yr + .05 units/yr	genetic and pheno- typic correlations + and high for most wn and post wn traits.		Inbreeding over 30%; + selection differential for all traits; strong + environmental trends; genetic trends - for all traits but feed efficiency.
Bailey et al.(1971)	+ Post wn gain	12	1488 (total in study)	He	Post wn gain Feed efficiency Yrl conf	+2.01 lb/yr + .51 /yr + .62 units/yr		.78	Replicated at two locations; generation interval 4.57 to 4.97 yr; average inbreeding 2%; response based on regression or dam birth yr.
	+ Feed efficiency (gain/TDN)	12			Post wn gain Feed efficiency Yrl conf	+ .34 lb/yr + .09 /yr + .06 units/yr		.52	
	+ Yrl conformation	12			Post wn gain Feed efficiency Yrl conf	- .13 lb/yr + .02 /yr - .05 units/yr		0	
Barlow et al.(1978)	+ Yrl gain (birth to yrl)	First generation results		An	Yrl gain		+ birth wt + pre wn gain + post wn gain + yrl wt		Used control line; all sires replaced each year; 56.4% of yrl wt response accounted for by changes in preweaning ADG; divergences for most measures of growth and skeletal sire significant; yrl wt divergence 44 lb.

TABLE IV (Continued)

Reference	Selection criteria	Number of years	Number of calves	Breed[a]	Trait	Response[b]	Correlated responses	Realized h^2	Comments
Benson et al.(1972)	Index (+ yrl wt per day of age; - backfat per CWT) equally weighed in standard measure	8	387 (from carcass lines)	He	Birth wt	+ .24 ; -1.26 lb/yr			Environmental trends est. by repeat matings; magnitude of responses usually greater than anticipated.
					Wn wt	-2.98 ; +3.06 lb/yr			
					Final wt ( )	+16.34 ; +46.85 lb/yr			
					Yrl wt/day of age ( )	+ .04 ; + .03 lb/yr			
					Fat thickness ( )	+ .03 ; + .01 in/yr			
					Yrl wt ( )	+ .35 ; -6.64 lb/yr			
					550 day wt ( )	+1.26 ; -1.87 lb/yr			
Brinks et al. (1961 & 1965)	+ Weights and gain + gain with some emphasis on conformation in closed lines	25	2027	He	Birth wt	.38 ; .37 lb/yr		–	Generation interval 4.93 yr; responses as large or larger than expected from selection; environmental trends est. by repeat matings; increased inbreeding detrimental effect on all traits studied.
					Wn wt	2.4 ; 1.2 lb/yr			
					Feed test gain	—— ; .81 lb/yr			
					Large + phenotypic response in all traits except post wn gain for heifers				
Chapman et al. (1969 & 1972)	+ Wn wt	7		Polled He	Birth wt	+.24 lb/yr		.33	Control line used; generation interval 5.4 yr; no selection in females; no partitioning of genetic and environmental trends; wn wt and ADG lines consistently outperformed type line.
					Wn wt	-8.3 lb/yr			
					Wn score	+ .01 units/yr			
					Gain to wn	-9.0 lb/yr			
	+ Post wn gain	7			Birth wt	+1.06 lb/yr		.54	
					Wn wt	-13.4 lb/yr			
					Wn score	+ .10 units/yr			
					Gain to wn	-14.3 lb/yr			
	+ Yrl type score	7			Birth wt	+1.19 lb/yr			
					Wn wt	-6.2 lb/yr			
					Wn score	+ .15 units/yr			
					Gain to wn	-7.6 lb/yr			
Chevraux & Bailey (1977)	+ post wn growth rate (closed line) on 140 day test	19	414 records to wn 390 records to yrl	He	Wn wt	+7.23 lb/yr	+ feed efficiency (gain/TDN)		Continuation of study reported by Bailey et al. (1971); 3.24 generations of selection; inbreeding increased from 1.5% in 1956 to 18.1% in 1974 calves.
					Post wn gain	+9.53 lb/yr		.35	

TABLE IV (Continued)

Reference	Selection criteria	Number of years	Number of calves	Breed[a]	Trait	Response[b]	Correlated responses	Realized h^2	Comments
Fahmy and Lelande (1973)	+ Pre wn gain			Sh	Birth wt Wn wt	—; .24 lb/yr —; 1.06 lb/yr			Used maternal and paternal half sib differences between years to adjust for environmental trends.
Flower et al.(1964)	Multiple trait plus progeny test	8	550	He	Birth wt Wn wt	-1.04 ; .64 lb/yr -4.9 ; 4.9 lb/yr			4.03 yr generation interval; used repeat matings to est. environmental trends.
Koch et al. (1974a & 1974b)	+ Wn wt (WWL)	10	2956	He	Birth wt Wn wt Yrl wt (bulls) Yrl wt (heifers)	+ .88 lb/yr +1.1 lb/yr -3.5 lb/yr +7.9 lb/yr	+ correlations in all traits in all lines except muscling score in WWL		Generation interval 4.6 yr; bulls used as 2 yr olds; ave. annual selection differential WWL + 9 lb, YWL + 16 lb, IL + 12.5 lb and + .5 units.
	+ Yrl wt (YWL)	10			Birth wt Wn wt Yrl wt (bulls) Yrl wt (heifers)	+ .88 lb/yr + .9 lb/yr -6.8 lb/yr +6.4 lb/yr			
	Index (+ Yrl wt and + muscling score) (IL)	10			Birth wt Wn wt Yrl wt (bulls) Yrl wt (heifers)	+1.10 lb/yr +1.1 lb/yr -4.6 lb/yr +10.1 lb/yr			
Koch (1978)	+ Wn wt + Yrl wt or index (of + yrl wt and + muscling score)	8	377 heifers (random sample from the 3 lines)	He			+ age adj. rate of gain + % wt adj retail product + % bone - fat trim % + carcass wt + rib eye area + fat thickness - marbling		Heifers fed for 252 days post wn.

TABLE IV (Continued)

Reference	Selection criteria	Number of years	Number of calves	Breed[a]	Trait	Response[b]	Correlated responses	Realized h^2	Comments
Nelms and Stratton (1967)	+ Wt at end of 168 day post wn feed test	12		He	Birth wt 180 day wt Post wn ADG Final wt	+.66 lb/yr +1.5 lb/yr +.02 lb/day/yr +5.6 lb/yr			Generation interval 4.29 yr; average inbreeding 11%; actual gains for 180 day wt, ADG and final wt less than expected; annual selection differental for final wt 13 lb; no est of genetic trends.
Newman et al.(1973)	+ Yrl wt	10		Sh	Yrl wt (bulls) Yrl wt (heifers)	+25.7 ; +9.8 lb/yr +18.4 ; +6.2 lb/yr		.50 .39	Used control line; accumulated annual selection differential last 6 yr 25.6 lb for bulls and 18.4 lb for heifers; cattle at two locations.
Nwalakor et al.(1976)	Inbred and line crosses selected on age and weight	26	1534 inbred 1874 line crosses	He	Wn wt (inbred) Wn wt (inbred adj for inbreeding) Wn wt (line crosses)	–.76 ; +2.59 lb/yr +.78 ; +4.13 lb/yr +1.27 ; +4.62 lb/yr			Inbreeding to 33.1% in calves and 21.8% in dams; environmental trends est. from repeat matings; most improvement last 2/3 of the study.
Scarsi et al. (1973)	4 inbred and 2 single trait selection lines; growth rate or conformation for each breed and one He line on index of type and conformation	17		An He Sh	Wn wt Wn wt (inbred lines)	range —; -2.6 to +5.0 lb/yr range —; -6.3 to +3.7 lb/yr			Environmental trends by adding and accumulating deviations between consecutive yr to base yr; all selection lines except the type line showed + phenotypic and genetic changes for wn wt.
Stanforth (1974)	+ Wn wt (WWL) + Yrl wt (YWL)	9 9	827	He	Wn wt Yrl wt Wn wt Yrl wt	+8.3 lb/yr +10.1 lb/yr +7.6 lb/yr +15.4 lb/yr	+ birth wt + post wn ADG + wn conformation	.43 .53	Earlier report of data in present study; generation interval 4.07 yr; cumulative selection differentials WWL + 98.2 lb, YWL 196.4 lb.

TABLE IV (Continued)

Reference	Selection criteria	Number of years	Number of calves	Breed[a]	Trait	Response[b]	Correlated responses	Realized h^2	Comments
Vanmiddlesworth et al. (1979)	No particular selection criteria given		2415	An	Birth wt	+ .02 ; - .07 lb/yr			Trends of the cattle raised at the experiment station; environmental trends est. by repeat sure method.
					120 day wt	+ .66 ; +1.08 lb/yr			
					205 day wt	+ .84 ; + .24 lb/yr			
					240 day wt	+1.39 ; - .90 lb/yr			
					360 day wt	+4.81 ; +1.28 lb/yr			
Willms et al.(1980)	+ Growth	15 to 20		He	Pre wn ADG (He)	—; +.007 lb/day/yr			Environmental trends est. by repeat matings; no selection in females; environmental trends +; more progress in synthetic lines.
				Beef	Wn wt (He)	—; +.22 lb/yr			
				Synthetic	Post wn ADG (H	—; +.003 lb/day/yr			
				(BS)	Yrl wt (He)	—; +2.87 lb/yr			
				Dairy	18 mo wt (He)	—; -10.1 lb/yr			
				Synthetic	Pre wn ADG (BS)	—; +.017 lb/day/yr			
				(DS)	Wn wt (BS)	—; _1.98 lb/yr			
					Post wn ADG (BS)	—; +.057 lb/day/yr			
					Yrl wt (BS)	—; +14.8 lb/yr			
					18 mo wt (BS)	—; -9.3 lb/yr			
					Pre wn ADG (DS)	—; +.020 lb/day/yr			
					Wn wt (DS)	—; +2.87 lb/yr			
					Post wn ADG (DS)	—; +.048 lb/day/yr			
					Yrl wt (DS)	—; +15.0 lb/yr			
					18 mo wt (DS)	—; -8.8 lb/yr			

[a]He = Hereford, An = Angus and Sh = Shorthorn.

[b]First listing or only listing is phenotypic trends; second listing or listing following "—;" is genetic trend.

in many growth traits was realized through selection, although selection criteria was not clearly defined or constant, indicating positive genetic correlations between many economically important traits in beef cattle.

In studies where genetic trends are estimated, the majority have used the repeat matings technique to estimate environmental trends (Brinks et al., 1961; Flower et al., 1964; Benson et al., 1972; Willms et al., 1980; and others). Fahmy and Lalande (1973) estimated environmental effects by using maternal and paternal half sib differences between years while Scarsi et al. (1973) added accumulating deviations between consecutive years to the base year as an estimate of environmental trend. Few studies have maintained a control line to moniter environmental flucuations (Newman et al., 1973; Anderson et al., 1974; and Barlow et al., 1978).

Some studies specifically designed to estimate response to selection for various growth traits merit further discussion. Brinks et al. (1961 and 1965) evaluated changes in closed lines of Hereford cattle over a 26 year period. Selection was for increased weights and gains with some emphasis on conformation. Large, positive phenotypic responses were observed in all traits except postweaning gain in heifers. Both genetic and phenotypic trends were as large or larger than anticipated response based on parameter estimates and indexes. Selection pressure was much greater on the sire side (top 18% of the population selected) than the dam side (top 89% selected). Selection indexes in retrospect were calculated as follows for sires (I_S) and dams (I_D), respectively: I_S = .21 birth weight + .13 weaning weight + .26 weaning score + 1.20 final weight and I_D = .01 birth weight + .14 weaning weight + .11 weaning score - .16 yearling weight + .39 18-month weight + .08 18-month score - .11 mature fall weight + .03 producing ability.

Newman et al. (1973) and Anderson et al. (1974) based selection solely on yearling weight for 10 years in two replicate herds of Shorthorn cattle from 1958 to 1969. Cumulative selection differentials were calculated by adding the mean cumulative selection differential of all parents of a contemporary group to an individual's own deviation from that group in contrast to the method used by Pattie (1965) in which the average of the individual's parents selection differential was added to the individual's deviation. Mean cumulative selection differentials realized through the 10 years of the study were 150.7 and 127.7 lb for sires and dams, respectively. Positive genetic increases were observed in yearling weight; however, although appreciable, these genetic increases only accounted for 40-45% of the total phenotypic increase in yearling weight. There were significant, positive correlated responses in birth weight and postweaning gain. Response in weaning weight, although not significant, was also positive.

Koch et al. (1974a,b) summarized the first 10 years of selection in three lines of Hereford cattle (150 cows and 6 sires per line) selected for weaning weight (WWL), yearling weight (YWL) or an index of yearling weight and muscling score (IL). Buchanan (1979), working with the same study, presented results through 1977 after 17 years or 3.7 generations of selection. Bulls were used first at two years of age and remained in service for three years. Selection intensity was quantified (1) as average annual selection differentials and (2) as accumulated selection differentials. Comparisons of actual with potential selection differentials (Koch et al., 1974a,b) showed from 77 to 97% of potential selection opportunity realized in bulls and 50 to 71% achieved in heifers, while Buchanan's (1979) estimates increased to 86 to 95% in bulls and

62 to 74% in heifers with the additional seven years of selection. Buchanan (1979) also reported sire (I_S) and dam (I_D) indexes in retrospect with their selection differentials per generation (ΔI) in standard measure. In the three lines, indexes were as follows:

I_S(WWL): ΔI = .22 birth weight + .65 weaning weight + .32 yearling weight + .01 muscle score = 1.65

I_D(WWL): ΔI = .09 birth weight + .84 weaning weight + .12 yearling weight + .07 muscle score = .44

I_S(YWL): ΔI = .07 birth weight - .05 weaning weight + 1.00 yearling weight - .01 muscle score = 1.80

I_D(YWL): ΔI = .17 birth weight + .26 weaning weight + .68 yearling weight + .10 muscle score = .34

I_S(IL): ΔI = .16 birth weight + .15 weaning weight + .40 yearling weight + .62 muscle score = 1.85

I_D(IL): ΔI = .21 birth weight + .09 weaning weight + .77 yearling weight + .13 muscle score = .43

Response to selection was estimated by five methods: expected genetic change based on paternal half-sib analysis of covariance, intra-year regression on generation coefficient, intra-year regression of progeny on midparent cumulative selection differentials and expected genetic change based on both intra-line and inter-line regressions of offspring on midparent in an unselected population. Average estimated response (over methods and in standard deviation units per generation) in WWL, YWL and IL were, respectively: .23, .17 and .15 in weaning weight; .36, .43 and .33 in yearling weight and -.03, .01 and .24 in muscling score for the first 10 years. Buchanan (1979) reported average estimated responses (in standard measure per generation) for WWL, YWL and IL as: .19, .22 and .15 for birth weight; .17, -.03 and .30 for weaning weight; .13, -.06 and .26 for preweaning gain; .42, .13 and .19 for postweaning gain; -.07, -.29 and .00 for muscle score and .29, -.06 and .37 for yearling weight, respectively.

Stanforth (1974) in preliminary analyses of selection lines that are the subject of this dissertation, quantified selection pressure and estimated response to selection in two lines of Hereford cattle selected for weaning weight (WWL) or yearling weight (YWL) from 1964 to 1973. Generation intervals averaged 4.09 and 4.06 years in WWL and YWL, respectively. By 1973, an average of 1.98 and 2.12 generations of selection had been practiced in the two lines, respectively. Cumulative selection differentials to that time were 98.2 lb for weaning weight in WWL and 196.4 lb for yearling weight in YWL. Male cumulative selection differentials accounted for 80% of total midparent cumulative selection differential for weaning weight in WWL and for 83% of total midparent cumulative selection differential for yearling weight in YWL. Progeny test data indicated sires from the 1970 calf crop had breeding values for weaning weight and yearling weight that were 58 and 108 lb, respectively, superior to breeding values of foundation sires. In YWL, breeding value of new sires were superior to breeding values of repeat sires for all traits except birth weight, while in WWL, breeding values of new sires were generally inferior to breeding values of repeat sires.

Genetic Parameters in Beef Cattle

Estimates of heritability and correlations are numerous in the literature. Workers at Texas A & M University have summarized these statistics for beef cattle (Woldehawariate *et al*., 1977) and Tables V and VI are constructed from information reported in that publication. Averages (and ranges) of heritability estimates for the ten traits are: birth weight .45(-.29 to .94); preweaning average daily gain .30(-.34 to .63); weaning weight .24(-.06 to .71); weaning conformation score

TABLE V

SUMMARY OF HERITABILITY ESTIMATES FOR GROWTH AND CONFORMATION TRAITS IN BEEF CATTLE (Woldehawarite et al., 1977)

Trait	Unweighted $\bar{X}$		Regression unweighted $\bar{X}$		Regression weighted $\bar{X}$		Paternal half sib[a] unweighted $\bar{X}$		Paternal half sib weighted $\bar{X}$			Weighted regression and weighted paternal half sib[b]
	No.	h^2	No.	h^2	No.	h^2	No.	h^2	No.	ANO[c]	h^2	
Birth wt	84	.39	7	.38	7	.42	68	.40	68	18	.45	.45
Preweaning ADG	70	.25	8	.04	8	.06	54	.28	54	15	.33	.30
Weaning wt	103	.31	11	.31	11	.13	72	.32	72	16	.26	.24
Weaning conf. score	61	.35	11	.25	11	.24	41	.38	41	14	.42	.38
Feedlot gain	44	.45	7	.53	7	.47	36	.44	36	9	.32	.34
Pasture gain	18	.34	4	.26	4	.21	10	.36	10	15	.34	.30
Final feedlot wt	37	.47	8	.46	8	.44	28	.47	28	9	.47	.46
Yearling pasture wt	21	.39	1	.43	—	—	18	.38	18	14	.44	.44
Final feedlot conf. score	18	.35	4	.22	4	.18	12	.45	12	NA[d]	.46	.36
Yearling pasture conf. score	15	.28	3	.15	3	.16	9	.32	9	11	.34	.30

[a] Average estimate used as appropriate.

[b] Weighted by number of offspring estimated per method.

[c] Average number of offspring per sire.

[d] Not available

TABLE VI

SUMMARY OF CORRELATION ESTIMATES BETWEEN VARIOUS TRAITS IN BEEF CATTLE
(Woldenhawariate *et al.*, 1977)

Traits	No. of studies	Overall average[a]		Weighted average[b]		
		r_p	r_g	ANO[c]	r_p	r_g
Birth wt - preweaning ADG	21	.23	.33	20	.23	.34
- weaning wt	26	.37	.55	21	.38	.54
- wn conformation	13	.10	-.06	17	.15	.33
- wn condition	3	.12	-.37	21	.12	-.37
- feedlot gain	9	.30	.48	NA[d]	.28	.51
- final feedlot wt	13	.44	.62	12	.43	.60
- feedlot conformation	2	.16	.12	NA[d]	.15	.07
- feedlot condition	1	.15	1.10			
- pasture gain	1	.17	.43			
- final pasture wt	2	.58	.67	NA[d]	.49	.63
- pasture conformation	1	.17	.23			
Preweaning ADG - weaning wt	21	.97	.95	17	.98	.99
- wn conformation	13	.39	.41	22	.34	.35
- wn condition	3	.48	.86	18	.47	.88
- feedlot gain	8	.13	.18	NA[d]	.12	.22
- final feedlot wt	8	.68	.65	NA[d]	.69	.67
- feedlot conformation	1	.39	1.29			
- feedlot condition	1	.32	.86			
- pasture gain	1	.13	.49			
- final pasture wt	2	.66	.74	NA[d]	.64	.72
- pasture conformation	1	.23	-.04			
Weaning wt - wn conformation	23	.37	.17	13	.40	.24
- wn condition	16	.16	.42	11	.16	.32
- feedlot gain	18	.68	.73	11	.70	.71
- final feedlot wt	6	.23	.16	NA[d]	.20	.12
- feedlot conformation	7	.05	.02	14	.20	-.06

TABLE VI (Continued)

Traits	No. of studies	Overall average[a]		Weighted average[b]		
		r_p	r_g	ANO[c]	r_p	r_g
- pasture gain	5	.51	.46	12	.64	.67
- pasture conformation	11	.15	-.07	9	.20	.02
Wn conformation - feedlot gain	7	-.01	.11	NA[d]	.00	.17
- final feedlot wt	7	.29	.28	NA[d]	.30	.33
- feedlot conformation	5	.42	.64	NA[d]	.40	.68
- pasture gain	6	-.13	-.05	12	-.13	-.02
- final pasture wt	6	.13	-.08	10	.21	-.03
- pasture conformation	8	.39	.57	14	.35	.56
Feedlot gain - final feedlot wt	17	.72	.78	11	.74	.82
- feedlot conformation	5	.39	.33	NA[d]	.40	.34
Final feedlot wt - feedlot conformation	6	.37	.25	NA[d]	.41	.34
Pasture gain - final pasture wt	4	.61	.83	13	.63	.81
- pasture conformation	6	.18	.15	10	.24	.27
Final pasture wt - pasture conformation	6	.28	.08	10	.40	.30

[a] Average over studies.

[b] Average taking number of offspring per study into consideration.

[c] ANO = average number of offspring per sire.

[d] NA = estimate not available.

.38(.00 to .71); feedlot gain .38(-.08 to .88); final feedlot weight .46(.03 to .92); feedlot conformation score .36(.07 to .92); pasture gain .30(.08 to .57); pasture yearling weight .44(.04 to .83; and pasture conformation score .30(.00 to .85). Table V summarizes heritabilty estimates of the above ten traits by various methods. Because of the number of correlations among these ten traits, average phenotypic and genetic correlations are reported in Table VI.

In general, available information indicates few antagonistic genetic relationships between economically important traits. Mostly positive genetic correlations are reported between growth rates at various stages, growth rate and feed efficiency, growth and carcass traits and between growth rate and mature size. However, not all of these relationships are favorable, for example increased calving difficulty is associated with heavy birth weights and feed requirements increase as cow size increases.

Maternal Influences on Growth

Growth of a calf from birth to weaning is influenced by its own genotype for growth plus the environment it is raised in. The environmental component is complicated by maternal environment supplied by the dam. Maternal effects exist, either as maternal genetic or permanent environmental variances, so knowledge of the genetics of maternal effects is necessary when evaluating responses to selection for traits such as weaning weight.

Koch and Clark (1955) reported the phenotypic correlations between dams weaning weight and weaning weights of her progeny, and progeny preweaning average daily gains as .06 and .03, respectively. Boston et al. (1975)

found similar correlations in analyzing 2030 Angus and 548 Hereford records of .15 to .20 for dam weaning weight and mean progeny weaning weight. Kress and Burfening (1972) reported the correlation in Hereford cows between cow 180-day weight and MPPA as .15, while Christian et al. (1965) found a .07 phenotypic correlation between dam weaning weight and progeny weaning weight. All are small, but positive correlations.

Willham (1972) developed and discussed formulas evaluating the fraction of the selection differential realized if various genetic components are included. If direct (G), maternal (Gm) and phenotypic (P) effects are included, the fraction realized if selection is based on calf phenotype is (Var(G) + 3/2 Cov(GGm) + 1/2 Var(Gm))/Var(P). Including grandmaternal effects (Gn), the fraction becomes (Var(G) + 2/3 Cov(GGM) + 5/4 Cov(GGn) + 1/2 Var(Gm) + 3/4 Cov(GmGn) + 1/4 Var(Gn))/ Var(P). From these formulas, selection for traits effected by maternal and grandmaternal components can be increased if the associated covariance terms are positive. However, the literature generally reports negative covariances between direct and maternal genetic effects.

It has been hypothesized that there is an alternating generation phenomena for weaning weight in beef cattle. Heifers raised by heavy milking dams are detrimentally effected by this good nutrition and in turn supply poor maternal environments to their calves; however, heifers of this second generation raised under poorer milking conditions of their dams produce heavier calves at weaning; thus the alternating generation effect. The basis of this hypothesis is suggested by reported genetic antagonism between calves preweaning performances and maternal effects. Christian et al. (1965) reported negative correlations between dam weaning weight and milk production (-.10 to -.20) and butterfat production

(-.18 to -.27).

Negative covariances between direct genetic and maternal genetic effects for many preweaning traits have been reported in the literature. Vesely and Robison (1971) reported negative covariances between direct and maternal effects for weaning weight, weaning type score and birth weight in 1962 Hereford cattle. Koch and Clark (1955) found negative correlations (-.65 to -.68) between direct and maternal effects on preweaning gain and Deese and Koger (1967) reported a near zero covariance between direct and maternal effects in purebred Brahman cattle, but it was negative and contributing 30% of the total variance in Brahman-Shorthorn crosses.

A negative correlation (-.28) between direct and maternal effects for weaning weight in Hereford cattle was found by Hohenboken and Brinks (1971). Brown et al. (1978) in an extensive analyses of 3220 Angus records, included grandmaternal effects in their model. Genetic correlations between direct and maternal effects were -.51 for birth weight and -.26 for weaning weight. The correlations for the two traits between direct and grandmaternal effects were .93 and -.12, while direct-maternal environmental correlations were .14 and -.55 for birth weight and weaning weight, respectively. Brown et al. (1978) suggested an alternate generation phenomena because of the pattern of negative covariances for direct-maternal effects and maternal-grandmaternal effects coupled with positive covariances for direct-grandmaternal effects.

According to Koch's (1972) review article, available estimates of genetic correlation between maternal environment and individual growth potential for weaning weight are all negative, averaging -.50 and direct-maternal correlations for preweaning gain are also negative. Kress et al. (1979), from 13,682 records on Simmental sired calves, reported the correlation of direct-maternal effects for weaning weight as -.68. This would reduce the portion of the selection differential realized by 56% when selecting for weaning weight.

Mangus and Brinks (1971) divided Hereford heifers into three groups based on their own weaning weight and then studied these heifers' progeny, grand progeny and great grand progeny. The high group's calves were lowest in weaning weight, grand offspring again highest and last generation back to being the lightest at weaning, again indicating high preweaning nutritional levels have detrimental effects upon cow productivity. The medium weight group did not change appreciably through the three generations while the low group came nearly to the level of the medium group in generation two and remained relatively constant in generation three. These workers also reported heifers out of two-year-old cows subsequently produced heavier calves at weaning than heifers out of mature cows, indicating lower levels of milk from young dams that are genetically superior for milking ability are beneficial to future productivity of heifers they produce at a young age. They also conclude that the low correlation of heifer's weaning weight and her subsequent productivity indicates heifer weaning weight is a poor criteria for selection to improve cow productivity.

Van Vleck et al. (1977) looked at theoretical responses to selection for weaning weight by various methods and derived formulas to estimate response. Their results suggested that if the antagonism between direct and maternal effects is genetic, long term response to selection for weaning weight can be enhanced by selecting bulls for direct genetic values and selecting heifers for maternal values, using performance of other relatives as aids to selection.

The literature supports the idea of a negative covariance between direct and maternal effects for preweaning growth in beef cattle. If these estimates are real, they decrease the effectiveness of selection for progeny weaning weight when using dam weaning weight as the selection criteria.

Summary of Literature Review

Evidence accumulated to date in laboratory and livestock species indicates differences among animals in most economically important traits, especially growth traits, are, to a considerable extent, genetic and selection for these traits would be expected to be effective in improving net merit of these species. Selection experiments have demonstrated reasonably rapid response for traits of moderate to high heritability in laboratory species and poultry, and varying degrees of response in swine and cattle. The majority of selection studies with cattle have relied on time trends to partition genetic and environmental components, with very few utilizing control lines.

Studies with beef cattle, in general, have shown:

(1) Favorable relationships between pre- and postweaning traits, making correlated responses possible and indicating various selection schemes can be effective in improving net performance. However, some correlated responses such as increased birth weights and mature weights may not be desirable.

(2) Generation intervals range from 4.03 to 5.40 years.

(3) Positive selection pressure can be achieved for measures of pre- and postweaning traits.

(4) Genetic changes per unit of time are not large,

> but positive response can be realized and because of the cumulative effect of selection, these changes can be substantial over a period of time.

Evidence indicates selection can be an effective tool in improving performance of beef cattle.

CHAPTER III

MATERALS AND METHODS

The Cattle

Data used in this study were collected from 1964 to 1979 as part of the beef cattle breeding project (1256) at the Oklahoma Agricultural Experiment Station. Performance records of 1273 purebred Hereford calves, 239 selected Hereford cows and 57 selected Hereford bulls were analyzed. In addition, records of 723 purebred Angus calves, 126 Angus cows and 31 Angus bulls were also analyzed from an unselected control line. Project 1256 was initiated at the Southwest Livestock and Forage Research Station in the early 1960's to measure direct and correlated response to selection for weaning and yearling weight in Hereford and Angus cattle. Foundation animals were assembled in 1960 and cows were randomly allocated to lines for the 1963 breeding season. Foundation females originated from several herds in the southwestern and midwestern United States. Hereford foundation cows originated from 16 sires, while Angus females were progeny of 30 sires. Foundation sires of each breed came from several sources with 10 sires representing Herefords and 25 sires representing Angus. These foundation sires were used from 1963 through 1966 in the Angus lines. In these breeding seasons, foundation sires were bred to cows from all selection lines within a breed. All lines were closed prior to 1967 and 1968 for Hereford and Angus lines, respectively, with all breeding stock selected on an intraline basis. The design of the selection project is given in Table VII. Since only data from the two Hereford lines and Angus control line were utilized in this study, the remainder of discussion will deal specifically with only these lines; however, general procedures were similar for all lines, regardless of breed.

Replacement breeding animals were selected on the basis of heaviest individual 205-day weaning weight in one line (WWL) and heaviest individual 365-day (bulls) or 425-day (heifers) yearling weights in the other line (YWL). Tables VIII and IX present number of calves with preweaning and postweaning records for WWL and YWL, respectively, along with actual number of selected individuals on an annual basis. An animal was considered "selected" if it produced at least one offspring in the selection line.

Each year two bulls were selected from each Hereford line along with an alternate based upon the respective selection criterian. Selected bulls were used two years, then discarded. Thus, four bulls were used per line per year, two being used for the first time and the other two being used for their second year. Bulls were used first as two-year-olds through the 1970 breeding season and as yearlings in subsequent years. No Hereford bulls were selected from the 1969 calf crop because of this procedure change to the use of yearling bulls. The only time an alternate Hereford bull was used occured during the 1972 breeding season in the YWL. Three bulls from WWL and YWL were selected from the 1976 and 1977 calf crops, so that an independent comparison between the lines could be made. The 1979 calf crop was produced by randomly mating these selected bulls to a group of Angus cows. Over the 15 year period, 28 and 29 Hereford bulls were selected from the WWL and YWL, respectively and used in these lines.

TABLE VII

DESIGN OF THE BEEF CATTLE SELECTION EXPERIMENT

Line	WWL	YWL	WWL	YWL	CL[b]	WWL
Breed[a]	H	H	A	A	A	A
Number cows per line	50	50	50	50	50	50
Trait selected:						
weight at specified age	205	365	205	365	-	205
selection criteria[c]	I	I	I	I	-	I/P[d]
Number of bulls selected per year	2	2	2	2	2	5/2[d]
Number of years bulls used	2	2	2	2	2	2
Number of heifers selected per year	10	10	10	10	10	10

[a]H = Hereford, A = Angus.

[b]Unselected control line.

[c]I = individual, P = progeny.

[d]Top five bulls selected on individual performance and two were subsequently selected on progeny performance.

TABLE VIII

NUMBER OF CALVES WITH PREWEANING AND POSTWEANING RECORDS AND NUMBER SELECTED IN THE WEANING WEIGHT LINE (WWL)

Year	Preweaning		Postweaning		Selected	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	11	13	10	13	2	6
1965	25	24	25	24	2	7
1966	28	16	18	11	2	8
1967	20	22	18	21	2	12
1968	22	23	21	23	2	10
1969	24	19	18	18	0	10
1970	23	26	21	26	2	10
1971	16	27	15	26	2	8
1972	24	20	21	20	2	9
1973	18	20	14	20	2	9
1974	19	20	16	19	2	11
1975	25	20	24	20	2	10
1976	17	27	16	27	3	5
1977	24	19	20	18	3	—
1978	11	24	11	23	—	—
Total	307	320	268	309	28	115

TABLE IX

NUMBER OF CALVES WITH PREWEANING AND POSTWEANING RECORDS AND NUMBER SELECTED IN THE YEARLING WEIGHT LINE (YWL)

Year	Preweaning		Postweaning		Selected	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	16	10	16	10	2	7
1965	22	25	20	25	2	7
1966	25	20	17	14	2	13
1967	25	20	25	19	2	10
1968	27	19	24	19	3	9
1969	23	21	23	20	0	9
1970	23	24	20	24	2	10
1971	22	25	22	25	2	10
1972	23	21	21	20	2	10
1973	16	20	15	20	2	10
1974	19	26	18	25	2	11
1975	18	24	17	24	2	10
1976	22	22	16	21	3	8
1977	32	13	29	13	3	—
1978	18	24	18	24	—	—
Total	331	314	301	304	29	124

Thirteen top ranking heifers based on the respective selection criteria were retained from WWL and YWL each year and bred as yearlings to calve as two-year-olds. All heifers were pregnancy checked after breeding season and on the average, the ten highest ranking pregnant heifers were selected to replace cows culled in each line. Fifty breeding age females were maintained per line. Cows were culled by the following criteria: (1) serious unsoundness, (2) open two years in a row and (3) oldest age. No Hereford heifers were selected from the 1977 or 1978 calf crops as the selection project was being terminated. A total of 115 and 124 heifers were selected in the WWL and YWL, respectively, during this study.

The first selections in the Hereford lines were made from the 1964 calf crop. The first calves produced by selected heifers were born in 1966 and selected bulls first sired calves in the 1967 calf crop.

Table X presents number of calves with preweaning and postweaning records, as well as numbers of replacement cattle for the control line (CL). Originally the Angus CL was designed as a progeny test line, where heifers were selected that excelled in yearling weight and five bulls selected on yearling weight performance, then each randomly mated to 25 Angus cows in a progeny test herd maintained at Stillwater. The top two bulls were then selected on the basis of progeny yearling performance to sire calves in the selection lines.

The Hereford and Angus selection lines were designed to start at the same time; however, detection of the dwarf gene in many of the Angus foundation cattle caused some delay in the initiation of the Angus lines. All cattle tracing back to this gene were removed from selection lines and 1964 was used as a foundation year for the Angus lines. First

TABLE X

NUMBER OF CALVES WITH PREWEANING AND POSTWEANING RECORDS AND NUMBER SELECTED IN THE CONTROL LINE (CL)

Year	Preweaning Bulls	Preweaning Heifers	Postweaning Bulls	Postweaning Heifers	Selected Bulls	Selected Heifers
1964	11	18	10	18	1	12
1965	20	22	20	22	5	10
1966	18	25	14	15	2	8
1967	25	21	24	15	—	10
1968	31	17	31	17	—	10
1969	25	14	25	14	2	10
1970	26	25	24	25	2	4
1971	28	17	28	17	3	7
1972	21	25	21	24	2	10
1973	23	23	22	23	2	10
1974	29	16	29	16	2	10
1975	26	22	23	21	2	10
1976	28	19	25	18	2	9
1977	33	15	33	15	2	6
1978	25	19	25	17	4	—
Total	369	298	354	277	31	126

selections in the Angus lines were made from the 1965 calf crop.

In 1969, the decision was made to convert this Angus progeny test line to an unselected control line to monitor yearly environmental fluctuations. Up to this time only two calf crops, 1968 and 1969, had been sired by progeny tested bulls, so very little selection had actually occured. Angus cows were artifically inseminated with semen collected from Angus foundation sires and two clean-up bulls were used with near zero selection differentials for both weaning and yearling weight. Because of the formation of the CL, only two bulls were used from the 1966 calf crop and no bulls from the 1967 and 1968 calf crops. In addition, foundation cows were retained in the line as long as possible, thus fewer heifer replacements were kept from the 1970 and 1971 calf crops.

From the 1970 calf crop on, bulls and heifers were selected to have, on the average, zero selection differentials for both weaning and yearling weights. Each year, as previously described for the Hereford lines, four bulls were used. Thirteen heifers were retained and up to ten used as replacements to maintain 50 cows in the CL. The same cow culling procedure was used in the CL as used in the Hereford WWL and YWL. Over the 15 year period, 31 bulls and 126 heifers were used as replacements in the CL.

Management and Data Collection

Selection lines were maintained at the Southwestern Livestock and Forage Research Station at El Reno, OK. All lines were managed as a single herd except during the breeding season and when forage availability prohibited doing such. Every effort was made to insure as uniform an environment as possible for all cattle. Cattle were pastured on native range typical of central Oklahoma during most of the year. In winter, the cow herd was maintained on native winter range, wheat pasture and milo stubble, as available and supplemented with prairie hay, alfalfa and cottonseed cake as necessary.

Breeding females were allocated to sires within lines by stratified randomization to obtain equal distribution of cow age groups within sires. Matings between closely related individuals were avoided to minimize inbreeding. Breeding season started May 1 of each year and lasted for 90 days through 1968, then was reduced to 60 days for the remaining years of the study. Calves were born in the spring, mostly in February and March. All calves were ear tagged, tatooed and weighed within 24 hours of birth. Suckling calves were pastured with their dams without creep feed and weaned at an average age of 205 days. At weaning, all calves were weighed following a 12 hour shrink off water and scored by a committee of at least three persons for conformation and condition.

After weaning bull calves were given a two week warm up period prior to being placed on a 160 day gain test during the first eight years of this study and for 140 day gain test from 1972 to 1978. Bulls were weighed following a 12 hour shrink off feed and water at the end of the test period and scored for conformation and condition. Test rations underwent three basic changes over the 15 year period. Table XI summarizes composition of the rations. The initial ration utilized whole ear corn, then in 1966, ground shell corn was substituted for ground ear corn, percentage cottonseed hulls was reduced and percentage whole oats was increased. The second change in 1970 involved the addition of preformulated supplemental pellets (Table XII), increasing the amount of ground shell corn and cottonseed hulls and dropping alfalfa hay, whole oats, wheat bran and protein supplement from the ration. In 1974, the final modification of the ration was

TABLE XI

COMPOSITION OF BULL TEST RATIONS

Ingredient	Years ration used			
	1964-1965	1966-1969	1970-1973	1974-1978
	%	%	%	%
Ground whole ear corn	35	--	--	--
Ground shell corn	--	30	57	57
Cottonseed hulls	20	15	23	22
Ground alfalfa hay	10	10	--	6
Whole oats	10	20	--	--
Wheat bran	10	10	--	--
Protein supplement[a]	10	10	--	--
Molasses	5	5	5	5
Supplemental pellets	--	--	15	10

[a]Cottonseed meal and soybean oil meal were used interchangeably depending on relative prices.

TABLE XII

COMPOSITION OF SUPPLEMENTAL PELLETS

Ingredient	Percentage in ration
Dehydrated alfalfa	33
Soybean oil meal	40
Wheat middlings	16
Urea	3
Salt	3
Dicalcium phosphate	2
Calcium carbonate	2
Aurofac-10 (Cyanamid Auromycin)	.3
Trace mineral	.1
Vitamin A (10,000 I.U./gram)	.2

made by adding 6% ground alfalfa hay and decreasing cottonseed hulls by 1% and decreasing supplemental pellets by five percent. All rations were fed ad libitum from self feeders.

Heifer calves were placed on pasture gain tests following weaning (including wheat pasture when available) and supplemented with prairie hay, alfalfa, cottonseed cake and grain as necessary to gain from .75 to 1.00 pounds per day to 425 days of age. This longer postweaning period was used for heifers to permit greater opportunity for genetic differences to be expressed under the lower nutritional level. Weights, conformation scores and condition scores were taken at an average age of 425 days.

Primary Traits Measured

Complete performance records were collected on each calf through a year of age for bulls and through 425 days of age for heifers. The following records were utilized in this study:

1. Birth weight: Calves were weighed within 24 hours of birth. Birth weights of all calves weaned were utilized in this study.
2. Preweaning average daily gain: Preweaning average daily gain was calculated by dividing the differences of actual weaning weight and birth weight by calf age at weaning.
3. Weaning weight: Calves were weaned and weighed at an average age of 205 days. Weaning weights were adjusted to 205 days of age by multiplying average daily gain from birth to weaning by 205 and adding birth weight then adjusted for age of dam.

4. Weaning grade: A committee of at least three persons independently scored each calf for muscling at weaning independent of fatness and size. The three scores were averaged for each calf. These subjective scores were based on a 17 point grading system with 13 representing average choice, 14 high choice and so on.
5. Weaning condition score: The same committee procedures were used to score each calf at weaning for fat cover. Again, a 17 point scale was utilized with 13 being average fatness.
6. Postweaning average daily gain: Postweaning average daily gain was calculated by dividing the difference between actual yearling weight and on test weight by days on test.
7. Yearling weight: 365-day yearling weights for bulls and 425-day weights for heifers were calculated by multiplying postweaning average daily gain by 160 for bulls and 220 for heifers and adding 205-day age of dam adjusted weaning weight.
8. Yearling grade: Bulls and heifers were scored for muscle at the end of their respective gain tests by the same system as outlined for weaning conformation.
9. Yearling condition score: Evaluation for fat cover of bulls and heifers at the end of the postweaning period was also by the same procedure previously

described for scoring at weaning.

Age of dam adjusted weaning weights used to make actual selections of bull and heifer calves in WWL were calculated through the 1969 calf crop by multiplying preweaning average daily gain by 205 and adding birth weight, then multiplying the entire quantity by the appropriate age of dam correction factor. The classifications of age of dam are given in Table XIII and the multiplicative age of dam correction factors utilized are presented in Table XIV.

Starting with the 1970 calf crop, additive age of dam correction factors, also presented in Table XIV were used as developed by Cardellino and Frahm (1971) from records on these lines of cattle from 1964 to 1968. No age of dam adjustments were made for calves from dams 5-years-old and older.

The age of dam adjusted yearling weights used for actual selection of bull and heifer calves in the YWL were calculated by multiplying postweaning average daily gain by 160 for bulls and by 220 for heifers and adding 205-day, age of dam adjusted weaning weight as previously defined.

After all data had been collected and the selection lines terminated, age of dam correction factors were developed from records of all Hereford and Angus cattle in retrospect for the nine primary traits measured. Analyses of calf records were done by least squares procedure within breed and sex, with year, age of dam and the year by age of dam interaction in the model. Calf records from dams over 11 years of age (a total of 1 Angus and 3 Hereford cows) were eliminated from the analyses. Table XV presents the additive correction factors obtained to adjust data for age of dam differences. The nine primary traits were each directly adjusted by these correction factors prior to any further analyses.

TABLE XIII

CLASSIFICATION OF VARIOUS AGES OF DAMS

Age classification	Age of dam (in months)
2 year old	24 ± 2
3 year old	36 ± 2
4 year old	48 ± 2
Mature	over 58

TABLE XIV

AGE OF DAM CORRECTION FACTORS USED TO ADJUST 205-DAY WEANING WEIGHT PRIOR TO SELECTIONS

Age of dam	Multiplicative correction factors, 1964-1969		Additive correction factors, 1970-1978 (lb)	
	Hereford	Angus	Hereford	Angus
2	1.15	1.15	+80	+60
3	1.10	1.10	+35	+35
4	1.05	1.05	+10	+10
Mature	1.00	1.00	+0	+0

TABLE XV

ADDITIVE AGE OF DAM CORRECTION FACTORS TO MATURE DAM BASIS

Trait	Age of dam	Hereford		Angus	
		Bulls	Heifers	Bulls	Heifers
Birth weight (lb)	2	+12	+11	+9	+7
	3	+ 4	+ 3	+4	+3
	4	+ 0	+ 2	+2	+1
Preweaning ADG (lb/day)	2	+.43	+.29	+.29	+.24
	3	+.21	+.15	+.18	+.14
	4	+.06	+.04	+.08	+.05
205-day weaning weight (lb)	2	+100	+70	+70	+55
	3	+ 48	+33	+40	+32
	4	+ 12	+10	+19	+12
Weaning condition score	2	+1.1	+1.0	+.7	+.7
	3	+ .7	+ .7	+.5	+.4
	4	+ .2	+ .3	+.3	+.2
Weaning conformation score	2	+1.4	+1.1	+1.0	+.8
	3	+ .9	+ .7	+ .7	+.5
	4	+ .3	+ .2	+ .4	+.2
Yearling weight (lb)	2	+81	+44	+71	+34
	3	+49	+24	+44	+21
	4	+ 1	+ 5	+16	+ 7
Postweaning ADG[a] (lb/day)	2	+0	-.11	+0	-.10
	3	+0	-.04	+0	-.05
	4	+0	-.02	+0	-.03
Yearling condition score	2	+.4	+.4	+.4	+.2
	3	+.4	+.4	+.4	+.1
	4	+.2	+.1	+.3	+.1
Yearling conformation score	2	+.5	+.7	+.4	+.3
	3	+.4	+.6	+.3	+.2
	4	+.1	+.4	+0	+.1

[a]Age of dam was not a significant source of variation for bull calves.

Traits Measured on Terminal Cross Calves in 1979

As previously discussed, the Hereford WWL and YWL were terminated with the 1978 calf crop. The final group of selected Hereford bulls in 1976 and 1977 from these lines were randomly mated to a group of Angus cows, producing 83 crossbred calves. All bull calves were castrated at birth and after weaning all steer and heifer calves were placed in feedlot and slaughtered when an anticipated low choice quality grade was obtained. Table XVI gives the feedlot ration fed ad libitum.

Besides the nine primary traits previously discussed, data was collected on feedlot and carcass traits. Feedlot traits included days in feedlot, average daily gain on test, final feedlot weight, weight per day of age and feed efficiency. Carcass traits measured were slaughter age, carcass weight, carcass weight per day of age, dressing percentage, single fat thickness, kidney, heart and pelvic fat percentage, marbling score, carcass grade and rib eye area. Also, wither and hip heights were measured the same day yearling weights were recorded.

Milk Production Data

Another portion of data in this study were obtained during the summer of 1979 from 35 Hereford dams and their calves, 18 from WWL and 17 from YWL representing a random sample of mature dams within each line. Lactational performance was determined monthly from April through September. Calves were separated for six hours, allowed to suckle their dams and then separated again for an average of 12 hours. Cows were given an intramuscular injection of 10 to 20 mg of the tranquilizer ace promazine approximately 15 minutes before milking. Immediately prior to milking,

TABLE XVI

COMPOSITION OF FEEDLOT RATION FOR 1979 CALF CROP

Ingredient	Percentage in ration
Corn	78
Alfalfa	8
Cottonseed hulls	4
Molasses	5
Supplemental pellets[a]	5

[a]Supplemental pellets consisted of 67.6% soybean oil meal (44%), 12% urea, 10% calcium carbonate, 8% salt plus Aurofac, Vitamin A and trace minerals.

cows were injected with 1.5 mg of Syntocin, a synthetic oxytocin, in the jugular to induce milk letdown. Cows were milked with a portable vacuum pump milking unit. Milking time per cow varied from 5 to 10 min and each cows udder was stripped out by hand to assure a complete milkout had been obtained. The milk was weighed and two samples taken, one for butterfat analysis, the other for protein and total solids analysis.

Samples for butterfat determination were transferred to the DHIA laboratory at Oklahoma State University for analysis by a milk-o-tester. Protein content was determined by the UDY dye method and color computer (Ashworth, et al., 1960; Udy, 1956) and total solids by oven-drying of samples in a 100^{o}C oven for four hours. Duplicate samples were analyzed for protein and total solids. All milk composition estimates were completed within four days of each milking.

Measurement of Selection Applied

Generations of Selection

Generation coefficients were calculated from a formula described by Brinks et al. (1961): CGC=(SGC + DGC)/2+1, where CGC, SGC and DGC are calf, sire and dam generation coefficients, respectively. Foundation sires and dams were assigned generation coefficients of zero, so calves produced by foundation sires and dams have a CGC of one; therefore generations of selection were obtained by subtacting one from the calculated CGC.

Cumulative Selection Differentials

Cumulative selection differentials (CSD) can be used to evaluate total selection applied for any individual or for the entire group. When considering the primary trait under selection, CSD can be compared with total response to evaluate effectiveness of selection. If generations are discrete, the CSD can be calculated by simply adding selection differentials of successive generations. Because of overlapping generations in species such as cattle, additional formulas are necessary. In this study, the method outlined by Newman et al. (1973) has been used where CSD is equal to the individual's own deviation from its contemporary (year-line-sex) group plus mean accumulated selection (MAS) for that sex of calf to that point in time. MAS is the average CSD of parents of a contemporary group. Each of the following components was calculated for MAS each year: MAS sires to sons (MASSS), MAS sires to daughters (MASSD), MAS dams to sons (MASDS) and MAS dams to daughters (MASDD). MAS for bulls is the sum of MASSS plus MASDS while MAS for heifers is the sum of MASSD plus MASDD. These values for each sex take sire and dam past histories of selection into account. Selection due to sire independent of dam selection was calculated as the sum of MASSS plus MASSD and correspondingly, selection due to dams independent of sire selection is MASDS plus MASDD. Midparent MAS or MAS over sexes is simply the average of bull and heifer MAS values or average of selection due to sire and dam MAS values. CSD for an individual can thus be viewed as the total selection practiced previously plus an additional selection practiced in the individual.

CSDs were calculated for the nine traits of primary interest in both selection lines and the control line. Foundation sires and dams were assigned zero selection differentials for all traits. CSDs were calculated in both actual units and standardized measure for each year. In addition, to estimate yearly trends, average (over sexes) MAS values for each year were regressed on year using simple linear regression.

The method employed differed from that presented by Pattie (1965a), in which an individuals MAS was the average cumulative selection of its parents. Newman's method was preferred because the deviation of selected bulls and heifers is from the mean of the entire year-line-sex group, not from the average for progeny of parents of selected individuals only.

Actual and Potential Selection Differentials

Selection differentials per generation were calculated for selected parents of calves and for the actual top bulls and heifers available for selection in each line according to line criteria. A comparison of actual vs potential selection differentials should give an estimate of the proportion of the possible selection pressure that was actually exerted in the primary trait of each line. Selection differentials for selected sires and dams were obtained by averaging deviated (and standardized) selection differentials of sires (and dams) for all progeny excluding those from foundation parents. Corresponding maximum potential selection differentials were calculated by averaging selection differentials for bulls and heifers (same number as actually selected each year) with the largest selection differentials for the primary criteria in each line, each year. "Maximum potential" for the control line was calculated for those individuals that were closest to zero selection differential for the average weaning and yearling weights.

Indexes in Retrospect

Although intentions were to select individuals having the best performance for a single trait, other factors may prevent this from being achieved in some cases. For example, a heifer that was heaviest at weaning or yearling time may not conceive at breeding and thus not be retained in the line. Perhaps top animals are not retained because of physical defects; or particular situations may strongly indicate a bull or heifer should not be selected, i.e. if the top weaning weight bull grows slowly on 140-day gain test, should he be selected?

If observed selection differentials are a function of multiple trait selection actually practiced, then an index showing relative emphases of component traits can be determined in retrospect (Dickerson et al., 1954). This index can be determined with the knowledge that the standardized selection differential of the k^{th} trait (ΔP_k) has the expectation $\Delta I \cdot r_{IP_k}$, where ΔI is the selection differential of the index (in standard measure) and r_{IP_k} is the correlation of P_k with the index. The following simultaneous equations can then be set up:

$$r_{IP_1} = \beta_{IP_1} + \beta_{IP_2} \cdot r_{P_1P_2} + \ldots + \beta_{IP_k} \cdot r_{P_1P_k}$$

$$\vdots$$

$$r_{IP_k} = \beta_{IP_i} \cdot r_{P_kP_1} + \beta_{IP_2} \cdot r_{P_kP_2} + \ldots + \beta_{IP_k}$$

where $r_{P_1P_k}$ is the phenotypic correlation between the first and k^{th} trait and β_{IP_k} is the standard partial regression of the index on the k^{th} trait.

Because ΔP_k has the expectation of $\Delta I \cdot r_{IP_k}$, we can multiply both sides of each simultaneous equation listed above by ΔI and solve for $\beta_{IP_k} \cdot \Delta I = \beta'_{IP_k}$. If all possible traits associated with selection are included, the multiple correlation of the index with all components is equal to one; therefore $\Delta I = (R^2_{I \cdot P_1 \cdots P_k} \cdot (\Delta I)^2)^{\frac{1}{2}} = (\sum_{i=1}^{k} r_{IP_k} \cdot \beta_{IP_k} \cdot (\Delta I)^2)^{\frac{1}{2}} = (\sum_{i=1}^{k} \Delta P_k \cdot \beta'_{IP_k})^{\frac{1}{2}}$. Once ΔI is calculated, $\beta_{IP_k} = \beta'_{IP_k} / \Delta I$ where β_{IP_k} gives the weighting of the k^{th} trait in the index.

Two sets of indexes were calculated. Index 1 included birth, weaning and yearling weights, weaning and yearling grades and weaning and yearling condition scores, while Index 2 substituted preweaning ADG for weaning weight and ADG weaning to yearling for yearling weight. Since Index 1 includes the primary selection traits, it provides the clearest picture of how closely selection criteria were followed and Index 2 shows the relative importance of gain at various stages of growth. Ideally the weighting for weaning weight in the weaning weight line would be one and all other traits have a weighting of zero for Index one.

Both Index 1 and Index 2 were calculated for sires, dams and parent average in the weaning weight line, yearling weight line and control line, based on actual selection differentials (in standard measure). Also, these indexes were obtained for sires and dams in each line, based on maximum potential selection differentials (in standard measure) to give indications of relative emphasis on the various traits if selection criteria had been followed exactly. Phenotypic correlations, used to calculate these indexes, were obtained from pooled sums of squares and cross products within years and lines, for each breed, for each sex. All Angus lines, although not the topic of this study as previously described, were used to calculate phenotypic correlations for development of indexes for the Angus control line.

Evaluation of Response to Selection

Phenotypic Trends

Means were obtained for each year-line-sex group for evaluation of phenotypic time trends for the nine traits of primary interest. Means were also pooled over sexes. All traits had been adjusted for age of dam differences as previously described. Year-line-sex means were regressed on year, using simple linear regression techniques, to estimate average phenotypic change per year. These coefficients of regression were averaged over sex, within each line, for each trait.

Yearling hip height was measured in the Hereford selection lines for the 1978 calf crop only. This trait was analyzed by ordinary least squares procedures to obtain line means. The linear model included line, sire within line, sex of calf and line by sex interaction as fixed effects and age of dam as a covariate (as these data were unadjusted for age of dam). The reduced model included all sources of variation that had $P<.20$ in the full model. Differences between lines were considered significant if the F value for line was $P<.05$.

Genetic Trends Measured as Deviations from the Control Line

Annual deviations from the control line were calculated for weaning weight averaged over sex and for yearling weight by sex. In addition, differences between coefficients of regression of the selection lines *vs* control line were obtained for all nine traits by sex and averaged over sex. Realized heritabilities for weaning weight in the weaning weight line and yearling weight in the yearling weight line were calculated by dividing the respective genetic response per year by average cumulative selection differential per year.

Genetic Trends Estimated from Repeat Sires and Dams over Years

Smith (1962) proposed the use of regression techniques to estimate genetic trends, assuming that sire and dam trends were equal, by estimating genetic change associated with sires. Zollinger (1981) developed this procedure further, to estimate genetic changes associated with dams.

Regression can be used to estimate genetic trend by holding either sires or dams constant. Expectation of the pooled regression of each trait (as a deviation of year-line-sex group) on year of calf birth within sire is negative genetic change associated with sires.

Since each sire has several progeny in one year, as well as over years, and a dam will produce calves over years, an estimate of genetic trend due to dams can be obtained by the pooled within dam regression of progeny performance deviated from the sire's year mean progeny performance on year of calf birth. This would compare the dam performance with other dams mated to the same sire. The negative of the regression coefficient is an estimate of genetic change occuring, due to dams. This estimate will also contain all components associated with change in the maternal environment provided to the calf. Since the genetic correlation between direct and maternal effects is probably negative, the dam component contributing to genetic trend will be lowered as maternal effects increase.

Total herd genetic trends per year thus were estimated to be the negative of the sum of the two regression coefficients calculated for each trait in each line.

Genetic Trends Estimated from Regression of Offspring on Generation Coefficient

In populations where generations overlap, intra-year regression of offspring deviation on calf generation coefficient provides a direct estimate of genetic trend per generation. These regressions were calculated for each trait, in each line and sex.

Analysis of Outcross Calves' Traits and Selected Sires Used to Produce this Calf Crop

Individual cumulative selection differentials were calculated for the 12 selected bulls used to produce the outcross calf crop in 1979 by addition of the mean accumulated selection differentials for males, for the year of the bull's birth plus his individual deviation from his year-line-sex group. These individual cumulative selection differentials were calculated for each trait, for each bull, then averaged over lines.

Also, inbreeding coefficients were obtained for each bull, then averaged for each line, by pedigree analysis (Pirchner, 1969). Pedigrees were traced back to foundation sires and dams. Foundation animals were assumed to have inbreeding coefficients of zero.

Ordinary least squares procedures were used to obtain line means for weaning, yearling, feedlot and carcass traits of the outcross calves. The linear model used for analysis of weaning and yearling traits included line, sire within line, sex of calf and line by sex interaction, all as fixed effects, and age of dam as a covariate. The model for analysis of feedlot and carcass traits included the fixed effects of line, sire within line, sex of calf, pen within line and line by sex interaction. Reduced models for each trait included all sources of variation that had P<.20 in the full models. Differences between lines were considered significant if the F value for line was P<.05.

Analysis of Cow Weight Trends and Milk Production Traits

Average cow weights were calculated by line and year for all mature cows (five year old or older) that raised a calf that particular year. A cow's weight was the average of her spring weight prior to breeding and fall weight after weaning. Simple linear regression analysis of cow weight means on year were used to estimate yearly phenotypic trends in each selection line.

Ordinary least squares procedures were used to analyze milk traits of the two Hereford lines. Monthly line means were obtained from a linear model containing line, sex of calf, week of milking, year of cow birth, line by sex of calf interaction and line by year of cow birth interaction as fixed effects and date of calving as a covariate. The same sources of variation were included in the full model for analysis of six-month means of each trait. Reduced models by month and over months contained all sources of variation with P<.20 in the full models.

Estimation of Population Parameters

Paternal Half-Sib Estimates

Estimates of heritabilities and genetic correlations were obtained from paternal half-sib analyses of variance and covariance for bulls and heifers separately. Estimates pooled over the Hereford lines and for the Angus control line were calculated. Heritabilities and genetic correlations obtained from this type of analysis do not include maternal effects which are important sources of genetic variation in growth of cattle (Koch, 1972 and Van Vleck et al., 1977).

The following formulas from Falconer (1960) were used to obtain heritabilities and genetic correlations from variance components of this analysis:

$$\hat{h}_i^2 = \frac{4\sigma_{s_i}^2}{\sigma_{s_i}^2 + \sigma_{e_i}^2} \quad \text{and} \quad \hat{r}_{g_{ij}} = \frac{\sigma s_{ij}}{(\sigma_{s_i}^2 \cdot \sigma_{s_j}^2)^{\frac{1}{2}}}$$

where $\sigma_{s_i}^2$ = sire component of variance of the i^{th} trait, $\sigma_{e_i}^2$ = error component of variance of the i^{th} trait and $\sigma_{s_{ij}}$ = the sire component of covariance between traits i and j.

Regression of Offspring on Parent

The regression of offspring on parent provides an opportunity to examine both direct and maternal effects in a population, as offspring-dam regression estimates contain maternal effects and a comparison of offspring-sire and offspring-dam regression provides some evidence of the magnitude of these maternal effects. Pooled within year offspring-sire and offspring-dam regressions were obtained for the control line and over the two Hereford lines for each sex, on each trait and for all pairs of traits. Within year offspring deviation was regressed on sire and dam deviations, with year of calf birth and year of sire (or dam) also included in the model to adjust for different selection histories behind the parents of calves born in one year.

The following formulas from Pirchner (1969) were used to obtain heritabilities and genetic correlations from regression analysis:

$$\hat{h}_i^2 = 2b_{o_i p_i} \quad \text{and} \quad \hat{r}_{g_{ij}} = \left(\frac{bo_i p_j \cdot bo_j p_i}{bo_i p_i \quad bo_j p_j} \right)^{\frac{1}{2}}$$

where $bo_i p_j$ is the regression coefficient of the i^{th} offspring trait regressed on the j^{th} parent trait. For estimates of genetic correlation, if the two covariances differ in sign, the average of the two covariances was used in the numerator instead of the geometric mean. Also, if both covariances are negative, the estimate was considered to be a negative correlation.

CHAPTER IV

RESULTS AND DISCUSSION

Intensity of Selection

Generations of Selection

Table XVII presents average number of generations of selection in the weaning weight line (WWL), yearling weight line (YWL) and control line (CL) for each calf crop. Both WWL and YWL had undergone 3.22 generations of selection in the 15 year period, while CL was similar involving 3.21 generations by the time the 1978 calf crop was produced. Interpretation of selection intensity and response was easier since all lines were at the same stage of selection. Actual range of calf generation coefficients was quite small, with a maximum range of 1.7 generations difference between selection histories of calves in any one year. Buchanan (1979) reported that after 17 years, 3.69, 3.56 and 3.67 generations of selection had been practiced in lines of Hereford cattle selected for weaning weight, yearling weight and an index, respectively.

Cumulative Selection Applied, Mean Selection Differentials per Generation and Maximum Potentials

The average cumulative selection differential (CSD) for a trait measures the amount of selection background in the parents of calves born

TABLE XVII

AVERAGE YEARLY GENERATIONS OF SELECTION

Year	Generations of selection		
	WWL	YWL	CL
1964	.00	.00	.00
1965	.00	.00	.00
1966	.06	.07	.09
1967	.38	.39	.18
1968	.67	.71	.63
1969	.80	.83	.92
1970	.99	1.18	.82
1971	1.32	1.50	.94
1972	1.74	1.77	1.53
1973	1.98	2.11	1.73
1974	2.16	2.28	2.08
1975	2.53	2.82	2.40
1976	2.67	2.89	2.68
1977	3.03	2.93	3.02
1978	3.22	3.22	3.21

in a given year. Averages for the nine primary traits of interest, birth weight (BW), preweaning average daily gain (WADG), weaning weight (WW), weaning grade (WG), weaning condition (WC) , yearling weight (YW), average daily gain weaning to yearling (YADG), yearling grade (YG) and yearling condition (YC) are given in Tables XVIII and XIX for the WWL and YWL, respectively. Parent average (ΔM) CSDs over the 13 year period are presented along with selection accumulated due to sires (ΔS) and dams (ΔD). In addition, CSDs in standard measure are reported for the 1978 calf crop, as well as ΔM regressed on year. Selection for WW in the WWL and YW in the YWL progressed at fairly regular rates throughout the study. In 1978, ΔM was 161 lb ($3.42\sigma_p$) for WW in the WWL and had accumulated at a rate of 12.11 ± .53 lb per year, while corresponding values for YW in the YWL were 279 lb ($3.61\sigma_p$) and 21.42 ± .70 lb per year. Cumulative selection differentials for WW in the WWL and YW in the YWL increased at the average rate of 1.06 and 1.12 σ_p per generation, respectively.

Correlated CSDs in the WWL were 14 lb, .72 lb/day, 198 lb, .26 lb/day, 1.98 units, 1.39 units, 2.17 units and .82 units for BW, WADG, YW, YADG, WG, WC, YG and YC, respectively. Comparisons for the various traits in standard measure CSDs indicate most selection pressure was practiced in WW ($3.42\sigma_p$) in the WWL, followed by WADG ($3.35\sigma_p$) or slightly more than one phenotypic standard deviation per generation of selection for both traits. It is of primary interest to evaluate the correlated CSD for YW in the WWL, because if appreciable selection can be applied for YW by selecting for WW, considerable savings in time and money can be realized by selecting animals at weaning instead of waiting until calves are a year of age. YW underwent 2.71 σ_p of selection pressure in the WWL or 75% as much pressure as direct selection for YW in the YWL. This suggests

TABLE XVIII

AVERAGE YEARLY CUMULATIVE SELECTION DIFFERENTIALS FOR SIRES (ΔS), DAMS (ΔD) AND PARENT AVERAGE (ΔM) IN THE WWL

Year	BW(lb)			WADG(lb/day)			WW (lb)			YW (lb)			YADG(lb/day)		
	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM
1966	0	.81	.40	0	.02	.01	0	4.48	2.24	0	5.28	2.64	0	0	0
1967	2.35	1.52	1.93	.04	.04	.04	11.77	8.94	10.36	-5.54	11.09	8.31	-.01	.01	0
1968	5.23	1.29	3.26	.18	.03	.11	43.35	6.92	25.14	34.93	9.87	22.40	-.02	.01	-.01
1969	2.79	1.99	2.40	.26	.07	.17	56.87	15.72	36.30	79.41	15.99	37.20	.07	.01	.04
1970	2.53	3.90	3.21	.26	.10	.18	55.21	24.62	39.91	82.39	15.31	53.85	.25	.01	.13
1971	3.45	3.76	3.61	.36	.16	.26	76.48	36.50	56.49	133.49	35.90	84.70	.39	.01	.20
1972	8.06	4.24	6.15	.49	.19	.34	109.16	44.48	76.82	134.79	51.93	93.36	.27	.06	.17
1973	13.37	4.77	9.07	.58	.26	.42	133.26	58.69	95.98	174.07	65.44	119.75	.36	.07	.21
1974	15.37	4.27	9.82	.61	.26	.44	140.35	58.68	99.52	234.09	72.02	153.06	.63	.11	.37
1975	14.39	6.69	10.54	.71	.31	.51	161.00	70.93	115.97	212.94	88.23	150.59	.41	.14	.28
1976	10.57	7.44	9.01	.74	.36	.55	161.64	80.64	121.14	194.04	107.36	150.70	.23	.19	.21
1977	17.27	8.99	13.13	.85	.43	.64	191.29	97.23	144.26	256.13	133.79	194.96	.42	.25	.34
1978	17.96	10.14	14.05	.93	.50	.72	209.22	113.63	161.42	250.47	146.00	198.19	.27	.24	.26
Standard measure (1978)	2.13	1.17	1.65	4.23	2.44	3.35	4.32	2.51	3.42	3.28	2.12	2.71	.74	.77	.76
Regression on year			1.04±.08			.05±.00			12.11±.53			15.94±.84			.03±.00

TABLE XVIII (Continued)

Year	WG[a]			WC[b]			YG[a]			YC[b]		
	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM
1966	0	.23	.12	0	.03	.02	0	.02	.01	0	-.01	-.01
1967	.53	.05	.29	.48	.07	.27	.30	.05	.18	.07	-.03	.01
1968	1.11	-.01	.55	1.12	.08	.59	.53	.03	.28	.43	-.01	.21
1969	.58	.11	.35	1.20	.09	.64	.57	0	.29	.58	0	.29
1970	.32	.26	.29	.81	.28	.55	.75	.19	.48	.30	.09	.19
1971	.85	.49	.67	.86	.53	.69	.78	.24	.52	.70	.15	.43
1972	1.52	.45	.99	1.40	.55	.98	.85	.43	.64	.59	.35	.47
1973	1.69	.65	1.17	1.16	.71	.94	1.11	.49	.80	.54	.40	.47
1974	1.51	.73	1.12	.99	.74	.87	1.33	1.73	1.53	.83	.48	.66
1975	2.35	.77	1.56	1.96	.78	1.37	1.86	.29	1.08	1.12	.58	.85
1976	2.63	.87	1.75	1.82	.82	1.32	2.08	1.69	1.88	1.15	.61	.88
1977	2.38	1.12	1.76	1.40	1.11	1.26	1.96	1.86	1.91	.86	.75	.81
1978	2.60	1.35	1.98	.153	1.26	1.39	2.30	2.04	2.17	.80	.84	.82
Standard measure (1978)	3.07	1.68	2.38	2.01	1.68	1.85	3.10	1.81	2.46	1.28	1.37	1.33
Regression on year			.15±.01			.11±.00			.18±.02			.07±.01

[a]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b]17 point scoring system where 13 = average fat cover.

TABLE XIX

AVERAGE YEARLY CUMULATIVE SELECTION DIFFERENTIALS FOR SIRES (ΔS), DAMS (ΔD) AND PARENT AVERAGE (ΔM) IN THE YWL

Year	BW(lb)			WADG(lb/day)			WW(lb)			YW(lb)			YADG(lb/day)		
	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM
1966	0	.72	.36	0	.02	.01	0	4.43	2.21	0	6.08	3.04	0	.01	.00
1967	5.90	.70	3.30	.14	.03	.08	34.99	6.28	20.64	71.95	5.52	38.74	.24	0	.12
1968	8.43	.61	4.52	.22	.03	.13	53.83	7.41	30.62	125.09	4.41	64.75	.47	0	.24
1969	10.02	2.03	6.03	.19	.06	.13	48.68	14.96	31.82	107.78	19.77	63.78	.41	.04	.23
1970	10.35	3.54	6.95	.33	.10	.17	58.86	24.98	41.92	151.98	38.75	95.37	.59	.10	.35
1971	5.44	3.85	4.65	.32	.11	.22	71.67	27.03	49.35	216.19	48.04	132.12	.90	.14	.52
1972	8.74	5.34	7.04	.43	.18	.30	96.10	41.47	68.74	232.58	74.11	153.34	.90	.21	.56
1973	12.42	7.66	10.04	.59	.23	.42	134.72	55.97	95.35	252.36	100.73	176.53	.80	.29	.54
1974	14.58	6.47	10.52	.53	.23	.38	123.79	53.11	88.45	264.74	102.84	183.79	.89	.32	.61
1975	13.50	8.45	10.98	.79	.28	.48	157.38	65.58	111.48	272.90	134.72	203.82	.79	.43	.61
1976	13.87	8.53	11.20	.69	.33	.51	154.73	75.60	115.17	305.39	154.35	229.87	.99	.50	.74
1977	16.54	8.58	12.56	.69	.41	.55	158.76	92.50	125.63	366.21	170.41	268.31	1.31	.50	.90
1978	21.80	10.48	16.14	.80	.44	.62	185.02	101.78	143.40	362.84	194.98	278.91	1.19	.59	.89
Standard measure (1978)	2.52	1.23	1.88	3.54	2.07	2.81	3.76	2.20	2.98	4.59	2.63	3.61	3.47	1.89	2.68
Regression on year			1.07±.07			.05±.00			10.76±.47			21.42±.70			.07±.00

TABLE XIX (Continued)

Year	WG[a]			WC[b]			YG[a]			YC[b]		
	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM
1966	0	.08	.04	0	.09	.05	0	0	0	0	.03	.01
1967	.42	.14	.28	.23	.14	.19	.64	.09	.37	.46	.11	.29
1968	.64	.06	.35	.40	.09	.25	1.23	-.01	.61	.89	.06	.48
1969	.34	.14	.24	.28	.16	.22	1.17	.13	.65	.94	.12	.53
1970	.51	.34	.43	.43	.29	.36	1.25	.39	.82	1.34	.27	.81
1971	.69	.32	.51	.50	.29	.40	1.21	.55	.88	1.38	.41	.90
1972	.91	.41	.66	.46	.33	.40	.98	.64	.81	1.21	.51	.86
1973	1.35	.50	.92	1.00	.43	.72	1.13	.83	.98	1.67	.63	1.15
1974	1.97	.46	1.22	.83	.43	.63	1.33	.77	1.05	1.48	.71	1.10
1975	1.88	.64	1.25	.85	.55	.70	1.33	.92	1.13	1.05	.91	.98
1976	1.53	.82	1.18	.84	.60	.72	1.34	1.02	1.18	1.24	1.00	1.12
1977	2.26	1.03	1.65	.95	.76	.86	1.06	1.19	1.63	1.80	1.07	1.44
1978	2.30	1.18	1.74	1.37	.82	1.10	2.32	1.27	1.79	1.60	1.14	1.37
Standard measure (1978)	2.74	1.45	2.09	1.87	1.10	1.49	3.03	1.54	2.29	2.53	1.64	2.08
Regression on year			.13±.01			.07±.00			.12±.01			.11±.01

[a]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b]17 point scoring system where 13 = average fat cover.

that animals selected for heaviest WW are also phenotypically above average for YW. Buchanan (1979) found a correlated selection differential achieved for YW in the WWL 86% as large as direct selection for YW.

In the YWL, correlated CSDs were 161 lb, .62 lb/day, 143 lb, .89 lb/day, 1.74 units, 1.10 units, 1.79 units and 1.37 units for BW, WADG, WW, YADG, WG, WC, YG and YC, respectively. Most selection pressure occured for YW ($3.61\sigma_p$) with considerable correlated pressure in WW ($2.98\sigma_p$). It has been postulated that selection for YW may improve WW as much or more than direct selection for WW (Koch *et al.*, 1974). This hypothesis is based on the higher heritability of YW relative to the heritability of WW and the high positive genetic correlation that apparently exists between the two traits. In this data, the correlated CSD for WW in the YWL was 87% as large as the CSD achieved from directly selecting for WW in the WWL, giving positive evidence for the above hypothesis. It is also of interest to note that WW accumulated relatively faster in the YWL than did YW in the WWL ($3.42\sigma_p$ *vs* $2.98\sigma_p$ for WW compared to $2.71\sigma_p$ *vs* $3.61\sigma_p$ for YW in the WWL and YWL, respectively). Also, more correlated CSD was realized for WADG than YADG ($2.81\sigma_p$ *vs* $2.68\sigma_p$) in the YWL while the reciprocal effect was not observed in the WWL ($3.35\sigma_p$ *vs* $.76\sigma_p$ for WADG and YADG, respectively).

Buchanan (1979) reported CSDs per generation slightly under one phenotypic standard deviation for WW in their WWL and slightly over one phenotypic standard deviation for YW in their YWL, which is very similar to the intensity of selection in the present study. Newman *et al.* (1973) reported selection pressures accumulated at an average rate of 22.0 lb/year for YW in two replicate herds of Shorthorn cattle which is in close agreement with selection pressure exerted for YW in the YWL of the present study. Nelms and Stratton (1967), selecting for weight at the end of a 168 day postweaning feed test, realized average selection differentials of 12.4 lb/yr for final weight off-test, which is considerably less selection pressure than for YW in the present study.

Weaning weight and yearling weight are both traits that are influenced by numerous components; therefore it is important to evaluate correlated selection intensity and response. BW is of specific concern, since heavy BWs have been associated with calving difficulties. CSD for BW in both lines was positive, increasing 1.06 lb/yr or approximately accumulating at 50% of the selection pressure exerted on primary selection traits for each line. Other studies have shown positive indirect selection intensities for BW when multiple trait selection was practiced (Flower et al., 1964; Brinks et al., 1965; Nelms and Stratton, 1967; and others).

Concern has also been expressed by some in the industry that selection for performance will result in deterioration of conformation unless conformation is included in the selection program. Another concern is that selection for increased weight will increase fatness of animals at a given age. WG and YG showed considerable positive selection pressure in both selection lines. Comparison of standard measure CSDs show selection pressure for WG and YG averaged approximately 71% and 61% the selection intensity of the trait of primary selection in the WWL and YWL, respectively. Correlated emphasis on fatness, although positive, was much smaller when comparing standard measure CSDs.

Table XX presents CSDs for the control line (CL) in the same manner as previously described for the Hereford lines. CSDs accumulated in a sporadic manner for most traits, as would be expected in a CL. Although positive CSDs were realized in all traits, they were generally small, ranging from $.08\sigma_p$ to $1.06\sigma_p$ for the various traits, with only 13.0 lb ($.36\sigma_p$) and 42.1 lb ($.70\sigma_p$) Csd for WW and YW, respectively by the 1978 calf crop.

In a population under long term selection, CSDs of parents are the combined result of sire and dam selection. Reports in the literature have shown that selection differentials of sires are generally much larger than selection differentials of dams. This would be expected as there is considerably more opportunity for selection among bulls than heifers because of the large proportion of heifers that must be saved for replacement.

A way of evaluating the proportion of male selection pressure is comparison of mean accumulated selection differentials of selected bulls and heifers. These values for each sex are independent of past sire and dam selection histories as the values simply are the average selected bull and heifer deviations from their contemporary year-line-sex group. Table XXI presents mean selection differentials per generation of selected bulls (ΔS), selected heifers (ΔS) and parent average (ΔM) in standard measure as well as mean maximum potential selection differentials per generation for each line. Table XXII gives the realized mean selection differentials per generation in actual units. The proportion of selection pressure attributable to sires was 74% for WW in the WWL and 83% for YW in the YWL. Replacement of females in the lines was somewhat faster than replacement rates in most commercial herds, thus in most practical situations the relative contribution of male selection to genetic improvement of the herd would be expected to be larger than experienced in this study.

The proportion of potential selection realized can be evaluated by

TABLE XX

AVERAGE YEARLY CUMMULATIVE SELECTION DIFFERENTIALS FOR SIRES (ΔS), DAMS (ΔD) AND PARENT AVERAGE (ΔM) IN THE CL

Year	BW(lb)			WADG(lb/day)			WW(lb)			YW(lb)			YADG(lb/day)		
	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM	ΔS	ΔD	ΔM
1966	0	.52	.26	0	0	0	0	.40	.20	0	1.51	.76	0	.01	0
1967	0	1.39	.70	0	0	0	0	1.96	.98	0	3.82	1.91	0	.01	0
1968	3.81	1.03	2.42	.04	.02	.03	12.04	5.02	8.53	74.05	2.63	38.34	.39	0	.20
1969	-.16	2.42	1.13	.04	.02	.03	7.50	6.31	6.91	74.47	1.59	38.03	.42	.01	.22
1970	-3.00	2.29	-.35	-.02	.02	0	-6.99	6.95	-.02	44.77	11.48	28.13	-.30	.06	.20
1971	-2.47	2.50	.01	.03	.02	.03	3.48	6.88	5.19	14.73	17.20	15.97	.07	.10	.09
1972	-1.80	2.65	.42	.02	.03	.03	3.39	8.27	5.83	41.82	20.21	31.02	.27	.11	.19
1973	1.43	2.21	1.82	.02	.04	.03	5.40	9.68	7.54	24.33	35.26	24.80	.15	.14	.15
1974	-3.22	1.86	-.69	.01	.04	.02	-2.14	10.58	4.22	19.96	30.69	25.32	.17	.16	.16
1975	.45	2.38	1.41	-.01	.04	.02	-.36	10.39	5.02	30.15	39.54	34.84	.22	.22	.22
1976	-2.97	2.02	-.47	-.01	.03	.01	-3.94	7.93	2.00	31.98	37.80	34.89	.25	.22	.24
1977	-1.85	2.16	.15	.05	.03	.04	8.09	8.30	8.19	40.14	41.81	40.98	.24	.24	.24
1978	-.42	1.57	.57	.05	.07	.06	10.08	15.91	12.99	36.81	47.29	42.50	.23	.22	.23
Standard measure (1978)	-.03	1.94	.08	.30	.40	.35	.30	.42	.36	.56	.83	.70	.99	.83	.93
Regression on year			.70±.06			.08±.03			10.92±.72			15.37±1.28			.17±.15

TABLE XX (Continued)

Year	WG[a] ΔS	WG[a] ΔD	WG[a] ΔM	WC[b] ΔS	WC[b] ΔD	WC[b] ΔM	YG[a] ΔS	YG[a] ΔD	YG[a] ΔM	YC[b] ΔS	YC[b] ΔD	YC[b] ΔM
1966	0	-.05	-.03	0	0	0	0	.04	.02	0	.01	0
1967	0	-.02	-.01	0	-.04	-.02	0	.11	.05	0	.05	.02
1968	.14	.04	.09	.22	.07	.15	.88	.17	.05	.68	.15	.41
1969	-.76	.11	-.33	-.76	.18	-.01	.45	.19	.32	.45	.22	.43
1970	-.63	.07	-.28	-.30	.06	-.13	.42	.32	.40	.28	.23	.26
1971	.04	-.07	-.02	-.02	.04	.01	.26	.26	.26	.26	.27	.26
1972	1.2	.03	.08	-.06	.13	.03	.72	.40	.56	.70	.38	.54
1973	-.36	.04	-.16	-.15	.09	-.08	.21	.47	.34	.03	.38	.21
1974	-.18	.11	-.03	-.32	.09	-.11	.51	.59	.55	.41	.50	.46
1975	.07	-.04	.02	.11	-.01	.05	.64	.58	.61	.50	.49	.50
1976	.35	-.11	.12	.11	-.07	.02	.74	.55	.65	.52	.49	.51
1977	.48	-.05	.21	-.04	-.03	-.03	.68	.68	.68	.28	.65	.47
1978	.29	.21	.25	.22	.14	.18	.42	.78	.60	.29	.64	.47
Standard measure (1978)	.48	.34	.41	.25	.06	.16	.53	1.06	.80	.29	.97	.63
Regression on year			.10±.01			.07±.01			.08±.01			.03±.01

[a]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b]17 point scoring system where 13 = average fat cover.

TABLE XXI

MEAN SELECTION DIFFERENTIALS PER GENERATION FOR SELECTED SIRES (ΔS), DAMS (ΔD) OR MIDPARENTS (ΔM) AND MAXIMUM POTENTIALS BASED ON LINE CRITERIA, EXPRESSED IN STANDARD MEASURE

Line	Item	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
		Average of selected parents of calves[a]								
WWL	ΔS	.586	1.353	1.368	1.065	.885	1.062	.433	.948	.593
	ΔD	.298	.547	.579	.263	.311	.536	.156	.304	.301
	ΔM	.442	.950	.974	.664	.598	.799	.295	.626	.447
YWL	ΔS	.749	1.152	1.219	.871	.496	1.599	1.254	.945	1.002
	ΔD	.263	.466	.484	.262	.263	.323	.503	.291	.271
	ΔM	.506	.809	.852	.567	.380	.961	.879	.618	.637
CL	ΔS	-.215	.020	-.013	.089	-.105	.267	.426	.289	.136
	ΔD	.211	.161	.193	.084	.057	.241	.342	.391	.343
	ΔM	-.002	.091	.090	.087	-.024	.254	.384	.340	.240
		Maximum potential for sire or dam selection[b]								
WWL	ΔS	.842	1.505	1.563	1.162	.910	.983	.118	.853	.583
	ΔD	.417	.795	.828	.468	.420	.616	.009	.192	.226
YWL	ΔS	.749	1.152	1.219	.871	.496	1.599	1.254	.945	1.002
	ΔD	.389	.533	.581	.349	.322	.755	.514	.463	.436
CL	ΔS	-.081	-.005	-.008	.238	.037	-.062	-.055	-.090	-.209
	ΔD	-.020	.095	.081	.140	.129	-.044	-.074	.052	.051

[a]Averages, weighted by the number of progeny, for ΔS and ΔD excluding foundation parents.

[b]Average selection differentials for the (same number as actually selected) bulls and heifers each year according to line criteria.

TABLE XXII

MEAN SELECTION DIFFERENTIALS PER GENERATION FOR SELECTED SIRES (ΔS), DAMS (ΔD) OR MIDPARENTS (ΔM)[a,b]

Line	Item	BW (lb)	WADG (lb/day)	WW (lb)	WG (units)[c]	WC (units)[d]	YW (lb)	YADG (lb/day)	YG (units)[c]	YC (units)[d]
	ΔS	5.12	.30	67.2	.92	.69	89.1	.16	.78	.41
WWL	ΔD	2.43	.10	23.1	.18	.21	27.0	.02	.57	.16
	ΔM	3.78	.20	45.2	.55	.45	58.1	.09	.68	.27
	ΔS	6.67	.26	60.7	.76	.36	134.9	.48	.79	.71
YWL	ΔD	2.13	.09	19.8	.19	.19	27.7	.05	.21	.16
	ΔM	4.40	.18	40.3	.48	.28	81.3	.27	.50	.44
	ΔS	-1.60	.00	-1.7	.02	-.01	18.6	.13	.21	.11
CL	ΔD	1.54	.02	6.6	.07	.06	11.1	.05	.28	.21
	ΔM	.03	.01	2.5	.05	.03	29.7	.09	.25	.16

[a]Expressed in deviated measure.

[b]Averages, weighted by the number of progeny, for ΔS and ΔD excluding foundation parents.

[c]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[d]17 point scoring system where 13 = average fat cover.

comparing selection differentials of actual and potential mean CSDs in Table XXI for the trait of primary selection in each line. In the WWL, 88% and 70% of potential selection was realized in WW for sires and dams, respectively while corresponding values in the YWL for YW were 100% and 43%, respectively. Selection criteria for bulls in the YWL was followed exactly; however, heifer selection in the YWL was quite a bit poorer than in the WWL. In heifers, failure to conceive was probably the largest reason for loss of selection pressure with other unsoundnesses also contributing. Another source of loss of selection pressure, especially in heifers, could be attributed to method of adjustments of calf records for age of dam differences. Actual selections were based on multiplicative age of dam correction factors during the early years of the study then switched to additive correction factors for the remainder of the study. As discussed in Materials and Methods, data in this analysis was adjusted for age of dam differences by correction factors developed upon completion of the study. Therefore, two different sets of age of dam correction factors were used on the field data to make actual selections each year while a third set of correction factors developed in retrospect were used on data from which maximum potential selection differentials were calculated. Top animals probably would remain in the same ranking by any method of adjustment, but rankings of animals close to mean performance might change with these various adjust ment factors; therefore, larger differences between actual and maximum potential selection would occur in heifers than bulls as more heifers were selected.

Indexes in Retrospect

Indexes in retrospect (in standard measure) were calculated for sires and dams using both actual and maximum potential selection differentials per generation given in Table XXI. Pooled within line phenotypic correlations for Hereford and Angus lines used in these calculations are in Appendix Tables LII and LIII, respectively. Tables XXIII and XXIV present the indexes in retrospect.

Midparent index selection differentials (ΔI_1) indicate that slightly over one standard deviation unit of selection for this index was applied each generation for the WWL ($1.001\sigma_p$) and YWL ($1.019\sigma_p$). Selection pressure in the CL for the index was less than half the selection applied in the two Hereford lines (approximately $.45\sigma_p$/generation). Ideally, ΔI_i for the CL would be zero.

The proportion of potential selection for this index which was realized can be evaluated by comparing I_1 of the actual and potential indexes. They reveal that 87% and 100% in the WWL and YWL, respectively, of potential selection was realized in sires, while corresponding values for dams were 73% and 71%. These values, except for YWL dams, agree closely with calculations based on only selection differentials of primary traits.

Index 1 weightings (β_{IP_k}) provide a check on how closely selection criteria were followed, since all primary traits are included and weightings indicate direct effects independent of phenotypic correlations with the primary traits. In the WWL, selection pressure (β_{IP_k}) for WW was substantial in both sires and dams. In WWL sires, there was a small amount of unintended selection for conformation. In dams, WW received a

TABLE XXIII

SELECTION INDEXES IN RETROSPECT (IN STANDARD MEASURE) FOR ACTUAL AND MAXIMUM POTENTIAL SELECTION APPLIED - B_{IP_k} FOR INDEX 1

Line	Parental type	BW	WW	WG	WC	YW	YG	YC	ΔI_1
				Actual sire, dam or midparent selection[a]					
WWL	Sire	.035	.760	.132	.024	-.021	.267	-.056	1.418
	Dam	.140	.838	-.469	.187	.210	.051	.134	.630
	Midparent	.074	.817	-.034	.037	.040	.243	-.038	1.001
YWL	Sire	.038	.039	.358	-.319	.880	-.183	.205	1.667
	Dam	.254	1.276	-.280	-.032	-.583	.323	.239	.547
	Midparent	.104	.345	.183	-.254	.547	-.026	.244	1.019
CL	Sire	-.635	-.557	.316	-.458	.887	.373	.095	.578
	Dam	.243	.551	-.168	-.369	-.406	.637	.574	.470
	Midparent	-.336	-.328	.174	-.476	.615	.598	.335	.438
				Maximum potential sire or dam selection[b]					
WWL	Sire	.218	.994	.144	-.053	-.399	.132	.104	1.637
	Dam	.168	.984	-.046	.000	.060	-.232	.011	.859
YWL	Sire	.038	.039	.358	-.319	.880	-.183	.205	1.667
	Dam	.159	.018	-.080	.108	.833	.034	.100	.767
CL	Sire	-.089	-.399	1.119	-.094	.341	-.441	-.659	.429
	Dam	-.037	1.460	.221	-.019	-1.682	.322	.233	.250

[a]Calculated with selection differentials of parents actually selected.

[b]Calculated with maximum potential selection differentials (same number as actually selected) bulls and heifers based on line criteria.

TABLE XXIV

SELECTION INDEXES IN RETROSPECT (IN STANDARD MEASURE) FOR ACTUAL AND MAXIMUM POTENTIAL SELECTION APPLIED - B_{IP_k} FOR INDEX 2

Line	Parental type	BW	WADG	WG	WC	YADG	YG	YC	ΔI_2
				Actual sire, dam or midparent selection[a]					
WWL	Sire	.161	.715	.135	.026	.042	.242	-.079	1.428
	Dam	.339	.946	-.471	.185	.131	.059	.129	.630
	Midparent	.215	.810	-.020	.051	.130	.203	-.074	1.014
YWL	Sire	.140	.523	.345	-.328	.589	-.160	.221	1.654
	Dam	.112	.692	-.040	.190	.830	-.199	-.102	.724
	Midparent	.130	.597	.231	-.165	.696	-.194	.110	1.187
CL	Sire	-.629	-.122	.326	-.405	.723	.313	.057	.611
	Dam	.167	.233	-.038	-.184	.412	.378	.419	.492
	Midparent	-.319	.067	.213	-.372	.604	.451	.245	.478
				Maximum potential sire or dam selection[b]					
WWL	Sire	.361	.725	.146	-.053	-.269	.118	.096	1.642
	Dam	.364	.991	-.052	-.004	.054	-.230	-.001	.870
YWL	Sire	.140	.523	.345	-.328	.589	-.160	.221	1.654
	Dam	.262	.602	-.060	-.113	.603	.010	.075	.786
CL	Sire	-.134	-.258	1.122	-.066	.330	-.458	-.667	.439
	Dam	-.257	.130	.575	.279	-.266	.064	.105	.162

[a]Calculated with selection differentials of parents actually selected.

[b]Calculated with maximum potential selection differentials (same number as actually selected) bulls and heifers based on line criteria.

greater proportion of total emphasis than in sires, with mild unintended selection on YW. Examination of potential indexes indicate if primary selection criteria had been followed exactly in the WWL, there would have been more unintentional selection on BW and negative emphasis on YW for sires. For dams, emphasis of all yearling traits would have been reduced. Actually, in practice, selection pressure exerted in the WWL may be more desirable than maximum potential as all the above mentioned changes in emphasis are not desirable from an industry viewpoint.

In the YWL, the sire index indicates the majority of selection pressure was on YW with some unintentional selection on WG, while selection pressure for WW was near zero. The actual vs maximum potential index for sires of the YWL is the same, as the top bulls for YW were actually used each year. YWL dam's index is difficult to explain. It indicates negative selection pressure on YW and extremely high unintentional selection emphasis on WW with milk positive pressure on BW, YG and YC. This may partially explain the low (43%) realized selection pressure for YW of dams in the YWL discussed in the previous section compared with the 71% of potential selection of the index for YWL dams realized as mentioned above. Comparisons of actual and potential YWL dam indexes indicate selection pressure could have been quite high for YW with little unintentional selection on any other trait. Conception failures at first breeding for heaviest YWL heifers or age of dam adjustment factor inconsistentcies between the data analyzed and actual selection practiced as discussed in the prior section may offer some explanation, but this result is quite surprising and mostly unexplainable.

CL indexes, based on actual selection practiced, showed emphasis on YW for sires, with some selection on conformation, but negative selection for WW and BW. In dams, selection was exerted on WW, YG and YC.

Index 2 provides evidence concerning growth periods that were important during selection. In the WWL, WADG received major emphasis in both sires and dams, with BW receiving more selection pressure in dam selection than expected from its contribution to WW. YADG emphasis was positive, but small in both sexes. In the YWL, the selection pressure exerted on YADG and WADG was nearly proportional for both sires and dams, indicating both periods of growth are important to YW selection.

When interpreting selection indexes in retrospect, it is important to realize they are a function of estimated phenotypic correlations between various traits in each index as well as primary or secondary selection differentials. Although indexes may indicate "unintentional selection" in various traits, other than the primary trait of selection, actual selection procedure could not have taken traits such as conformation and condition into account above their actual contribution due to correlations with weaning, yearling weight, or reproductive ability.

Brinks et al. (1965) reported indexes in retrospect for sires and dams and the average ΔI was .93. Buchanan (1979) also reported indexes in retrospect with traits included similar to the present study. ΔI values in the study reported by Buchanan had more emphasis on sire selection and less on dam selection. Generally, except for Index 1, YWL dams, emphasis on various traits was similar for both indexes.

Response to Selection

Phenotypic Trends

Annual phenotypic trends for each line are presented in Figures 1-7 for BW, WADG, WW, WG, YW, YADG and YG. Tables of annual means for each of these traits plus WC and YC are presented in Appendix Tables LIV-LXII by sex of calf. Since the two Hereford lines were derived from a common base, they should not differ except for sampling error until 1966 when the first calves from selected parents were produced. Differences between the Angus CL and Hereford selection lines until 1966 should be due mostly to breed differences. As described in materials and methods, the CL originally was a progeny tested selection line until the 1970 calf crop, so one set of selected sires were used to produce the 1968 calf crop, thus introducing some selection pressure for growth. In total, as previously discussed, the cumulative selection differentials realized in the CL were $.42\sigma_p$ and $.70\sigma_p$ for WW and YW, respectively. From 1970 on, any increase in differences between the selection lines and CL should be due to genetic response to selection in the selection lines.

Generally, WWL and YWL followed similar patterns of phenotypic response for all traits. When considering the phenotypic trends for YW for each sex, note selection line means were consistently above CL for heifers, while rankings of the three lines for phenotypic response in bulls changed quite often.

To help clarify phenotypic time trends for the nine traits, regression coefficients of performance on year are given in Table XXV by sex and line. There were negative trends over time for WW and YW for both sexes in all three lines, with larger negative coefficients in the CL. This indicates

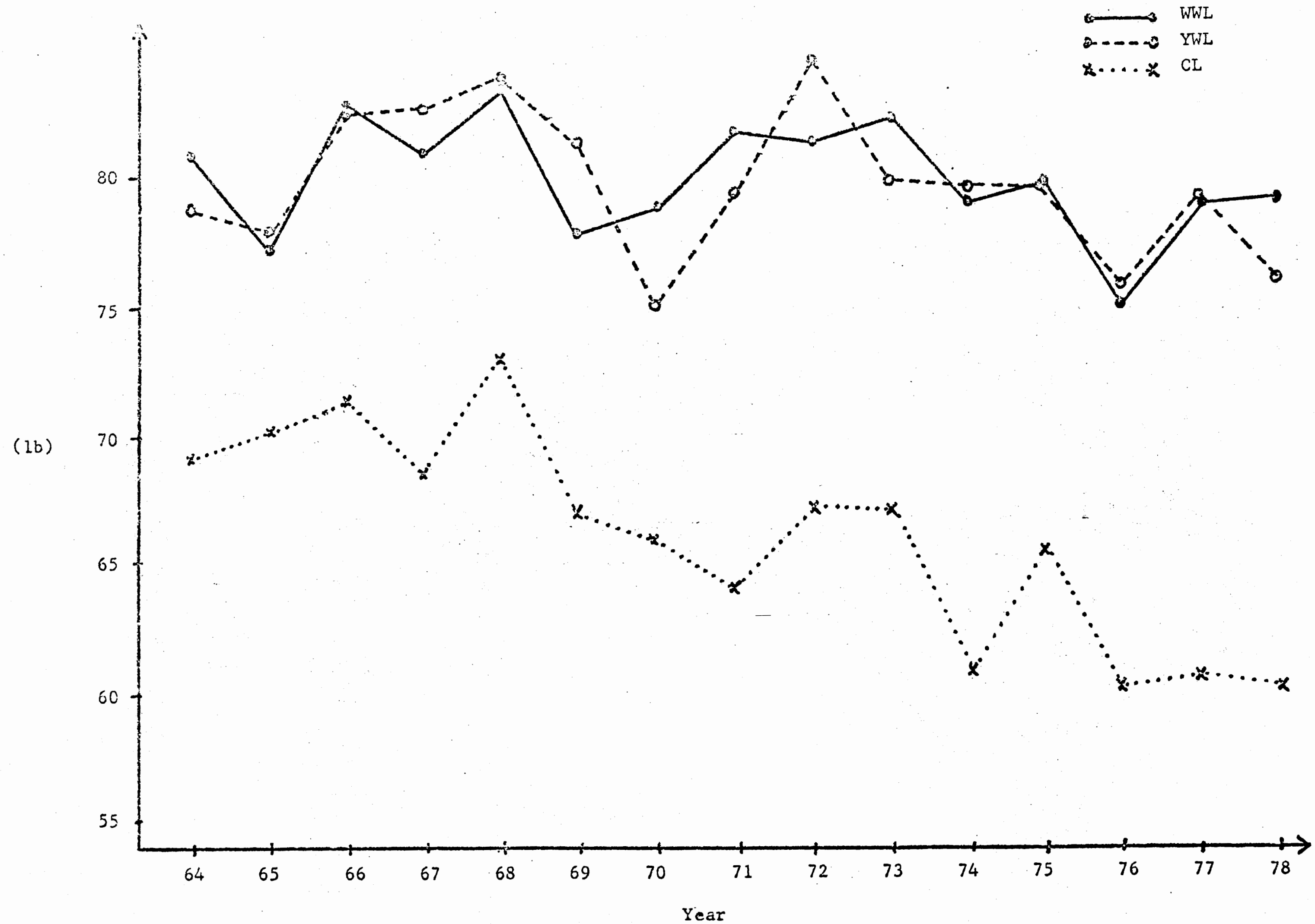


Figure 1. Annual Phenotypic Means for Birthweight Averaged Over Sex

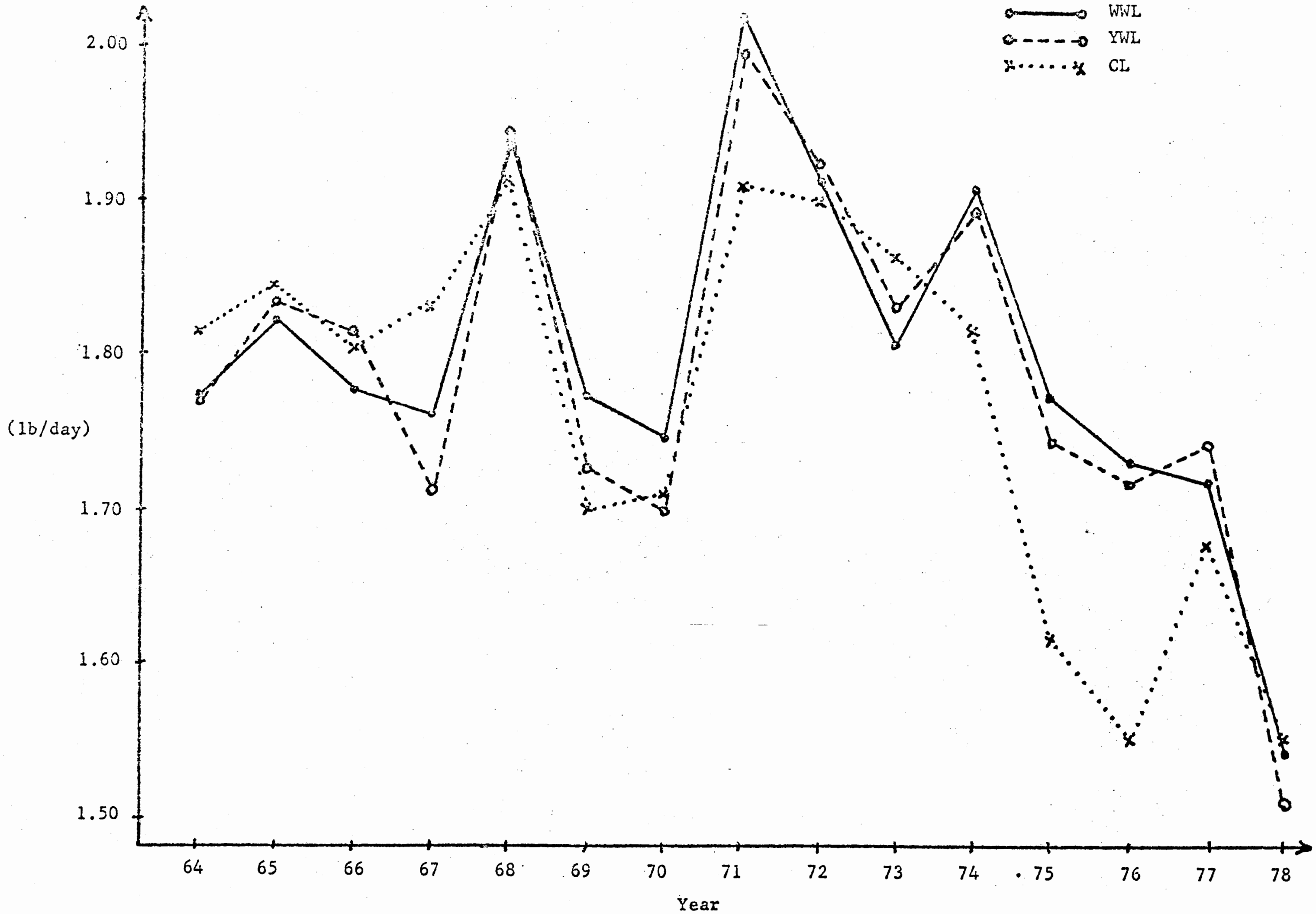


Figure 2. Annual Phenotypic Means for Preweaning Average Daily Gain Averaged Over Sex

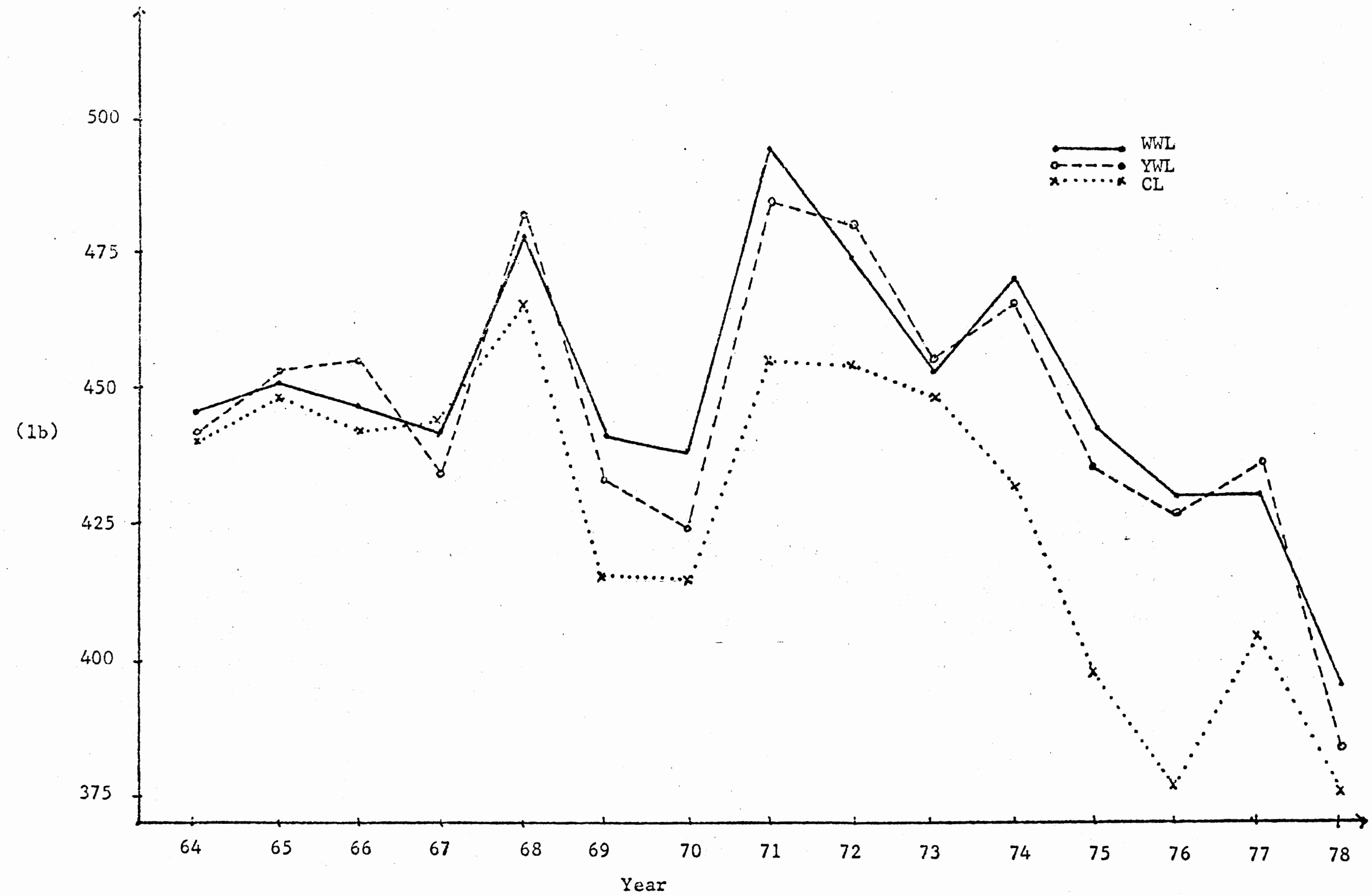
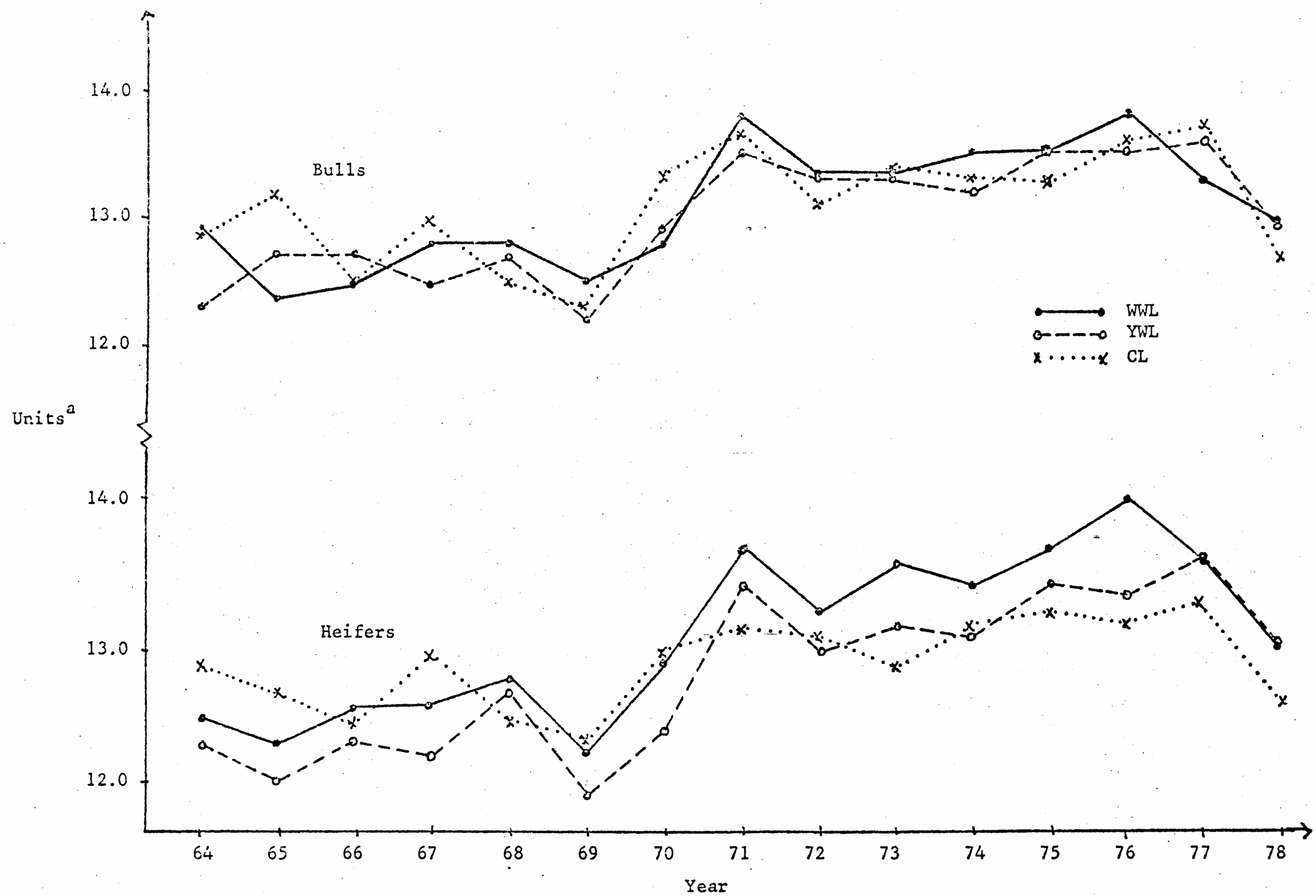


Figure 3. Annual Phenotypic Means for Weaning Weight Averaged Over Sex



[a]13 = average choice, 14 = choice plus, etc.

Figure 4. Annual Phenotypic Means for Weaning Conformation Scores of Bulls and Heifers

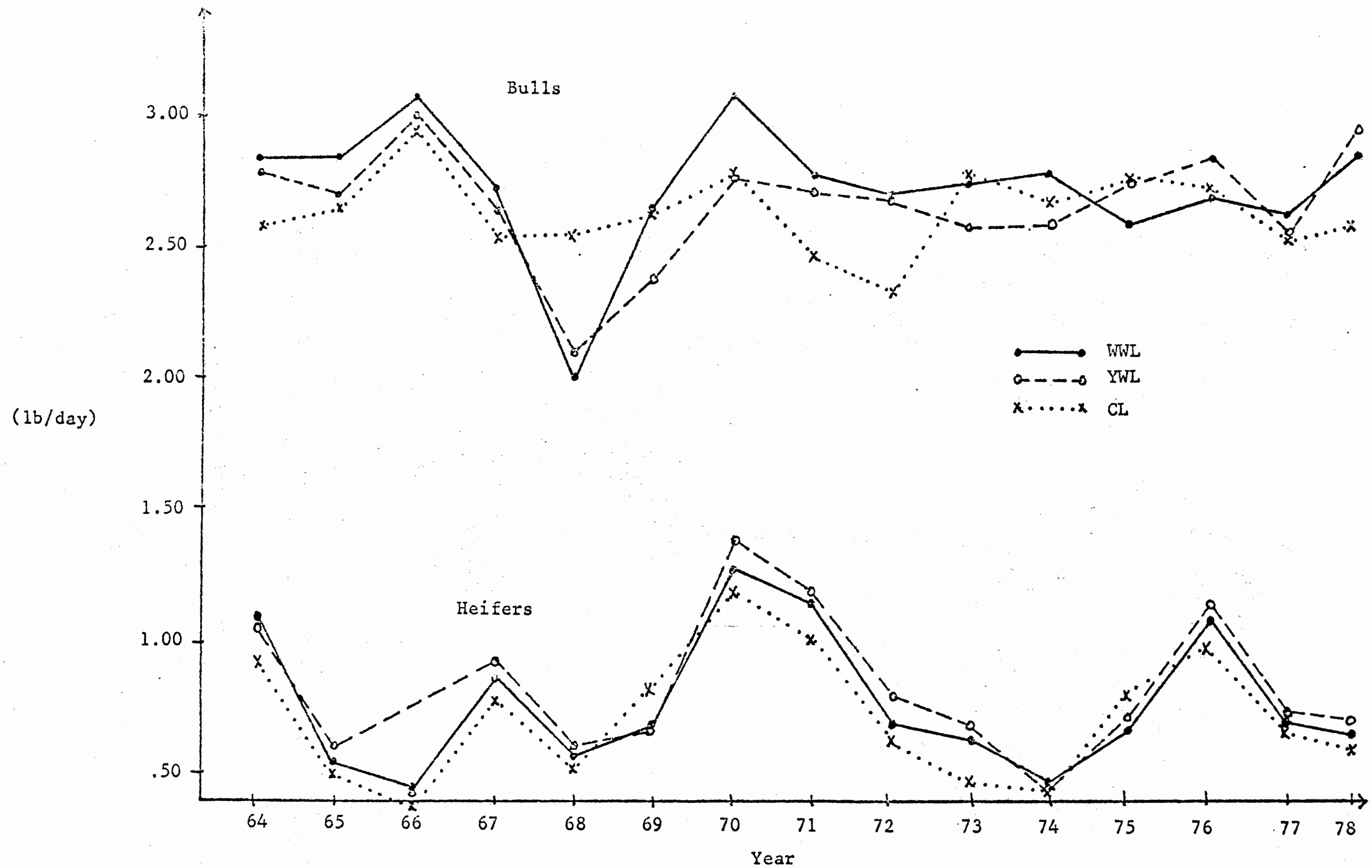


Figure 5. Annual Phenotypic Means for Postweaning Average Daily Gain for Bulls and Heifers

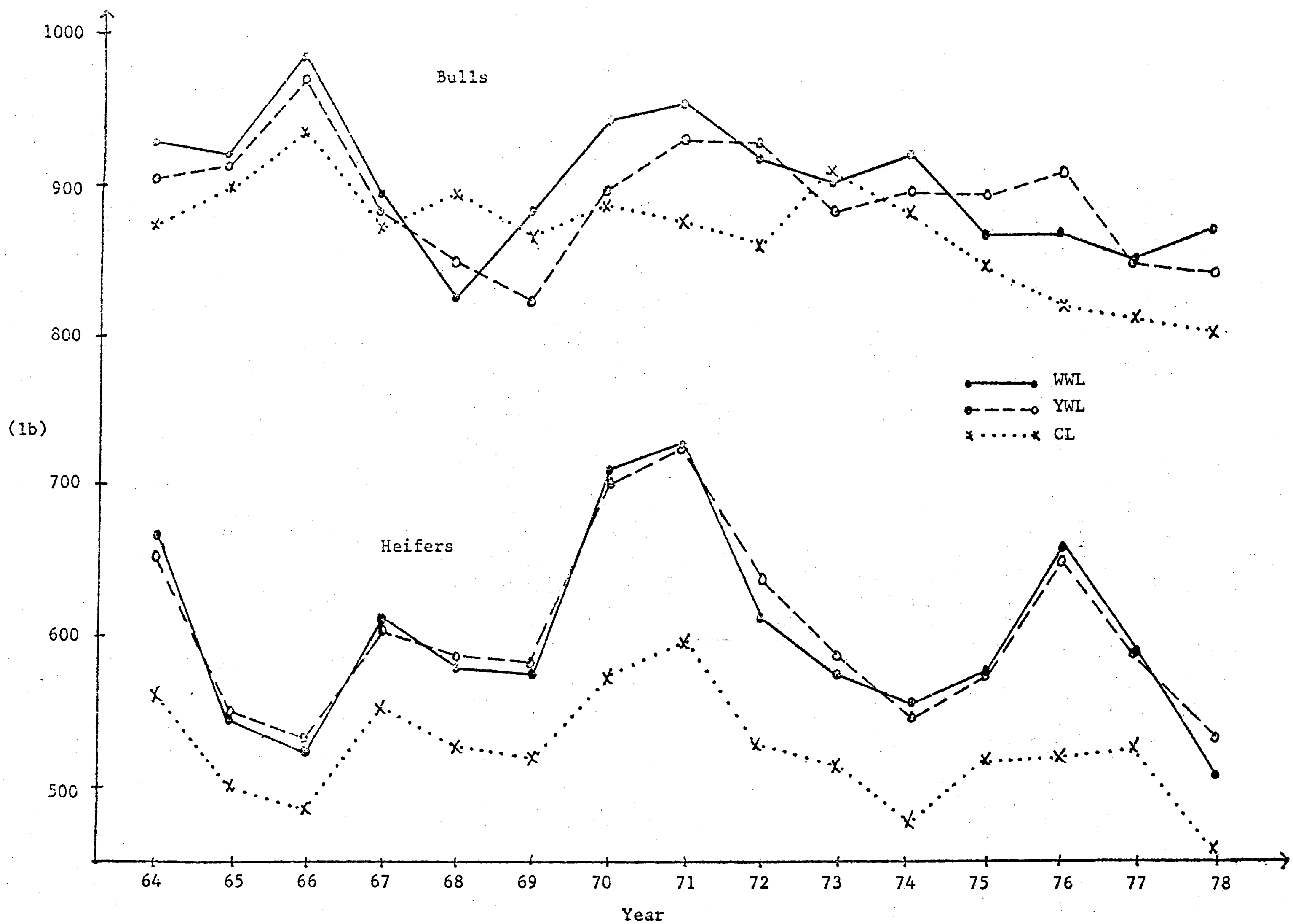


Figure 6. Annual Phenotypic Means for Yearling Weight for Bulls and Heifers

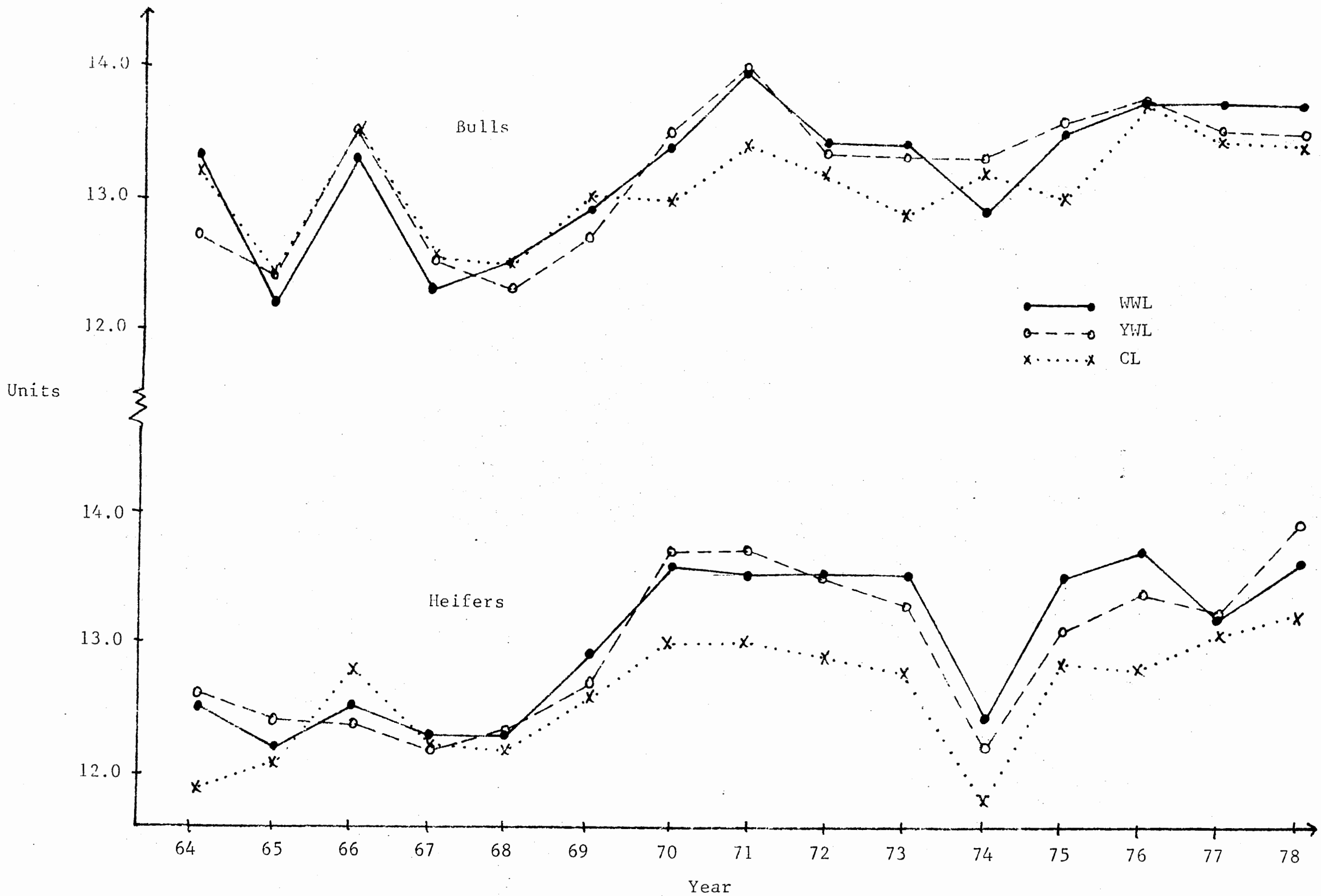


Figure 7. Annual Phenotypic Means for Yearling Conformation Scores of Bulls and Heifers

TABLE XXV

COEFFICIENTS OF REGRESSION OF PERFORMANCE ON YEAR

Trait	WWL			YWL			CL		
	Bulls	Heifers	Average	Bulls	Heifers	Average	Bulls	Heifers	Average
BW (lb/yr)	-.26±.12	-.16±.12	-.21	-.31±.12	-.17±.12	-.24	-.84±.10	-.66±.09	-.75
WADG (lb/day/yr)	-.011±.003	-.006±.003	-.009	-.015±.003	-.005±.003	-.010	-.023±.002	-.012±.002	-.018
WW (lb/yr)	-2.53±.74	-1.39±.62	-1.96	-3.43±.70	-1.13±.64	-2.28	-5.59±.52	-3.07±.48	-4.33
WG (units/yr)[a]	.082±.012	.101±.010	.092	.079±.011	.107±.011	.093	.058±.009	.042±.009	.050
WC (units/yr)[b]	.108±.011	.086±.009	.097	.092±.010	.085±.011	.089	.078±.008	.051±.009	.065
YW (lb/yr)	-4.52±1.30	-1.53±1.14	-3.03	-2.75±1.21	-1.09±1.11	-1.92	-6.02±.90	-3.76±.68	-4.89
YADG (lb/day/yr)	-.006±.007	.000±.004	-.003	.004±.005	.001±.004	.003	-.004±.004	-.003±.004	-.004
YG (units/yr)[a]	.090±.013	.103±.048	.097	.083±.012	.084±.013	.084	.059±.009	.059±.010	0.59
YC (units/yr)[b]	.065±.012	.049±.011	.057	.079±.010	.060±.011	.070	.064±.009	.068±.012	.066

[a] 17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b] 17 point scoring system where 13 = average fat cover, etc.

a negative environmental trend over the 15 year period. A trend for hotter, drier climatic conditions as the study progressed could have contributed to deterioration in the environment at the experiment station which resulted in less available forage for beef production on the experimental range. The standard errors of the regression coefficients indicate there was considerable variation in mean WW and YW year to year, with more variation observed in WWL and YWL than CL. Literature estimates of phenotypic trend are varied, however many observed negative environmental trends. Flower et al. (1964) and Benson et al. (1972) both have reported negative phenotypic trend in WW with positive genetic response. Koch et al. (1974a,b) observed a negative phenotypic trend in YW of bulls when selecting for WW or YW, while Chapman et al. (1969 and 1970) reported phenotypic trends that are negative for WW when selecting for WW.

A correlated phenotypic response in frame is also of interest when selecting for weights at various ages. In 1978, yearling hip height was measured on the two selection lines. Differences between the WWL and YWL were not significant (P=.23) while individual sires within line approached significance as a source of variation (P=.06). Least squares means for the WWL and YWL were 42.5 in and 42.1 in, respectively, thus the phenotypic correlated change in yearling hip height apparently is the same when selecting for WW or YW.

Genetic Change Estimated as Deviations from the Control Line

Phenotypic trends are the combined result of genetic and environmental effects. Direct estimation of environmental trend was obtained from the CL (although confounded by some selection pressure as discussed previously);

thus genetic trends due to selection pressure in WWL and YWL can be obtained simply by deviation from CL, Figure 8 portrays annual genetic trends in WW averaged over sex for WWL and YWL. Genetically, the two lines progressed at similar rates over time, improving until the 1977 calf crop. Genetic differences during 1964 and 1965 between the selection lines and CL were small, indicating little genetic difference for WW of the two breeds in the foundation population. In 1967 WW for both selection lines was genetically below CL. Up until the 1969 calf crop some selection pressure had been exerted in the CL as discussed previously.

Figures 9 and 10 represent genetic trends for YW of bulls and heifers, respectively in WWL and YWL. Again the annual genetic means for both Hereford lines followed similar patterns; however, there was considerably more flucuation in genetic trends of bulls than heifers. Selection line heifers genetically outperformed CL heifers throughout the study while progress for bulls in YW was quite sporadic.

To better quantify genetic trends, Table XXVI presents differences between selection line and CL coefficients of regression of phenotypic means in years (Table XXV) to give genetic change realized per year of bulls, heifers and averaged over sex for the nine traits of primary interest.

Direct genetic response for WW in the WWL was estimated to be 3.06 lb/yr in bulls and 1.68 lb/yr in heifers for an average of 2.37 lb/yr. Correlated response of WW when selecting for YW was 2.16 lb/yr and 1.94 lb/yr for bulls and heifers, respectively, averaging 2.05 lb/yr. More genetic response in WW was realized by direct selection than indirect selection in bulls while the opposite was true for heifers. When considering YW, direct genetic response was 3.27 lb/yr in bulls and 2.67 lb/yr in heifers (averaging 2.97 lb/yr) while correlated response was considerably

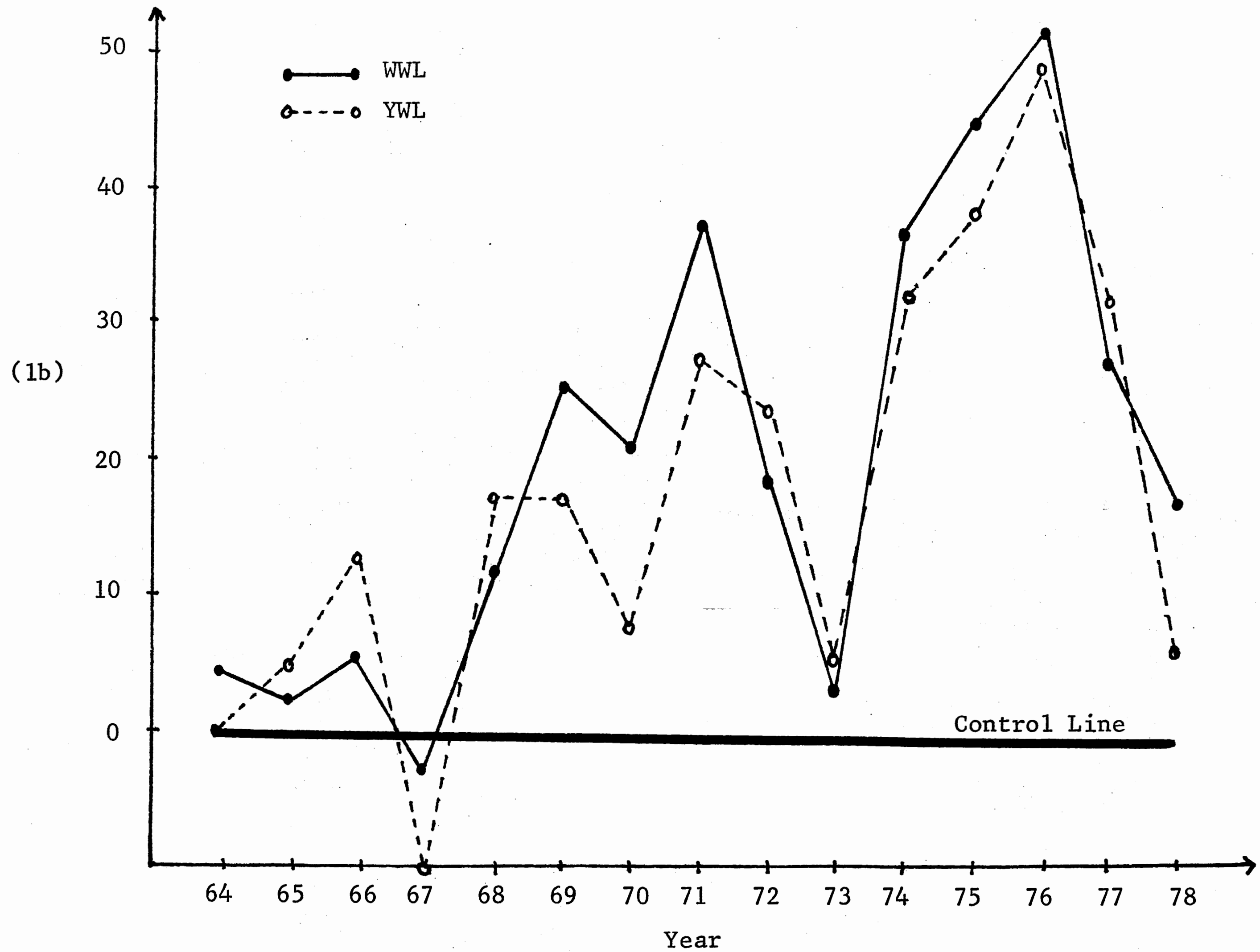


Figure 8. Annual Genetic Trend for Weaning Weight Averaged Over Sex as Deviations from Control

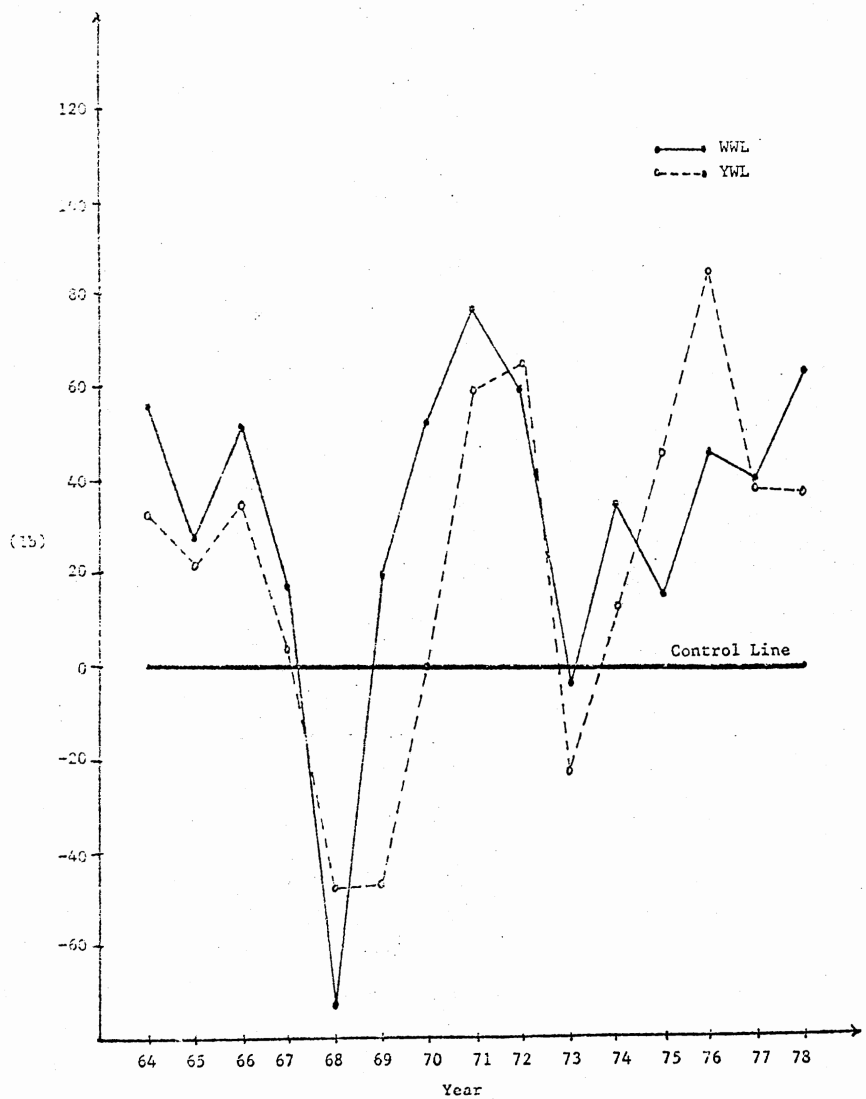


Figure 9. Annual Genetic Trend for Yearling Weight of Bulls as Deviations from the Control

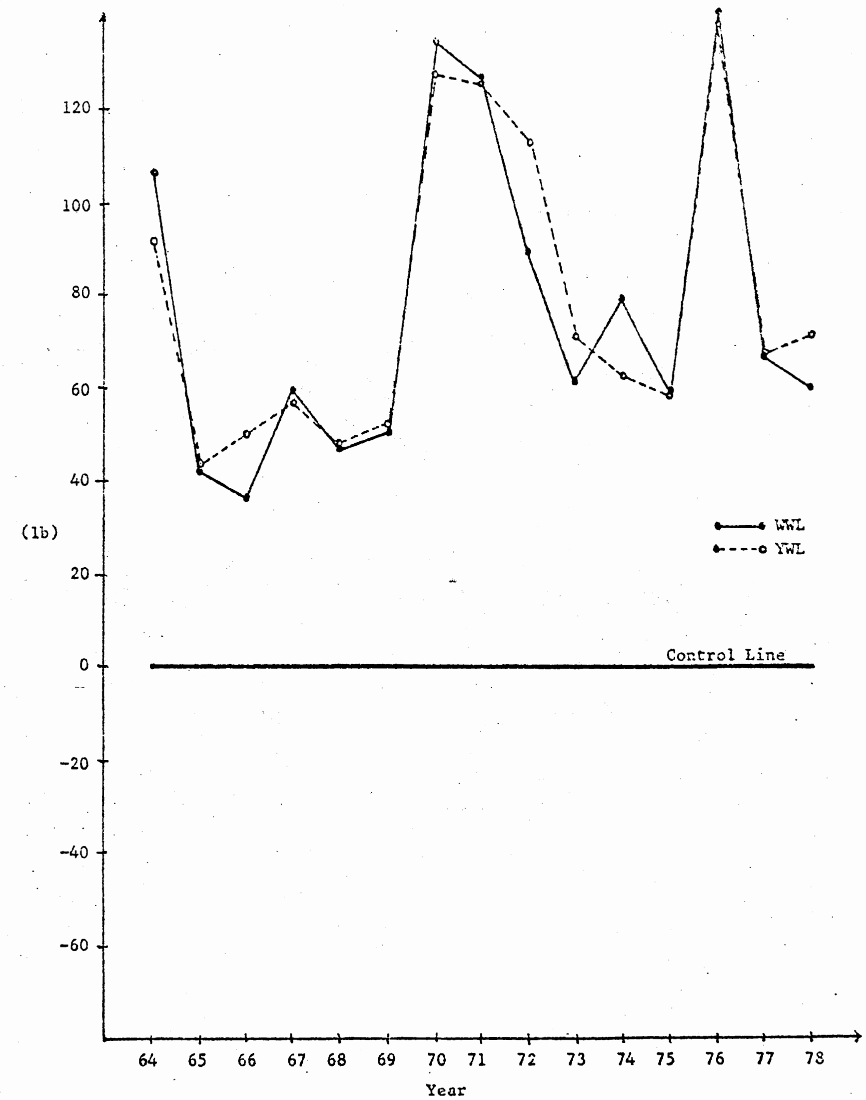


Figure 10. Annual Genetic Trend for Yearling Weight of Heifers as Deviations from the Control

TABLE XXVI

ESTIMATES OF GENETIC TREND FROM DIFFERENCES OF THE CONTROL LINE AND SELECTION LINES[a]

	WWL			YWL		
Trait	Bulls	Heifers	Average	Bulls	Heifers	Average
BW	.58	.50	.54	.53	.49	.51
WADG	.012	.006	.009	.008	.007	.008
WW	3.06	1.68	2.37	2.16	1.94	2.05
WG[b]	.024	.059	.042	.021	.065	.043
WC[c]	.030	.035	.033	.014	.034	.024
YW	1.50	2.23	1.86	3.27	2.67	2.97
YADG	.002	.003	.003	.008	.004	.006
YG[b]	.031	.044	.038	.024	.025	.025
YC[c]	.001	-.019	-.009	.015	-.008	.004

[a]Based on coefficients of regression in Table XXV.

[b]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[c]17 point scoring system where 13 = average fat cover.

lower in bulls (1.50 lb/yr) and similar in heifers (2.23 lb/yr).

Realized heritabilities based on genetic response and mean cumulative selection differentials were .20 for WW and .14 for YW. These realized heritabilities are probably underestimated, as there was some selection pressure in the CL for WW and YW, as previously discussed. Selection pressure realized in the CL would also tend to make the deviation from CL an underestimate of genetic changes in WWL and YWL.

Correlated genetic changes also occured. BW increased in both lines by .54 and .51 lb/yr for WWL and YWL, respectively. Correlated response in bulls and heifers was similar (.55 vs .50 lb/yr). Thus, selecting for increased weight, at either weaning or yearling, also increases BW. WADG also had positive correlated genetic change per year in both lines, with bulls in the WWL increasing twice as much as heifers (.012 vs .006 lb/day/yr). In the YWL, correlated WADG increase was similar in both sexes averaging .008 lb/day/yr. This data indicate selection for WW or YW give similar effects on WADG. Correlated response for YADG was twice as large in YWL as the WWL (.006 vs .003 lb/day/yr) indicating, unlike WADG, YW selection puts more emphasis on YADG than does WW selection. Also, correlated response in the YWL for bulls was twice the magnitude of response in heifers.

Another concern of beef cattle producers are indirect responses in conformation and fatness when selecting for weight traits. Conformation, or degree of muscling, as a correlated response at weaning increased in both lines by a similar magnitude (.043 units/yr). Unexpectedly, increases in heifer WG were more than twice that of bulls (.062 vs .023 units/yr). Correlated YG responses were greater in the WWL (.038 units/yr) than the YWL (.025 units/yr). Condition scores measure degree of finish at a particular weight. Correlated genetic changes in WC were similar in WWL bulls, WWL heifers and YWL heifers, averaging .033 units/yr, while YWL bulls were lower (.014 units/yr). Negative genetic changes occured in YC for heifers of both lines (average -.013 units/yr) and a positive change was observed in YWL bulls (.015 units/yr). Essentially no change occured in YC of WWL bulls. All correlated measures of response in conformation and condition were quite small, with more positive change occuring in degree of muscling than fatness, which is desirable from an industry viewpoint.

Few studies in the literature used control line-selection line deviations to estimate genetic change. Anderson et al. (1974), in a herd of Shorthorn cattle selected for increased YW found yearly response for YW to be 9.81 lb and 6.17 lb for bulls and heifers, respectively, with positive correlated responses in BW, YADG and WW. This is the same data utilized by Newman et al. (1973). Barlow et al. (1978) and Chapman et al. (1969 and 1972) also utilized control lines, but did not report estimates of genetic response. Genetic trends estimated by other various techniques are also reported in the literature and have been summarized in the literature review (Table IV). Most estimates of genetic trend and realized heritability reported from other studies are higher than estimated by the present study. Again, this can be at least partially explained by unintended selection pressure for WW and YW in the control line. Chapman et al. (1969 and 1972) obtained realized heritability estimate of .33. Newman et al. (1973) obtained a pooled estimate of realized heritability for YW of .45 from two selection lines.

Estimates of correlated responses in the literature tend to be in agreement with the present study in terms of direction of response. When selecting for weight at weaning or yearling, studies show positive indirect response in BW, WADG, YADG and weight at various ages (Newman et al., 1973; Anderson et al., 1974; Koch et al., 1974 and Buchanan, 1979). Other studies in which growth rate during a particular period was the selection criteria all tend to show positive correlated responses in WW and YW (Scarsi et al., 1973; Barlow et al., 1978; Willms et al., 1980 and others).

Stanforth (1974) utilized data up until 1973 from the present study on the two selection lines. Genetic trend was estimated by comparison of two foundation sires and four selected bulls from the 1970 calf crop. Semen had been stored on the foundation bulls, and this along with the four selected bulls, was used to produce calves in a progeny test herd in 1972. Progeny produced through these matings provided data for quantifying genetic differences of foundation sires vs selected bulls produced after seven years of selection. Genetic change was estimated by doubling the difference between means for the progeny produced by each group of sires; in other words it is an estimate of differences in breeding values. Although this type of comparison does not quantify genetic response in relation to the population mean, it does provide information which can be used to evaluate the relative effectiveness of selection. Least squares means and standard errors are presented in Table XXVII for progeny of foundation and selected sires. Offspring of selected sires outperformed foundation sires for all triats analyzed. Selected sires' progeny were 29 lb heavier at weaning on the average ($P<.01$); however, differences for YW were not significant ($P=.25$) although progeny of selected sires were 54 lb heavier at yearling time. Estimates of genetic change are given in Table XXVIII. The data indicate yearly changes of 1.06 lb, 8.29 lb, .023

TABLE XXVII

LEAST SQUARES MEANS AND STANDARD ERRORS FOR FOUNDATION AND SELECTED SIRES[a]

Trait	Foundation sires	Selected sires	Difference
Number of progeny	56	47	
BW (lb)	66.6±1.1	70.3±1.8	3.7 (P<.10)
WW (lb)	490±5	519±8	29 (P<.01)
WG[b]	13.4±.1	13.5±.1	.1 (NS)
YW (lb)	778±18	832±30	54 (P=.25)
YADG (lb/day)	1.84±.05	2.01±.08	.17 (P<.10)

[a]Data taken from Stanforth (1974).

[b]17 point scoring system was used where 13 = average choice, 14 = high choice, etc.

TABLE XXVIII

ESTIMATED IMPROVEMENT IN BREEDING VALUES OF SELECTED SIRES OVER FOUNDATION SIRES[a]

Trait	Total change	Change/year
BW (lb)	7.4±3.1	1.06±.45
WW (lb)	58.0±14.6	8.29±2.08
WG[b]	.16±.24	.023±.03
YW (lb)	108.0±51.7	15.4±7.31
YADG (lb/day)	.34±.14	.049±.021

[a]Data taken from Stanforth (1974).

[b]17 point scoring system used where 13 = average choice, 14 = high choice, etc.

units, 15.4 lb and .049 lb/day for BW, WW, WG, YW and YADG, respectively. All estimates, except WG, are considerably higher than the present analysis of genetic trend as a deviation from the control line. But, the estimates obtained from foundation vs selected sires cannot be related directly to effectiveness of selection for improving the population mean performance since selected bulls are not "average" and genetic improvement in the cow herd was not quantified. It does point out, however, selection for WW and YW was effective as selected sires had superior breeding value to foundation sires.

Other techniques have been utilized to estimate genetic change in studies where no control line was maintained to monitor environmental fluctuations. Two of these techniques have been utilized to estimate genetic trend from the present study. Tables XXIX, XXX and XXXI present genetic changes per year in each line due to changes in sire and dam breeding values by a method developed by Smith et al. (1962) and further developed by Zollinger (1981). This method uses regression techniques to obtain genetic trend due to sires and dams by utilizing the fact that sires were used in more than one year and dams usually have more than one off-spring during their productive herd life. In the WWL (table XXIX), average genetic trends per year were estimated to be positive for all traits but YG and YC. BW, WADG and WW were all underestimated when compared to yearly genetic trend values obtained as deviations from the control line (.22 vs .54 lb; .001 vs .009 lb/day; and 1.58 vs 2.37 lb, respectively), while YW and YADG were overestimated (3.40 vs 1.86 lb and .027 vs .003 lb/day, respectively). The results from the YWL (Table XXX), however, are quite unexplainable, as this technique estimated negative genetic trends, averaged over sexes, for BW, WADG, WW, WG and YW. Comparison of these

TABLE XXIX

ESTIMATES OF GENETIC TREND PER YEAR IN THE WWL BY WITHIN PARENT REGRESSIONS

Trait	Bulls			Heifers			Average		
	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires	Due to dams	Total
BW(lb)	.433±.992	-.121±.213	.312	.295±.992	-.168±.172	.127	.364	-.144	.220
WADG(lb/day)	-.0180±.0274	.0064±.0051	-.0116	.0144±.0239	-.0008±.0036	.0136	-.0018	.0028	.0010
WW(lb)	-.698±5.491	1.790±1.008	1.092	2.856±4.726	-.793±.770	2.063	1.079	.499	1.578
WG[d]	-.0920±.0964	.4701±.0201	.3781	-.0429±.0798	.0014±.0159	-.0415	-.0675	.2358	.1683
WC[e]	-.0972±.0873	.0354±.0191	-.0618	.0500±.0733	-.0009±.0146	.0491	-.0236	.0345	.0109
YW(lb)	2.930±10.252	1.136±2.541	4.066	2.388±6.802	.340±1.289	2.728	2.659	.738	3.397
YADG(lb/day)	.0374±.0492	.0119±.0135	.0493	.0016±.0200	.0031±.0048	.0047	.0195	.0075	.0270
YG[d]	.0233±.1013	-.0055±.0396	.0178	-.5854±.4258	-.0494±.1056	-.6348	-.2811	-.0275	-.3086
YC[e]	.0089±.0917	-.0006±.0250	.0083	-.0185±.0703	.0001±.0147	-.0184	-.0048	-.0003	-.0051

[a]Trend due to sires = -b (deviated trait raito · year)/sire.

[b]Trend due to dams = -b ((deviated trait ratio (progeny)-(sire group))·year)/dam.

[c]Sum of sire and dam contributions to genetic trend.

[d]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[e]17 point scoring system where 13 = average fat cover, etc.

TABLE XXX

ESTIMATES OF GENETIC TREND PER YEAR IN THE YWL BY WITHIN PARENT REGRESSIONS

Trait	Bulls			Heifers			Average		
	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires	Due to dams	Total
BW(lb)	.028±.304	-.066±.193	-.038	-.133±.245	.048±.187	-.085	-.053	-.009	-.062
WADG(lb/day)	-.0061±.0076	-.0003±.0047	-.0064	-.0068±.0060	-.0013±.0041	-.0081	-.0065	-.0008	-.0073
WW(lb)	-1.935±1.524	.067±.993	-1.868	-1.466±1.183	-.342±.822	-1.808	-1.701	-.138	-1.839
WG[d]	-.0170±.0278	.0082±.0194	-.0088	-.0268±.0229	.0077±.0165	-.0191	-.0219	.0080	-.0139
WC[e]	.0007±.0234	.0146±.0159	.0153	-.0248±.0231	.0146±.0160	-.0102	-.0121	.0146	.0025
YW(lb)	.221±3.559	1.374±2.135	1.595	-1.606±1.694	-.450±1.299	-2.056	-.693	.462	-.231
YADG(lb/day)	.0042±.0145	.0020±.0100	.0062	-.0003±.0051	-.0006±.0042	-.0009	.0020	.0007	.0027
YG[d]	-.0107±.0358	-.0084±.0204	-.0191	.0178±.0246	.0246±.0188	.0424	.0004	.0081	.0085
YC[e]	-.0042±.0290	.0022±.0176	-.0020	.0139±.0191	.0055±.0138	.0194	.0049	.0039	.0088

[a]Trend due to sires = -b (deviated trait ratio·year)/sire.

[b]Trend due to dams = -b ((deviated trait ratio (progeny)-(sire group))·year)/dam.

[c]Sum of sire and dam contributions to genetic trend.

[d]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[e]17 point scoring system where 13 = average fat cover, etc.

TABLE XXXI

ESTIMATES OF GENETIC TREND PER YEAR IN THE CL BY WITHIN PARENT REGRESSIONS

Trait	Bulls			Heifers			Average		
	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires[a]	Due to dams[b]	Total[c]	Due to sires	Due to dams	Total
BW(lb)	.129±.418	-.160±.165	-.031	-.014±.405	-.034±.193	-.048	.058	-.097	-.039
WADG(lb/day)	.0071±.0092	-.0024±.0033	.0047	.0063±.0083	.0055±.0037	.0118	.0067	.0016	.0083
WW(lb)	-1.435±1.930	-.555±.690	-1.990	1.224±1.808	1.323±.833	2.547	-.106	.384	.139
WG[d]	-.0755±.0361	.0392±.0130	-.0363	.0062±.0360	.0014±.0175	.0076	-.0345	.0203	-.0142
WC[e]	.0345±.0284	.0207±.0112	-.0138	.0013±.0349	-.0178±.0156	-.0165	-.1712	.0015	-.1697
YW(lb)	-.540±3.660	-.496±1.430	-1.036	2.495±2.203	1.072±1.191	3.567	.978	.288	1.266
YADG(lb/day)	.0047±.0167	-.0008±.0069	.0039	.0050±.0082	.0013±.0044	.0063	.0049	.0003	.0052
YG[d]	.0202±.0357	.0127±.0148	.0329	.0237±.0390	.0149±.0202	.0386	.0220	.0138	.0358
YC[e]	.0282±.0326	.0079±.0149	.0361	.0404±.0360	.0018±.0186	.0422	.0341	.0049	.0390

[a]Trend due to sires = -b (deviated trait ratio·year)/sire.

[b]Trend due to dams = b-((deviated trait ratio (progeny)-(sire group))·year)/dam.

[c]Sum of sire and dam contributions to genetic trend.

[d]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[e]17 point scoring system where 13 = average fat cover, etc.

values to those obtained by control line-selection line deviations (-.06 vs .51 lb/yr for BW; -.007 vs .008 lb/day/yr for WADG; -1.84 vs 2.05 lb/yr for WW; -.014 vs .043 for WG and -.23 vs 2.97 for YW) show large under estimation of genetic trend for all traits. This technique also estimated positive genetic change per year in the CL for WW (.14 lb) and YW (1.27 lb).

Another method of estimating genetic change on a per generation basis involves regressing calf performance as a deviation of year-line-sex contemporary group (or in standardized measure) on calf generation coefficient. These results are presented in Tables XXXII and XXXIII by line and sex. Genetic trend estimates in the WWL were positive for all traits in both sexes and generally much larger in magnitude than the estimates obtained from selection vs control line deviations. Just as in the above method of estimation of genetic change, results obtained in the YWL were quite puzzling. Although the estimate for WW in bulls is of similar magnitude to the CL-YWL deviation (8.38 vs 8.72 lb/generation), estimates for BW, WW, WG, WC, YW and YADG were all negative in heifers as well as estimate for YW, YG and YC response in bulls. CL estimates for genetic trend in WW and YW were negative in both bulls and heifers. This technique may have given unrealistic estimates because of the small amount of variation in calf generation coefficients in any given year.

Because of the unrealistic estimates of genetic trend obtained by these various methods and large inconsistencies observed between these methods and selection line, control line deviations, value of genetic trends estimated by these alternative procedures is questionable. Sizeable positive selection pressure was exerted on all traits of primary concern, either direct or correlated, yet these methods give negative

TABLE XXXII

REGRESSION OF OFFSPRING DEVIATION ON GENERATION COEFFICIENT

Trait	WWL Bulls	WWL Heifers	YWL Bulls	YWL Heifers	CL Bulls	CL Heifers
BW (lb/gen)	3.75±1.74	2.81±1.49	.09±1.56	-.55±1.43	-2.49±1.16	-1.82±1.28
WADG (lb/day/gen)	.088±.047	.051±.034	.026±.037	.004±.033	-.018±.024	.005±.026
WW (lb/gen)	23.60±9.42	8.98±6.70	8.38±7.57	-1.29±6.48	-4.64±5.17	-.311±5.72
WG (units/gen)[a]	.238±.162	.150±.114	.256±.140	-.143±.127	-.093±.098	-.228±.113
WC (units/gen)[b]	.217±.146	.004±.104	.148±.116	-.049±.127	-.067±.075	-.166±.114
YW (lb/gen)	31.37±15.30	19.39±9.54	-2.72±13.61	-1.18±8.94	-4.49±9.73	-5.05±6.92
YADG (lb/day/gen)	.132±.074	.035±.028	.017±.055	-.004±.027	-.009±.045	-.002±.026
YG (units/gen)[a]	.203±.154	-.352±.593	-.014±.136	.097±.129	.010±.093	-.256±.123
YC (units/gen)[b]	.065±.136	.042±.099	-.014±.110	.000±.098	.052±.088	-.095±.111

[a] 17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b] 17 point scoring system where 13 = average fat cover, etc.

TABLE XXXIII

REGRESSION OF STANDARDIZED OFFSPRING DEVIATIONS ON GENERATION COEFFICIENTS

Trait	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
BW	.396±.195	.349±.177	.005±.173	-.075±.167	-.273±.137	-.169±.158
WADG	.395±.209	.226±.173	.097±.167	.068±.172	-.076±.118	-.008±.151
WW	.454±.206	.266±.173	.100±.169	.028±.171	-.090±.119	-.059±.149
WG	.316±.201	.250±.163	.341±.170	-.101±.172	-.150±.129	-.285±.159
WC	.401±.199	.077±.156	.273±.171	.026±.177	-.062±.124	-.187±.164
YW	.414±.185	.332±.175	-.064±.164	.004±.164	-.012±.113	-.090±.147
YADG	.400±.199	.186±.171	.031±.152	-.096±.166	.015±.117	.026±.158
YG	.265±.188	.175±.169	-.020±.165	.117±.169	.012±.121	-.396±.174
YC	.096±.193	.062±.171	-.087±.156	-.004±.166	.076±.128	-.144±.178

[a]17 point scoring system where 13 = average choice, 14 = high choice, etc.

[b]17 point scoring system where 13 = average fat cover, etc.

estimates of genetic trend for many of the traits. Comparison to selection line, control line deviation estimates, points out the value of maintaining a control population in selection line studies to quantify genetic selection response instead of relying on other techniques to estimate genetic trends.

Terminal Outcross Calves

Another comparison of the WWL and YWL was made by using the top three bulls in 1976 and 1977 in both lines to produce calves in 1979 when mated to a group of Angus cows. Differences between calves sired by WWL selected bulls *vs* YWL selected bulls would show if 13 years of selection for WW gives different results than selection for YW

To characterize the last set of selected Hereford bulls, individual cumulative selection differentials (CSD) for each trait are presented in Table XXXIV as well as line averages. In the WWL, the average CSD for WW was 190.5 lb, ranging from 144.9 to 234.9 lb in the six bulls, while the average CSD for YW was 239.7 lb. Similar CSDs for WW (189.6 lb average) was realized in the six YWL bulls; however, YW CSDs in the YWL were considerably higher, averaging 346.8 lb (ranging from 298.4 lb to 377.9 lb). Apparently, at least in this set of bulls, direct selection pressure for YW lead to a correlated selection pressure in WW of similar magnitude to direct selection emphasis on WW, while the reverse was not observed. However, it is important to note this is a very small sample from which to draw inferences.

Another concern in selection studies is the amount of inbreeding accumulated in closed lines. Conscious effort was made throughout the study to avoid half-sib and parent-offspring matings, since closed lines were maintained of 50 cows per line. Inbreeding coefficients of each

TABLE XXXIV

CUMULATIVE SELECTION DIFFERENTIALS[a] FOR BULLS USED TO SIRE TERMINAL CROSS CALVES-1979 (LAST SELECTED HEREFORD BULLS)

Bull	BW (lb)	WADG (lb/day)	WW (lb)	WG (units)	WC (units)	YW (lb)	YADG (lb/day)	YG (units)	YC (units)
					WWL				
5711	17.4	.766	173.5	1.80	1.11	235.5	.496	3.06	.47
5724	23.7	.936	217.5	3.10	2.11	384.5	1.076	3.66	1.37
5742	19.0	.866	196.5	2.40	1.91	264.5	.466	3.66	.97
5602	5.5	.831	175.9	2.50	1.79	199.6	.147	2.37	1.28
5605	7.4	.671	144.9	2.80	1.49	157.6	.077	1.97	1.28
5617	33.5	.981	234.9	3.50	1.78	196.6	-.243	2.37	.68
Average	17.8	.842	190.5	2.68	1.70	239.7	.337	2.85	1.01
					YWL				
6717	13.2	1.02	221.8	2.58	1.86	340.9	.724	2.05	2.05
6719	19.3	.746	171.8	2.58	1.16	377.9	1.274	3.05	1.75
6736	26.3	.836	197.8	2.08	.66	369.9	1.064	2.05	1.05
6602	18.4	.673	157.0	2.51	1.43	298.4	.971	2.36	2.05
6608	23.4	.883	204.0	2.81	1.73	373.4	1.151	2.76	1.25
6637	24.4	.783	185.0	1.51	1.43	320.4	.931	1.96	1.45
Average	20.8	.824	189.6	2.35	1.38	346.8	1.019	2.37	1.60

[a]Deviated from contemporary group within line, year of birth and sex.

[b]CSD=MASM + individual's deviation (MASM = mean accumulated selection differential for males).

bull used to sire the outcross calf crop are given in Table XXXV. Overall, inbreeding for the WWL bulls was 7.7% while YWL bulls averaged 6.0%. Chevraux and Bailey (1977) showed an increase of inbreeding from 1.5% in 1956 to 18.1% in 1974 in a closed selection line, while Nelms and Stratton (1967) observed average inbreeding of 11% in their selection study. Levels of inbreeding in the WWL and YWL presented by Buchanan (1970) were less than the present study (4.4% and 5.5%, respectively in the 1977 calf crop after 15 years of selection); however, their selection lines were maintained with 150 cows and calves had less chance to be produced from related parents.

Traits of outcross progeny produced by these selected bulls were analyzed by least squares procedures. Mean squares of the full model analyses are presented in Table XXXVI and sources of variation that were included in reduced models are given in Table XXXVII for traits through one year of age. Selection line was not a significant source of variation ($P < .05$) for any trait; however, sire differences with line and sex of calf were significant ($P<.05$) for all traits, except YC. Age of dam was included in the model as a covariate to adjust for age of dam differences. Apparently, differences between individual sires within a selection line was much greater than differences between lines.

Least squares means and standard errors for traits through one year of age are reported in Table XXXVIII. Although WW of progeny from sires of the WWL was heavier than progeny of sires from the YWL (469 lb vs 452 lb) and YW was heavier (by 14 lb) for offspring produced by YWL selected bulls, neither difference was significant. On the average, calves produced by WWL sires were 3 lb lighter at birth, gained faster (.08 lb/day

TABLE XXXV

INBREEDING COEFFICIENTS OF BULLS USED TO
SIRE TERMINAL CROSS CALVES-1979
(LAST SELECTED HEREFORD BULLS)

WWL		YWL	
Bull	Inbreeding coefficient	Bull	Inbreeding coefficient
5711	.0918	6717	.0781
5724	.1113	6719	.0391
5742	.0996	6736	.0000
5602	.0625	6602	.0781
5605	.0625	6608	.1250
5617	.0313	6637	.0391
Average	.0765	Average	.0599

TABLE XXXVI

MEAN SQUARES FOR TRAITS THROUGH A YEAR OF AGE ON TERMINAL LINE CROSS CALVES IN 1979 - FULL MODEL

Trait	Source: Selection Line (L)	Sire within Line (SL)	Sex of Calf (S)	L*S	Age of Dam	Error
df:	1	11	1	1	1	67
Birth weight (lb)	97.5	156.9**	914.1**	1.3	929.8**	45.4
Preweaning ADG (lb/day)	.018	.049	.514**	.013	.580**	.049
205-Day weaning weight (lb)	314.0	2750.5	31417.7**	1392.3	34847.6**	2278.0
Weaning conformation	.187	.271	1.864*	.151	3.318**	.354
Weaning condition	1.175*	.530	1.488*	.086	3.916**	.355
ADG weaning to yearling (lb/day)	.271*	.264*	.852**	.069	.102	.101
365-Day weight (lb)	4306.4	15893.1**	105580.5**	6276.3	56525.2**	4926.0
Yearling conformation	.000	.284	3.085**	1.912**	.836+	.257
Yearling condition	.149	.524	.424	.035	1.485*	.336
365-Day hip height (in)	4.03	4.77*	33.04**	.95	3.69	2.18

+P<.10, *P<.05, **P<.01.

[a]Covariate source of variation.

TABLE XXXVII

SOURCES OF VARIATION FOR TRAITS THROUGH A YEAR OF AGE ON TERMINAL LINE CROSS CALVES IN REDUCED MODELS[a]

Trait Source:	Selection Line (L)	Sire within Line (SL)	Sex of calf (S)	L*S	Age of dam[b]
Birth weight (lb)	X	X	X		X
Preweaning ADG (lb/day)	X		X		X
205-Day weaning weight (lb)	X		X		X
Weaning conformation	X		X		X
Weaning condition	X	X	X		X
ADG weaning to yearling (lb/day)	X	X	X		
365-Day weight (lb)	X	X	X		X
Yearling conformation	X		X		X
Yearling condition	X	X			X
365-Day hip height (in)	X	X	X		X

[a]'X' indicates effect in reduced model for that particular trait.

[b]Covariate source of variation.

TABLE XXXVIII

LEAST SQUARES MEANS AND STANDARD ERRORS FOR TRAITS THROUGH A YEAR OF AGE ON TERMINAL LINE CROSS CALVES IN 1979

Trait	WWL	YWL	Difference (WWL-YWL)
Number of animals	41	42	
birth weight (lb)	77.3$\pm$1.1	80.1$\pm$1.6	-2.8
Preweaning average daily gain (lb/day)	1.91$\pm$.04	1.83$\pm$.03	+.08$^+$
205-Day weaning weight (lb)	469$\pm$8	452$\pm$7	+17
Weaning conformation score[a]	13.5$\pm$.1	13.3$\pm$.1	+.2
Weaning condition score[b]	13.4$\pm$.1	13.1$\pm$.1	+.3$^+$
Average daily gain weaning to yearling (lb/day)	2.29$\pm$.05	2.42$\pm$.07	-.13
365-Day weight (lb)	837$\pm$12	851$\pm$16	-14
Yearling conformation score[a]	13.4$\pm$.1	13.2$\pm$.1	+.2
Yearling condition score[b]	13.2$\pm$.1	13.1$\pm$.1	+.1
365-Day hip height (in)	44.4$\pm$.2	44.9$\pm$.3	-.5

$^+P<.10$.

[a]Conformation scores: 13 = average choice, 14 = high choice.

[b]Condition scores: 13 = average fatness.

more) in the preweaning period, had higher conformation (+.2 units average) and condition scores (+.2 units average) at weaning and yearling, gained slower (-.13 lb/day) postweaning and were shorter at the hip (-.5 in) at yearling time than offspring of the YWL sires, none of these differences were significant.

Tables XXXIX and XL give full model mean squares and sources of variation included in reduced models, respectively, for feedlot and carcass trait analyses of these outcross calves. Selection line of sires was a significant source of variation for final feedlot weight and hot carcass weight, while again differences between sires within line were significant for many traits as well as sex of calf.

Feedlot and carcass trait least squares means and standard errors are reported in Table XLI by line of selected sires. Calves were slaughtered as an anticipated low choice carcass was attained. In general, differences between progeny of sires from the two selection lines were small and non-significant for feedlot and carcass traits. Final feedlot weight was heavier ($P < .10$) for calves of YWL sires (+38 lb) and thus hot carcass weight was also heavier ($P < .05$) for progeny of YWL sires (+32 lb). Although ADG between the two lines on test was not significant offspring of the YWL gained .12 lb/day faster, plus went on test 15 lb lighter on the average than WWL sires' progeny and remained on feed for an average of 7 days longer, to contribute to the significant difference in final feedlot weight and hot carcass weight. YWL sires' calves also were more efficient on feed (-.11 lb feed per lb gain); however, this difference was not significant. Differences in carcass traits between these outcross calves were small, although a significant difference ($P < .05$) in marbling score (+.5 units) and thus a difference approaching significance ($P < .10$) for

TABLE XXXIX

MEAN SQUARES FOR FEEDLOT AND CARCASS TRAITS ON TERMINAL
LINE CROSS CALVES IN 1979 - FULL MODELS

Trait	Source:	Selection line (L)	Sire within line (SL)	Sex of calf (S)	L*S	Pen within line	Error
	df:	1	11	1	1	2	66
Initial weight on test (lb)		222.8	3647.2	22013.6*	195.8	121.9	3481.2
Final weight (lb)		22658*	15783*	101012**	7418	2137	5152
ADG on test (lb/day)		.277	.300**	.460*	.224	.008	.104
Days on feed		549.5	1298.6*	270.0	4.3	730.5	539.9
Age at slaughter (days		955.5	1511.1*	.1	39.4	800.4	625.5
Hot carcass weight (lb)		17469*	6258.0*	46233**	7748+	116	2554
Carcass weight per day of age (lb)		.042	.062*	.271	.056	.005	.022
Dressing percentage		11.37+	3.47	1.32	10.59	5.06	4.05
Single fat thickness (in)		.019	.027	.015	.019	.003	.020
Average fat thickness (in)		.003	.037	.061	.030	.003	.023
KHP fat (%)		.343	.614*	5.25**	.068	.098	.281
Marbling score		.697	.601	1.094	.394	1.449	.844
Carcass grade		.928	1.238	3.018	.045	2.431	1.586
Carcass conformation		.288	1.270	9.657**	.053	3.872	.876
Rib eye area (sq in)		4.26+	1.08	12.0**	.8	4.6*	1.3
Cutability(%)		.597	1.767	5.380+	.661	2.975	1.915

+P<.10.
*P<.05.
**P<.01.

TABLE XL

SOURCES OF VARIATION FOR FEEDLOT AND CARCASS TRAITS ON TERMINAL LINE CROSS CALVES IN REDUCED MODELS[a]

Trait Source:	Selection line (L)	Sire within line (SL)	Sex of calf (CA)	L*S	Pen within line
Initial weight on test (lb)	X		X		
Final weight (lb)	X	X	X		
ADG on test (lb/day)	X	X	X		
Days on feed	X	X			
Age at slaughter (days)	X	X			
Hot carcass weight (lb)	X	X	X		
Carcass weight per day of age (lb)	X	X	X		
Dressing percentage	X				
Single fat thickness (in)	X				
Average fat thickness (in)	X		X		
KHP fat (%)	X	X	X		
Marbline score	X		X		
Carcass grade	X		X		
Carcass conformation	X	X	X		
Rib eye area (sq in)	X		X		
Cutability (%)	X		X		

[a]'X' indicates effect in reduced model for that particular trait.

TABLE XLI

LEAST SQUARES MEANS AND STANDARD ERRORS FOR FEEDLOT AND CARCASS TRAITS ON TERMINAL LINE CROSS CALVES IN 1979

Trait	WWL	YWL	Difference (WWL-YWL)
Number of animals	41	42	
Initial weight on test (lb)	467±9	552±9	+15
Final weight (lb)	925±12	963±17	-38^{+}
Average daily gain on test (lb/day)	2.19±.05	2.31±.07	-.12
Days on feed	212±4	219±5	-7
Feed efficiency (lb feed/lb gain)	7.35	7.24	+.11
Age at slaughter (days)	415±4	424±6	-9
Hot carcass weight (lb)	585±8	617±12	-32*
Carcass weight per day of age (lb)	1.42±.02	1.46±.03	-.04
Dressing percentage	63.2±.3	63.6±.3	-.1
Single fat thickness (in)	.63±.02	.62±.02	-.01
Average fat thickness (in)	.76±.03	.75±.02	-.01
KHP fat (%)	2.9±.1	3.1±.1	-.2
Marbling score[a]	5.2±.1	4.7±.1	+.5*
Carcass grade[b]	10.1±.2	9.6±.2	+.5^{+}
Carcass conformation[c]	12.2±.2	12.0±.2	+.2
Rib eye area (sq in)	11.0±.2	11.1±.2	-.1
Cutability[d] (%)	49.1±.2	49.1±.2	0

+P<.10, *P<.05.

[a]Marbling score: 4 = slight, 5 = small.

[b]Carcass grade: 9 = high good, 10 = low choice.

[c]Carcass conformation: 11 = choice, 12 = high choice.

[d]Cutability: Murphey's equation.

carcass grade, gave advantage to calves from WWL sires.

Overall, these data indicate selection for WW or YW tend to give similar responses in correlated traits from birth to the rail. Thus, it might be advantageous to select for WW instead of YW as selection can be made earlier in a calf's life for a savings of time and money. Most other studies have found similar results for the end product of WW or YW selection (Koch et al., 1974; Buchanan, 1979). Also, correlated responses in carcass traits have been shown to be small or nonexistent in other reports as well as the present study (Anderson et al., 1974 and Koch et al., 1978).

Cow Traits - Weight and Milk Production

A correlated response for increase in mature size of cattle would be expected (Brinks et al., 1961 and 1965) when selecting for increased weight at an earlier age. Although genetic response was not measured for cow weight in this study, phenotypic trends were observed and are given for the WWL, YWL and CL in Table XLII. Annual mature cow weights for cows producing a calf that particular year and given along with the regression coefficients of cow weight means on year. These data indicate negative phenotypic trends over time, however indications of negative environmental trends for this study have already been discussed. Standard errors of the regression coefficients indicate substantial yearly variation in mean cow weight for all lines and differences between lines was small.

Selection, especially for WW, would be expected to increase cow milk producing ability ability as a large proportion of variation in calf weaning weights can be explained by differences in cow milk production. Although, estimates of correlated genetic improvement could not be made

TABLE XLII

AVERAGE MATURE[a] COW WEIGHTS BY YEAR[b]

Year	WWL No. of cows	WWL Average wt (lb)	YWL No. of cows	YWL Average wt (lb)	CL No. of cows	CL Average wt (lb)
1964	18	1054	15	1046	6	1063
1965	28	1185	27	1199	9	1029
1966	24	1084	27	1084	13	1024
1967	21	1072	22	1065	19	960
1968	22	1033	25	1039	18	976
1969	17	988	17	1019	13	893
1970	16	1040	14	1003	19	941
1971	18	1208	21	1151	21	1070
1972	22	1186	19	1166	28	1052
1973	17	1062	15	1061	30	995
1974	21	1066	26	1025	28	1021
1975	26	1002	24	986	23	1024
1976	26	1027	22	1049	27	986
1977	25	1094	26	1076	27	985
1978	19	1078	23	1038	20	926
Regression on year		-1.96 ± 14.66		-3.86 ± 13.04		-2.53 ± 11.19

[a]Mature cows are 5 years old or older, producing a calf on their respective lines that year.

[b]Average of spring weight prior to entering the breeding pastures and fall weight after weaning.

from this data, a comparison of the two Hereford lines was made during the summer of 1979 by machine milkout procedures. Monthy trends for 24 hour milk yield and percentage butterfat, protein and total solids are presented in figures 11-14. Differences between selection lines for all traits were generally small and not significant. Analysis was also done on the six month means for all milk production traits by least squares proceedures. Mean squares from full model analysis and sources of variation included in reduced models are given in Tables XLIII and XLIV, respectively, while least square means and standard errors are presented in Table XLV. No significant differences ($P<.05$) were observed between cows of the two Hereford lines for any milk trait; however dams of the weaning weight line tended to produce more milk (+.5 lb/day), containing less butterfat (-.4%) and less total solids (-.3%), but similar protein content, indicating selection for WW or YW both effect dam milk production in a similar manner, however selection for WW may increase milk yields slightly more than selection for YW.

Population Parameter Estimates

Population parameters were estimated for the Hereford cattle pooled over selection lines and for the Angus control line by paternal half-sib analysis, regression of offspring performance on sire performance and regression of offspring performance on dam performance, separately for bulls and heifers. Results are presented in Tables XLVI - LI. All methods gave some negative estimates of heritability, causing some genetic correlations to be nonestimatable because of negative variances. Also, all three methods estimated extremely large and unrealistic genetic

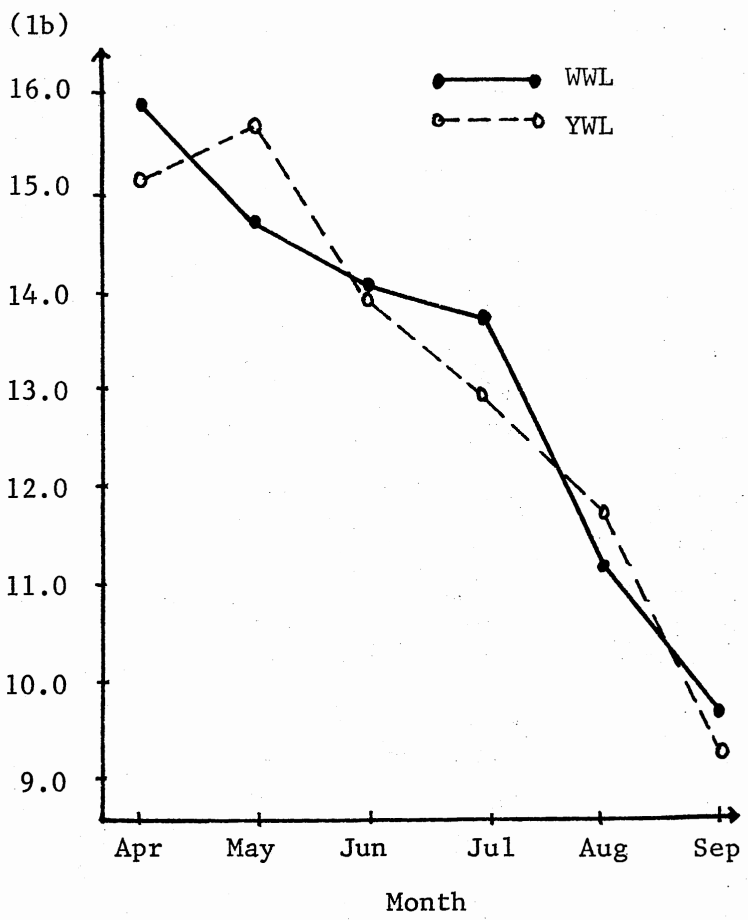


Figure 11. Least Squares Means for 24-Hour Milk Yields by Month

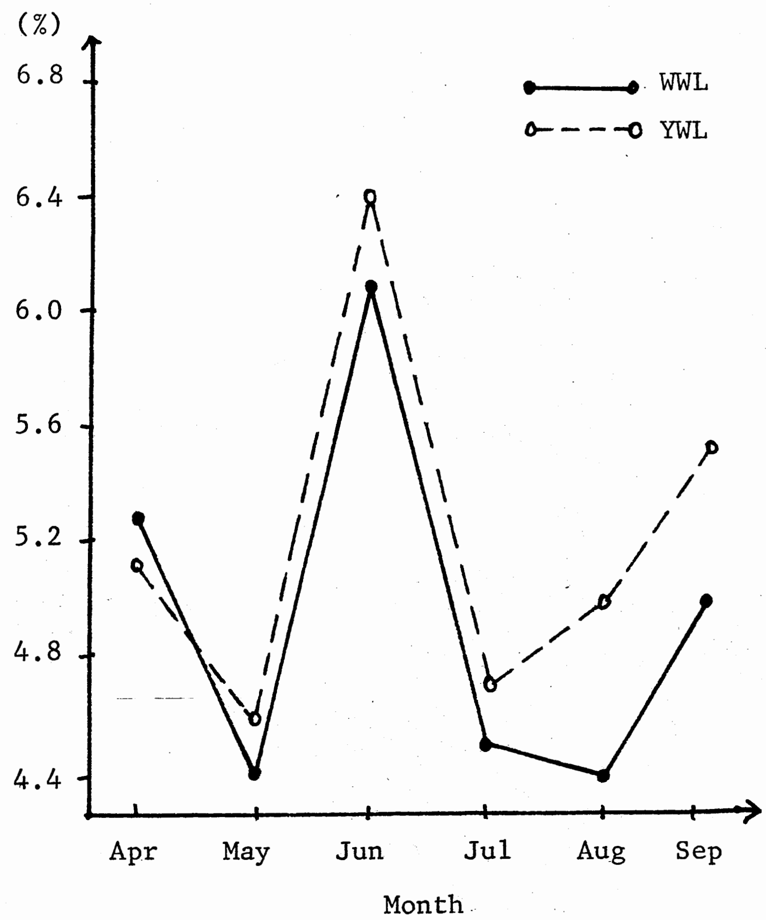


Figure 12. Least Squares Means for Butterfat Percentage by Month

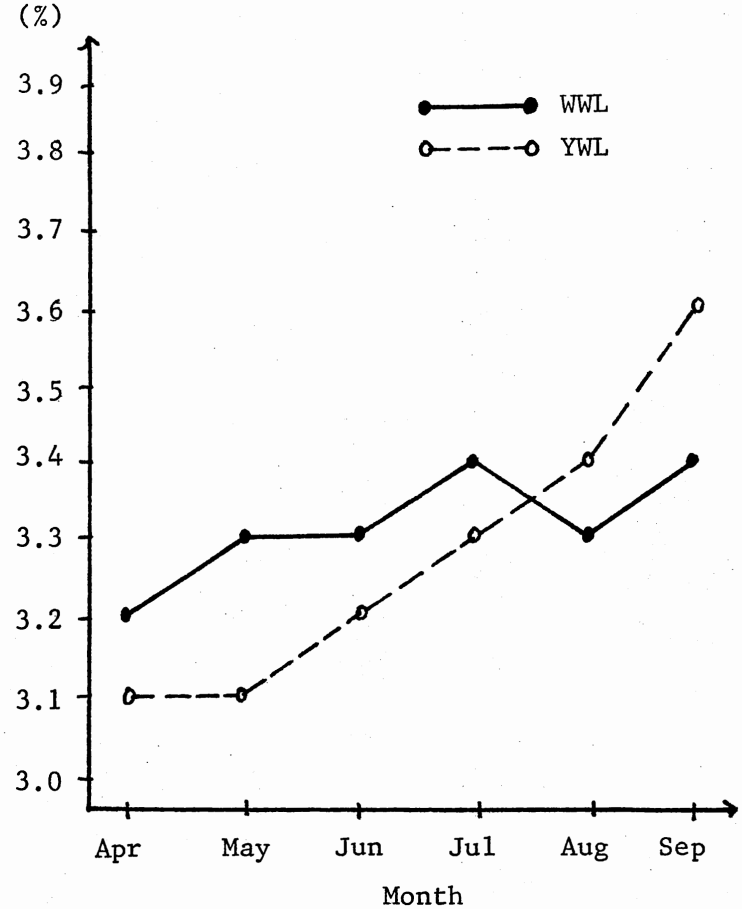


Figure 13. Least Squares Means for Protein Percentage by Month

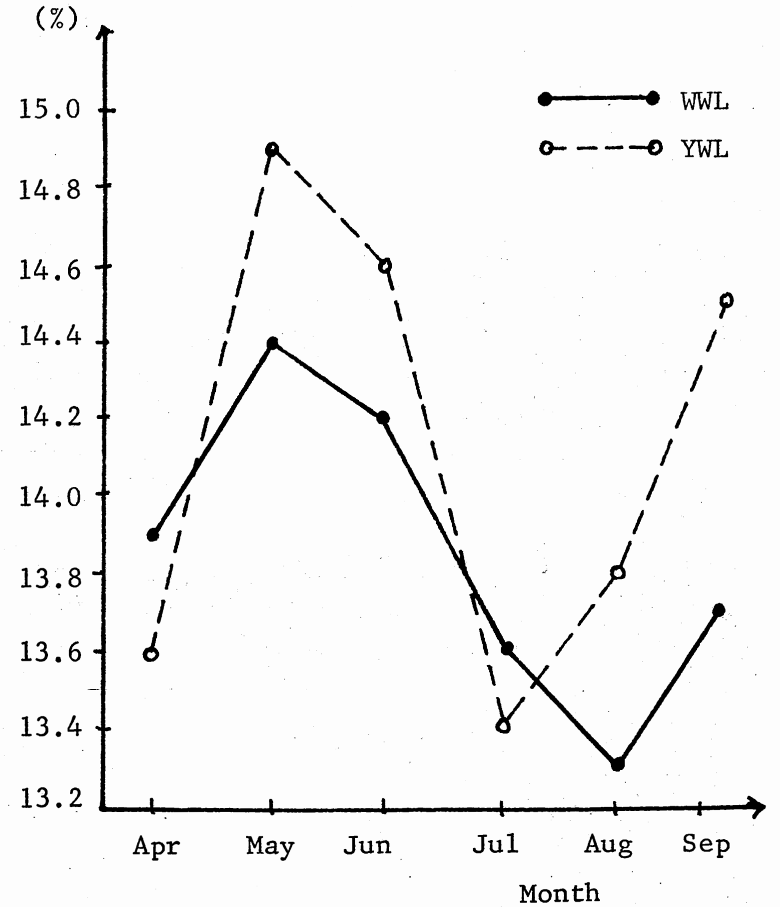


Figure 14. Least Squares Means for Total Solids Percentage by Month

TABLE XLIII

MEAN SQUARES FOR MILK YIELD AND COMPOSITION TRAITS - FULL MODELS

Trait / Source:	Selection line (L)	Sex of calf (S)	Week of milking (W)	Cow age (CA)	L*S	L*CA	Calving date[a]	Error
df:	1	1	1	7	1	7	1	15
Milk yield (lb/day)	3.76	2.94	44.77+	12.60	.02	15.53	14.67	14.67
Butterfat (%)	1.002+	.131	.029	.473	.174	.312	.714	.312
Butterfat yield (lb/day)	.001	.001	.163+	.042	.012	.063	.005	.052
Protein (%)	.001	.077*	.001	.042	.001	.011	.009	.014
Protein yield (lb/day)	.005	.001	.048+	.012	.000	.016	.013	.014
Total solids (%)	.706	.928	.081	.818	.015	.285	.878	.383
Total solid yield (lb/day)	.029	.003	.828	.249	.005	.344	.154	.271

+P<.10, *P<.05.

[a]Covariate source of variation.

TABLE XLIV

SOURCES OF VARIATION FOR MILK YIELD AND COMPOSITION TRAITS IN REDUCED MODELS[a]

Trait Source:	Selection line (L)	Sex of calf (S)	Week of milking (W)	Cow age (CA)	L*S	L*CA	Calving date[b]
Milk yield (lb/day)	X		X				
Butterfat (%)	X						X
Butterfat yield (lb/day)	X		X				
Protein (%)	X	X	X				
Protein yield (lb/day)	X		X				
Total solids (%)	X	X		X			X
Total solids yield (lb/day)	X		X				

[a]'X' indicates effect in reduced model for that particular trait.

[b]Covariate source of variation.

TABLE XLV

LEAST SQUARES MEANS AND STANDARD ERRORS FOR MILK YIELD AND COMPOSITION TRAITS

Trait	WWL	YWL	Difference (WWL-YWL)
Number cow-calf pairs	18	17	
24-Hour milk yield (lb)	13.5±.6	13.0±.9	+.5
Butterfat (%)	4.9±.1	5.3±.1	-.4+
24-Hour butterfat yield (lb)	.68±.05	.69±.05	-.01
Protein (%)	3.3±.1	3.3±.1	0
24-Hour protein yield (lb)	.44±.03	.42±.03	+.02
Total solids (%)	13.9±.1	14.2±.2	-.3
24-Hour total solid yield (lb)	1.89±.12	1.84±.13	+.05

+P<.10

TABLE XLVI

ESTIMATES OF HERITABILITIES AND GENETIC CORRELATIONS[a] FROM POOLED WITHIN LINE PATERNAL HALF-SIB ANALYSES OF COVARIANCE IN HEREFORD LINES

Trait	Sex	BW	WADG	WW	WG	WC	YADG	YW	YG	YC
BW	Bull	.42	NE	NE	NE	NE	.70	1.07	1.30	1.21
	Heifer	.54	.18	.78	.04	-.23	.11	.43	.13	.14
WADG	Bull		-.12	NE	NE	NE	NE	NE	NE	NE
	Heifer		.04	.76	.84	-.33	.63	.79	-.26	-.10
WW	Bull			-.02	NE	NE	NE	NE	NE	NE
	Heifer			.07	.56	-.64	.49	.79	-.12	.01
WG	Bull				-.13	NE	NE	NE	NE	NE
	Heifer				.18	.50	.27	.43	.53	1.00
WC	Bull					-.18	NE	NE	NE	NE
	Heifer					.17	.24	.03	1.76	1.21
YADG	Bull						.13	1.36	-.56	-.61
	Heifer						.30	.93	.62	.76
YW	Bull							.13	-1.92	-1.51
	Heifer							.26	.38	.58
YG	Bull								.04	.55
	Heifer								.29	.95
YC	Bull									.03
	Heifer									.30

[a]Heritabilities on diagonal genetic correlations on off-diagonal.
NE = not estimatible due to negative sire components of variance.

TABLE XLVII

ESTIMATES OF HERITABILITIES AND GENETIC CORRELATIONS[a] FROM PATERNAL HALF-SIB ANALYSES OF COVARIANCE IN THE CONTROL LINE

Trait	Sex	BW	WADG	WW	WG	WC	YADG	YW	YG	YC
BW	Bull	.49	NE	3.69	.10	NE	.52	.96	.24	.57
	Heifer	.00	-8.95	-5.94	NE	.92	1.38	.27	1.92	-4.30
WADG	Bull		-.13	NE	NE	NE	NE	NE	NE	NE
	Heifer		.05	.84	NE	.84	.85	1.16	3.01	-.65
WW	Bull			.03	-.07	NE	.97	1.24	-2.16	.93
	Heifer			.04	NE	.94	.82	1.27	1.04	-.93
WG	Bull				.35	NE	-.37	-.25	-.02	.72
	Heifer				-.05	NE	NE	NE	NE	NE
WC	Bull					-.06	NE	NE	NE	NE
	Heifer					.60	-.31	.14	.90	-.25
YADG	Bull						.41	.94	.60	1.00
	Heifer						.25	.82	-.05	-.09
YW	Bull							.35	.18	.97
	Heifer							.35	.41	-.27
YG	Bull								.12	1.13
	Heifer								.57	.88
YC	Bull									.26
										.44

[a]Heritabilities on diagonal genetic correlations on off-diagonal.
NE = not estimatible due to negative sire components of variance.

TABLE XLVIII

ESTIMATES OF HERITABILITY AND GENETIC CORRELATIONS[a] FROM OFFSPRING-SIRE REGRESSION ANALYSIS OF THE HEREFORD LINES

Trait	Sex	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW	Bulls	.48	NE	NE	-.77	-.45	1.23*	.12	.02	1.61*
	Heifers	.53	NE	NE	.14*	-1.32	2.90*	.28	-.26	NE
WADG	Bulls		-.29	NE	NE	NE	NE	NE	NE	NE
	Heifers		-.26	NE	NE	NE	NE	NE	NE	NE
WW	Bulls			-.25	NE	NE	NE	NE	NE	NE
	Heifers			-.03	NE	NE	NE	NE	NE	NE
WG	Bulls				.08	.16	-.01	.06	.47	.85*
	Heifers				.18	.68*	-42.96*	2.71*	-.16*	NE
WC	Bull					.15	-44.17*	.18*	.48	1.32
	Heifers					.03	-180.64*	5.42*	.78	NE
YW	Bulls						.23	1.19	-41.79	.19
	Heifers						.11	301.86*	4.56	NE
YADG	Bulls							.37	.49*	.44
	Heifers							.11	2.55	NE
YG	Bulls								.31	.71
	Heifers								.40	NE
YC	Bulls									.24
	Heifers									-.05

[a]Heritabilities on diagonal, genetic correlations on off-diagonal.
NE = not estimatible due to negative variances.
*Computed with arithmetic mean instead of geometric mean of the covariances.

TABLE XLIX

ESTIMATES OF HERITABILITY AND GENETIC CORRELATIONS[a] FROM OFFSPRING-SIRE REGRESSION ANALYSIS OF THE CONTROL LINE

Trait	Sex	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW	Bulls	.64	-.88	.01	4.79*	-.15	-2.36	-2.31*	1.87	NE
	Heifers	.31	-.46	-.23	-2.41	-1.34	.11	NE	NE	-.49
WADG	Bulls		.36	.93	2.08*	.65*	221.71*	.06*	8.38*	NE
	Heifers		.43	.08	.94	-.08	.92	NE	NE	5.86*
WW	Bulls			.25	-23.55*	-35.93*	1.02*	-125.90*	-137.81*	NE
	Heifers			.32	.11	-.46	1.14	NE	NE	-36.18*
WG	Bulls				.26	.16	-1.54	-2.00	-4.30*	NE
	Heifers				.04	-.86	126.72*	NE	NE	-.68*
WC	Bulls					.29	-69.15*	-.40	-2.20	NE
	Heifers					.27	19.66	NE	NE	1.24
YW	Bulls						.26	-46.75*	-94.81*	NE
	Heifers						.19	NE	NE	-85.95*
YADG	Bulls							.27	.02	NE
	Heifers							-.08	NE	NE
YG	Bulls								.02	NE
	Heifers								-.32	NE
YC	Bulls									-.27
	Heifers									.07

[a]Heritability on diagonal, genetic correlations on off-diagonal.
NE = not estimatible due to negative variances.
*Computed with arithmetic mean instead of geometric mean of the covariances.

TABLE L

ESTIMATES OF HERITABILITY AND GENETIC CORRELATIONS[a] FROM OFFSPRING-DAM REGRESSION ANALYSIS OF THE HEREFORD LINES

Trait	Sex	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW	Bulls	.61	13.42*	-.72*	-5.54*	.92	.67	.66	-.78*	1.09
	Heifers	.86	NE	1.89	NE	NE	NE	NE	NE	-6.33*
WADG	Bulls		.49	.96	.58	1.11	.71	.47	-.70*	-.22*
	Heifers		-.43	NE	NE	NE	NE	NE	NE	NE
WW	Bulls			.32	.11	1.04	.98	2.72	36.99*	.81
	Heifers			.05	NE	NE	NE	NE	NE	-3.55
WG	Bulls				.04	3.22	-.98*	1.63	2.30	2.25
	Heifers				-.57	NE	NE	NE	NE	NE
WC	Bulls					.24	.83	.77	1.11	1.06
	Heifers					-.13	NE	NE	NE	NE
YW	Bulls						.71	.94	.27	55.88*
	Heifers						-.05	NE	NE	NE
YADG	Bulls							.55	.72	-.56*
	Heifers							-.31	NE	NE
YG	Bulls								.43	1.42
	Heifers								-.17	NE
YC	Bulls									.04
	Heifers									.20

[a]Heritabilities on diagonal, genetic correlations on off-diagonal.
NE = not estimatible due to negative variances.
*Computed with arithmetic mean instead of geometric mean.

TABLE LI

ESTIMATES OF HERITABILITY AND GENETIC CORRELATIONS[a] FROM OFFSPRING-DAM REGRESSION ANALYSIS OF THE CONTROL LINE

Trait	Sex	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW	Bulls	.80	.31	.58	NE	NE	.55	NE	NE	NE
	Heifers	.15	-115.67*	-2.63	-2.08	-9.54*	3.28	NE	-2.37	-12.60*
WADG	Bulls		.45	.95	NE	NE	1.25	NE	NE	NE
	Heifers		.12	2.07	8.84*	-1.60	978.97*	NE	12.07	3.58*
WW	Bulls			.74	NE	NE	1.68	NE	NE	NE
	Heifers			.02	-74.62*	-136.34*	2.92	NE	-163.15*	-134.86*
WG	Bulls				-.48	NE	NE	NE	NE	NE
	Heifers				.25	.13	-.88	NE	.76	-1.20
WC	Bulls					-.16	NE	NE	NE	NE
	Heifers					.10	-1.34	NE	-.19*	1.34*
YW	Bulls						.67	NE	NE	NE
	Heifers						.11	NE	-62.41*	-233.99*
YADG	Bulls							-.44	NE	NE
	Heifers							-.50	NE	NE
YG	Bulls								-.40	NE
	Heifers								.24	.74*
YC	Bulls									-.04
	Heifers									.14

[a]Heritabilities on diagonal, genetic correlations on off-diagonal.
NE = not estimatible due to negative variances.
*Computed with arithmetic mean instead of geometric mean.

correlations because of extremely small variances used in the denominator of the calculations. These unrealistic estimates of heritablities and genetic correlations were quite surprising and unexplainable as postive selection pressure was exerted in all traits and positive genetic response was realized when evaluating genetic trends from selection line deviations from the control line; indicating there should have at least been positive estimates of heritability for the nine traits of primary concern in this study.

CHAPTER V

SUMMARY

The objectives of this study were to quantify selection pressure and estimate response to selection in two lines of Hereford cattle selected for weaning weight and yearling weight, respectively. An Angus control line was also maintained to moniter environmental fluctuations. The primary data were collected on 1273 Hereford calves and 723 Angus calves raised from 1964 to 1978 as part of the Oklahoma beef cattle selection project. Replacement animals were selected on basis of heaviest weight at 205 days of age (WWL) and heaviest weight at yearling (YWL), 365 day weight for bulls following gain tests and 425 day weight for heifers following a grazing period. Four bulls were used per line each year, two in their first year of service and two in their second year of service. The top 13 heifers, based on their respective selection criteria, were kept from each line, each year and bred to calve as two-year-olds. The ten highest ranking pregnant heifers were selected to remain in the line as ten cows in each line were culled. Fifty breeding age females were maintained in each line. The first calves produced from selected parents were born in the 1966 calf crop.

The Angus control line was orginally designed as a progeny test line, but in 1969 the decision was made to change it to an unselected control line (CL). From 1970 on, bulls and heifers in the CL were selected to have, on the average, zero selection differentials for both wean-

ing and yearling weights. In the CL, as in the selection lines, four bulls were used per year and up to ten replacement heifers chosen to maintain a 50 cow line.

Complete performance records were collected on each calf through a year of age for bulls and through 425 days for heifers. The records used in the primary portion of this study were birth weight (BW), weaning weight (WW), preweaning average daily gain (WADG), weaning grade (WG), weaning condition (WC), yearling weight (YW), average daily gain weaning to yearling (YADG), yearling grade (YG) and yearling condition (YC). All traits were adjusted for age of dam effects using additive correction factors developed from all available Hereford and Angus records in the selection study. Conformation scores (grade) were determined for each animal as the average score assigned by a committee of at least three persons where 13 represented average choice. Condition scores were assigned by a similar manner, with 13 representing average fat cover.

The final group of selected Hereford bulls born in 1976 and 1977 from the WWL and YWL were randomly mated to a group of Angus cows to produce calves in 1979. All steer and heifer calves were placed in feedlot and slaughtered when an anticipated low choice quality grade was obtained. Besides the nine traits previously mentioned, data was also collected on feedlot and carcass traits.

Another portion of the study involved the collection of milk production data during the summer of 1979 from 18 Hereford dams of WWL and 17 from the YWL. Lactational performance was determined monthy by machine milkout techniques. Milk composition traits (butterfat, protein, and total solids) were also analyzed.

Cumulative selection differentials (CSD) are equal to the individuals own deviation from its contempory year-line-sex group plus mean accumulated selection (MAS) for that sex of calf, to that point in time. MASs each year were calculated for sires to sons (MASSS), sires to daughters (MASSD) dams to sons (MASDS) and dams to daughters (MASDD). MAS for bulls is the sum of MASSS plus MASDS, while MAS for heifers is the sum of MASSD plus MASDD. CSD for an individual can be viewed as the total selection practiced previously plus any additional selection practiced in the individual.

CSDs were calculated for the nine traits of primary interest in all three lines, in both actual units and in standard measure. To estimate yearly trends, MAS values were regressed on year.

Potential maximum selection differentials were also calculated for the actual top bulls and heifers (based on number actually selected each year) available for selection each year based on line criteria. Indexes in retrospect, showing relative emphasis of componet traits were determined by using pheneotypic correlations calculated from the data and generation mean cumulative selection differentials in standard measure. Index 1 included BW, WADG, WW, WG, WC, YW, YADG, YG and YC and was calculated for both sexes in each line.

Phenotypic trends were evaluated by annual means and regression of annual means on year. Genetic trends were estimated by deviations of the selection lines from control on both a yearly and over year basis. Realized heritabilities were estimated as genetic response per year divided by average cumulative selection differential per year.

Another method used to estimate genetic trend was regression of each trait, as a deviation of year-line-sex group, on year of calf birth within sire (to estimate negative of the genetic change associated with sires) plus the pooled within dam regression of progeny deviated traits as a deviation from sire progeny means on year of calf birth (to estimate negative of the genetic change associated with dams). Another technique employed to measure genetic trend was regression of offspring performance on calf generation coefficient.

Analysis of terminal outcross calf traits by the final set of selected WWL and YWL bulls and cow milk production data were done by generalized least squares proceedures.

Parameter estimates of heritability and genetic correlations were obtained by paternal half-sib analysis, regression of offspring on sire and regression of offspring on dam.

Generations of selection were identical for the WWL and YWL (3.22 generations) in the 15 year period, while the CL was similar, involving 3.21 generations. In 1978, the cumulative selection differentials (CSD) averaged 161 lb ($3.42\sigma_p$) for WW in the WWL and had accumulated at a rate of 12.11 $\pm$ .53 lb/yr, while corresponding values for YW in the YWL were 279 lb ($3.61\sigma_p$) and 21.42 $\pm$ .70 lb per year. These results indicate over one phenotypic standard deviation of selection pressure was applied each generation. Annual correlated selection differentials for YW in the WWL were 75% as large as selecting directly for YW. In the YWL, correlated selection response for WW was 87% as intense as direct selection for WW. Postitive correlated selection differentials were realized for all traits in the selection lines. Results indicate quite a bit of selection pressure for WADG ($2.81\sigma_p$) and WW ($2.98\sigma_p$) in the YWL.

Postive CSDs were realized in the CL for all traits; however, they generally were small, with CSD in 1978 for WW and YW of 13.0 lb ($.36\sigma_p$) and 42.1 lb ($.70\sigma_p$), respectively. Mean accumulated selection differentials, showed selected bulls accounted for 74% and 83% of the selection pressure for WW in the WWL and YW in the YWL, respectively, independent of male selection. The proportions of potential selection realized for WW in the WWL were 88% and 70%, respectively, for sires and dams, while corresponding values in the YWL for YW were 100% and 43%, respectively.

Indexes in retrospect, in standard measure, indicated mild unintended selection for conformation in bulls and for YW in heifers, with the majority of emphasis on WW in both sexes for the WWL. In the YWL, the sire index indicated the majority of selection pressure was on YW with WW selection pressure essentially zero. The YWL's dam index was difficult to explain as it indicated negative selection pressure on YW and extremely high unintentional pre-sure on WW. The CL indexes showed emphasis on YW for sires with negative pressure on WW and BW, while unintentional dam selection pressure was on WW.

Evaluation of phenotypic time trends indicated the WWL and YWL followed similar patterns of response for all traits. There were negative time trends for WW and YW in both sexes for all three lines, with larger negative regression coefficients in the CL, indicating genetic response had occured, but a negative environmental trend had occured over the 13 year period.

Genetic change estimated as deviations from the CL showed direct response for WW in the WWL was 3.06 lb/yr in bulls and 1.68 lb/yr in heifers for an average of 2.37 lb per year. Correlated response of WW in the YWL was 2.16 lb/yr and 1.94 lb/yr for bulls and heifers, respectively, indicating more genetic response in WW was realized by direct selection than indirect selection in bulls with the opposite being true for heifers. The direct response for YW was 3.27 lb/yr for bulls and 2.67 lb/yr in heifers, averaging 2.97 lb/yr in the YWL, while as a correlated response in the WWL, it was considerably lower in bulls (1.50 lb/yr) and similar in heifers (2.23 lb/yr). Realized heritabilities were .20 for WW and .14 for YW. All genetic responses and realized heritabilities were probably underestimated as there was some selection pressure for WW and YW in the control line.

Correlated genetic changes also occured. BW increased in both lines (.54 and .51 lb/yr for WWL and YWL, respectively). Correlated response for WADG was .009 and .008 lb/day/yr for the WWL and YWL, respectively, while response for YADG was twice as large in the YWL as the WWL (.006 vs .003 lb/day/yr). All correlated measures of response in conformation and condition were quite small, with more positive change occuring in degree of muscling than fatness.

Other methods were also employed to evaluate genetic response to selection. An overview of data presented by Stanforth (1974) was given, which was based on an earlier report from a portion of the data in the present study. Estimation of genetic trend by comparison of foundation vs selected sire progeny showed offspring of selected sires outperformed foundation sires for all traits analyzed after only seven years of selection.

Two techniques, regression of performance on generation coefficient and regression techniques involving repeat matings of sires and dams, used in other studies to evaluate genetic trend in the absence of a CL gave unrealistic estimates of genetic response, including many negative values. There were large inconsistencies observed between these methods and selection CL deviations, making the value of these techniques questionable.

An independent comparison of selected WWL and YWL bulls showed both lines were similar for all progeny traits measured through one year of age, although calves from WWL bulls tended to be heavier at weaning (469 vs 452 lb) while the YWL sires' calves tended to be heavier at yearling by 14 pounds. Final feedlot weight was heavier for offspring of the YWL sires, but most other feedlot and carcass traits were similar for both lines. This data indicates selection for WW or YW tend to give similar response in correlated traits from birth to rail.

No correlated phenotypic response was observed for mature cow size. A comparison of the two selection lines for milk production traits showed no significant differences for milk yield or composition traits, although WWL dams tended to produce more milk (+.5 lb/day) than YWL dams.

All methods employed of estimating population parameters gave some negative estimates of heritability, causing some genetic correlations to be nonestimable because of negative variances. Also, these methods estimated some extremely large, unrealistic genetic correlations.

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APPENDIX

TABLE LII

PHENOTYPIC CORRELATIONS AMONG TRAITS IN THE HEREFORD LINES FOR BULLS AND HEIFERS[a,b]

TRAIT	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW		.233	.407	.157	.030	.424	.278	.233	.092
WADG	.151		.982	.654	.586	.689	.174	.465	.357
WW	.344	.978		.644	.556	.728	.217	.478	.350
WG	.142	.664	.659		.715	.436	.095	.509	.350
WC	.032	.629	.604	.756		.378	.082	.422	.405
YW	.402	.696	.744	.432	.364		.811	.627	.561
YADG	.229	-.047	.000	-.093	-.131	.641		.483	.498
YG	.171	.400	.415	.483	.440	.553	.370		.603
YC	.092	.388	.384	.430	.385	.501	.327	.654	

[a]Correlations for bulls are to the right of the diagonal and to the left of the diagonal for heifers.

[b]Pooled within lines.

TABLE LIII

PHENOTYPIC CORRELATIONS AMONG TRAITS IN THE ANGUS LINES FOR BULLS AND HEIFERS[a,b]

Trait	BW	WADG	WW	WG	WC	YW	YADG	YG	YC
BW		.213	.392	.079	.029	.414	.284	.252	.090
WADG	.274		.981	.532	.474	.678	.220	.428	.251
WW	.459	.979		.517	.454	.717	.260	.450	.253
WG	.198	.559	.556		.613	.300	.041	.432	.312
WC	.048	.474	.446	.599		.227	-.013	.306	.401
YW	.510	.785	.831	.372	.266		.855	.575	.339
YADG	.202	-.118	-.069	-.190	-.217	.479		.464	.291
YG	.258	.365	.390	.370	.332	.521	.330		.330
YC	.081	.161	.165	.224	.401	.288	.252	.545	

[a]Correlations for bulls are to the right of the diagonal and to the left of the diagonal for heifers.

[b]Pooled within lines.

TABLE LIV

ANNUAL MEANS AND STANDARD ERRORS FOR BIRTHWEIGHT[a] (LB)

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	80.9±1.8	81.3±2.3	81.2±2.9	75.7±3.3	73.1±3.0	65.6±2.6
1965	81.5±1.9	73.4±2.2	83.0±1.6	73.0±1.8	71.2±1.6	69.5±1.2
1966	86.3±1.5	80.8±2.0	84.7±1.9	81.5±1.5	75.4±1.8	67.5±1.0
1967	83.4±1.4	78.8±1.9	86.1±1.5	80.2±2.0	70.2±1.5	67.0±1.3
1968	85.0±2.1	82.1±1.7	88.7±1.8	81.3±1.5	76.5±1.7	70.1±1.6
1969	78.5±1.8	78.2±1.7	81.9±2.1	79.0+2.2	67.8±1.6	6.61±1.9
1970	80.1±1.7	77.8±1.3	77.8±1.8	72.3±1.8	70.5±1.7	61.3±1.4
1971	83.0±2.6	79.0±1.6	81.5±2.4	76.9±1.3	65.9±2.0	63.5±2.0
1972	82.0±1.8	81.1±1.7	89.1±1.9	82.9±1.5	70.0±1.7	63.0±1.4
1973	86.7±2.2	78.2±1.9	82.9±2.0	76.4±1.3	68.2±2.0	66.4±1.5
1974	80.1±2.0	77.8±1.9	84.2±2.0	75.1±1.6	64.4±1.6	58.5±1.2
1975	81.9±1.6	77.3±1.6	81.7±1.8	77.1±1.2	66.4±1.7	64.7±1.8
1976	76.1±2.4	74.1±1.1	76.8±1.6	75.0±1.7	63.0±1.6	57.5±1.8
1977	78.1±1.8	80.5±2.2	82.8±1.6	77.2±2.1	60.5±1.5	61.5±2.1
1978	84.2±2.2	75.2±2.6	77.7±2.2	74.1±2.7	63.5±1.3	57.2±1.5

[a]Adjusted for age of dam.

TABLE LV

ANNUAL MEANS AND STANDARD ERRORS FOR PREWEANING AVERAGE DAILY GAIN[a] (LB/DAY)

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	1.87±.06	1.68±.06	1.86±.06	1.68±.07	1.92±.05	1.71±.03
1965	1.90±.05	1.75±.03	1.96±.04	1.71±.03	1.95±.04	1.74±.03
1966	1.89±.04	1.66±.03	1.94±.03	1.69±.04	1.90±.04	1.71±.03
1967	1.85±.05	1.67±.03	1.81±.03	1.61±.05	1.94±.03	1.72±.03
1968	2.08±.04	1.80±.03	2.10±.04	1.79±.05	1.00±.03	1.83±.04
1969	1.83±.05	1.71±.03	1.76±.04	1.69±.04	1.81±.04	1.59±.03
1970	1.79±.06	1.72±.04	1.80±.06	1.60±.03	1.84±.03	1.58±.03
1971	2.14±.07	1.90±.04	1.08±.06	1.88±.05	2.03±.04	1.79±.04
1972	1.96±.05	1.87±.04	1.98±.05	1.86±.03	2.04±.04	1.75±.03
1973	1.86±.06	1.76±.04	1.90±.05	1.76±.03	1.93±.04	1.79±.04
1974	1.98±.05	1.84±.04	1.98±.05	1.79±.04	1.91±.03	1.72±.03
1975	1.81±.05	1.73±.05	1.80±.05	1.68±.04	1.64±.03	1.59±.03
1976	1.77±.07	1.70±.03	1.79±.04	1.64±.04	1.62±.04	1.48±.04
1977	1.72±.04	1.72±.07	1.76±.04	1.72±.05	1.67±.04	1.68±.04
1978	1.64±.04	1.44±.04	1.54±.05	1.48±.05	1.62±.03	1.48±.03

[a]Adjusted for age of dam.

TABLE LVI

ANNUAL MEANS AND STANDARD ERRORS FOR 205-DAY WEANING WEIGHT[a] (LB)

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	465±14	462±13	462±13	420±16	467±11	415±6
1965	471±10	431±8	485±9	422±7	470±9	427±7
1966	473±9	422±7	482±9	428±8	465±9	419±6
1967	463±11	420±7	458±6	410±10	469±7	419±6
1968	505±8	451±7	520±9	448±10	487±8	445±8
1969	454±10	429±8	442±9	424±7	438±8	391±7
1970	447±13	430±8	448±12	400±7	447±7	385±7
1971	521±16	468±9	508±14	462±11	482±9	431±9
1972	484±10	464±10	496±11	464±6	488±8	423±6
1973	468±12	438±8	474±11	437±7	465±9	434±9
1974	487±12	455±9	490±11	442±9	456±6	411±6
1975	454±10	431±11	451±11	421±10	404±7	391±6
1976	438±16	423±7	444±10	411±9	395±9	361±9
1977	431±7	434±16	443±9	431±11	404±8	406±8
1978	421±9	370±7	393±10	376±9	396±6	361±6

[a]Adjusted for age of dam.

TABLE LVII

ANNUAL MEANS AND STANDARD ERRORS FOR WEANING CONFORMATION SCORE[a]

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	12.9±.4	12.5±.2	12.3±.3	12.3±.4	12.9±.3	12.9±.2
1965	12.4±.2	12.3±.1	12.7±.2	12.0±.2	13.2±.2	12.7±.1
1966	12.5±.1	12.6±.2	12.7±.2	12.3±.1	12.5±.2	12.5±.1
1967	12.8±.2	12.6±.1	12.5±.1	12.2±.2	13.0±.2	13.0±.2
1968	12.8±.1	12.8±.1	12.7±.1	12.7±.2	12.5±.1	12.5±.1
1969	12.5±.1	12.2±.1	12.2±.1	11.9±.1	12.3±.1	12.3±.1
1970	12.8±.2	12.9±.1	12.9±.1	12.4±.1	13.3±.1	13.0±.1
1971	13.8±.1	13.8±.1	13.5±.2	13.5±.2	13.7±.2	13.2±.2
1972	13.3±.2	13.3±.2	13.3±.2	13.0±.1	13.1±.2	13.1±.1
1973	13.3±.2	13.7±.1	13.3±.1	13.2±.1	13.4±.1	12.9±.1
1974	13.5±.2	13.5±.2	13.2±.3	13.1±.2	13.3±.1	13.2±.1
1975	13.5±.2	13.8±.2	13.5±.2	13.5±.2	13.3±.2	13.3±.1
1976	13.8±.3	14.0±.1	13.5±.2	13.4±.1	13.6±.2	13.2±.2
1977	13.3±.1	13.5±.2	13.6±.1	13.7±.1	13.7±.1	13.4±.1
1978	12.9±.2	13.0±.1	12.9±.1	13.0±.1	12.7±.1	12.6±.1

[a]Adjusted for age of dam.

TABLE LVIII

ANNUAL MEANS AND STANDARD ERRORS FOR WEANING CONDITION SCORE[a]

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	12.4±.3	12.5±.2	12.1±.3	12.1±.4	12.4±.2	12.8±.2
1965	11.8±.2	12.5±.2	12.3±.2	12.2±.2	12.6±.1	12.7±.2
1966	12.0±.2	12.6±.2	12.1±.2	12.4±.2	12.3±.2	12.6±.2
1967	12.4±.1	12.4±.1	11.8±.1	12.0±.2	12.3±.1	13.0±.2
1968	12.3±.1	12.5±.1	12.3±.1	12.3±.1	12.2±.1	12.4±.1
1969	12.2±.1	12.4±.2	12.0±.1	12.1±.1	12.3±.1	12.4±.1
1970	12.5±.2	12.7±.1	12.5±.1	12.2±.1	12.7±.1	12.7±.1
1971	13.7±.1	13.9±.1	13.4±.1	13.6±.1	13.7±.1	13.5±.1
1972	13.2±.1	13.2±.2	13.1±.1	13.2±.1	13.0±.1	13.1±.1
1973	12.3±.2	12.8±.2	12.3±.2	12.3±.1	12.7±.1	12.8±.2
1974	13.3±.1	13.4±.1	13.3±.1	13.0±.2	13.4±.1	13.4±.1
1975	13.3±.1	13.8±.1	13.1±.2	13.2±.1	13.2±.1	13.4±.2
1976	13.4±.2	13.7±.1	13.1±.1	13.2±.1	13.2±.1	13.3±.2
1977	13.1±.1	13.4±.1	13.2±.1	13.7±.2	13.5±.1	13.8±.2
1978	13.0±.2	12.9±.1	12.8±.1	12.8±.1	12.7±.1	12.8±.1

[a]Adjusted for age of dam.

TABLE LIX

ANNUAL MEANS AND STANDARD ERRORS FOR YEARLING WEIGHT[a,b] (LB)

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	927±25	667±17	904±27	652±22	871±22	560±9
1965	922±13	544±12	917±16	546±8	895±16	502±7
1966	988±17	522±10	971±17	536±7	936±18	486±6
1967	896±23	614±8	883±14	611±14	879±11	554±9
1968	824±24	574±8	850±18	575±11	898±15	527±8
1969	886±17	571±9	820±15	573±8	867±13	521±11
1970	947±17	710±12	895±25	703±12	895±15	575±10
1971	953±26	719±11	935±21	719±15	876±15	592±11
1972	919±15	612±10	925±15	636±11	860±11	523±8
1973	902±26	572±17	883±17	582±16	906±17	511±13
1974	920±24	559±18	898±21	543±21	885±13	480±9
1975	863±15	576±14	894±23	575±12	848±17	517±8
1976	868±20	660±9	907±17	655±11	822±17	518±10
1977	851±14	588±18	849±15	588±15	811±13	522±9
1978	872±21	509±10	845±19	530±9	808±13	459±8

[a]Adjusted for age of dam.

[b]365-day weight for bulls and 425-day weight for heifers.

TABLE LX

ANNUAL MEANS AND STANDARD ERRORS FOR POSTWEANING AVERAGE DAILY GAIN[a] (LB/DAY)

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	2.83±.11	1.10±.03	2.79±.10	1.06±.04	2.57±.11	.92±.03
1965	2.83±.07	.52±.03	2.70±.02	.57±.02	2.65±.08	.48±.02
1966	3.09±.09	.44±.03	3.01±.07	.42±.04	2.95±.07	.31±.04
1967	2.71±.11	.86±.02	2.68±.07	.92±.04	2.56±.05	.77±.04
1968	2.00±.12	.56±.02	2.10±.08	.58±.03	2.57±.07	.52±.02
1969	2.67±.08	.65±.03	2.39±.06	.68±.05	2.67±.07	.82±.04
1970	3.09±.07	1.28±.03	2.78±.11	1.38±.03	2.77±.07	1.20±.03
1971	2.76±.10	1.14±.02	2.71±.08	1.17±.03	2.47±.06	1.02±.03
1972	2.68±.07	.68±.03	2.70±.06	.78±.05	2.32±.05	.62±.02
1973	2.73±.11	.61±.07	2.58±.07	.66±.06	2.78±.07	.48±.06
1974	2.78±.16	.46±.05	2.60±.10	.44±.03	2.68±.07	.44±.03
1975	2.60±.07	.66±.04	2.75±.10	.70±.03	2.75±.07	.80±.04
1976	2.71±.09	1.08±.03	2.84±.05	1.13±.03	2.63±.08	.97±.04
1977	2.62±.06	.69±.05	2.57±.05	.72±.05	2.54±.05	.74±.02
1978	2.86±.11	.64±.03	2.86±.07	.70±.02	2.57±.06	.61±.03

[a]Adjusted for age of dam

TABLE LXI

ANNUAL MEANS AND STANDARD ERRORS FOR YEARLING CONDITION SCORE[a]

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	13.4±.3	12.9±.2	12.6±.2	12.6±.2	13.0±.3	12.0±.1
1965	13.2±.2	12.2±.1	12.8±.2	12.3±.1	13.1±.1	12.1±.1
1966	12.5±.1	13.1±.2	12.7±.2	12.2±.2	13.0±.2	12.7±.3
1967	12.8±.2	11.9±.1	12.6±.2	11.9±.1	13.1±.1	12.0±.1
1968	12.1±.1	11.9±.1	12.0±.1	11.7±.1	12.8±.1	12.0±.1
1969	12.9±.2	12.3±.1	13.2±.2	12.2±.1	13.6±.1	12.4±.1
1970	13.9±.2	14.2±.1	13.3±.2	14.1±.1	13.5±.2	14.4±.2
1971	13.8±.2	13.2±.1	13.6±.1	13.1±.2	13.9±.1	13.1±.1
1972	13.4±.1	13.2±.1	13.2±.1	13.1±.1	13.3±.1	13.0±.1
1973	12.9±.2	12.9±.1	12.8±.1	12.8±.1	13.2±.2	12.8±.1
1974	13.1±.2	11.9±.1	12.9±.2	11.9±.1	13.2±.1	11.9±.1
1975	13.4±.1	12.9±.1	13.5±.2	12.7±.1	13.5±.1	13.3±.1
1976	13.5±.1	13.1±.1	13.3±.1	12.9±.1	14.1±.1	13.3±.2
1977	13.9±.2	12.8±.1	13.6±.1	12.9±.2	14.1±.1	13.2±.1
1978	13.7±.2	13.3±.1	13.7±.1	13.5±.1	13.6±.1	13.3±.1

[a]Adjusted for age of dam.

TABLE LXII

ANNUAL MEANS AND STANDARD ERRORS FOR YEARLING CONFORMATION SCORE[a]

Year	WWL		YWL		CL	
	Bulls	Heifers	Bulls	Heifers	Bulls	Heifers
1964	13.3±.4	12.5±.2	12.7±.3	12.6±.2	13.2±.4	11.9±.2
1965	12.2±.2	12.2±.2	12.4±.2	12.4±.1	12.4±.2	12.1±.2
1966	13.3±.2	12.5±.1	13.5±.3	12.4±.2	13.5±.2	12.8±.3
1967	12.3±.2	12.3±.1	12.5±.2	12.2±.2	12.5±.1	12.2±.1
1968	12.5±.2	12.3±.1	12.3±.1	12.3±.2	12.5±.1	12.2±.2
1969	12.9±.2	12.9±.2	12.7±.2	12.7±.1	13.0±.1	12.6±.2
1970	13.4±.2	13.6±.2	13.5±.2	13.7±.1	13.0±.2	13.0±.2
1971	14.0±.3	13.5±.1	14.0±.2	13.7±.2	13.4±.2	13.0±.1
1972	13.4±.1	13.5±.2	13.3±.1	13.5±.1	13.2±.1	12.9±.1
1973	13.4±.3	13.5±.2	13.3±.2	13.3±.2	12.9±.2	12.8±.1
1974	12.9±.2	12.4±.2	13.3±.2	12.2±.1	13.2±.1	11.8±.2
1975	13.5±.2	13.5±.2	13.6±.2	13.1±.2	13.0±.1	12.9±.1
1976	13.7±.2	13.7±.1	13.7±.2	13.4±.2	13.7±.1	12.8±.2
1977	13.7±.1	13.1±.2	13.5±.1	13.2±.2	13.5±.1	13.1±.1
1978	13.7±.2	13.6±.1	13.5±.2	13.9±.1	13.4±.1	13.2±.1

[a]Adjusted for age of dam.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Thesis: DIRECT AND CORRELATED RESPONSES TO SELECTION FOR INCREASED WEANING AND YEARLING WEIGHTS IN HEREFORD CATTLE

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