SELECTION IN HEREFORD CATTLE

II. EXPECTED AND REALIZED RESPONSE

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SUMMARY

Data from 14 inbred lines and 14 linecross groups of Hereford cattle at the San Juan Basin Research Centre, Hesperus, were used to evaluate expected and realized response in birth and weaning traits and postweaning traits in males and females over a 28-year period.

There were large differences in the means and variations of the performance traits among the inbreds and linecrosses, the inbreds showing inbreeding depression and greater variability while the linecrosses manifested within-breed heterosis. Except for gain from weaning to 12 months, genetic progress was expected in all traits studied, mainly due to sire selection. Regressions of annual trait means on years indicated positive phenotypic trends in the inbreds for heart girth circumference, adjusted weaning weight (adjusted for inbreeding), weaning score, final weight and feed consumption of males and the yearling weights and gains of females. **Changes were negative for other traits. In the linecross group phenotypic trends were positive in all traits except heart girth circumference, weaning age, initial test weight and feed efficiency.**

Estimated genetic progress per generation due to within line selection was negative in the inbreds but was considerably positive for the linecrosses in most of the traits. As expected, between line selection yielded greater genetic improvement in the inbred than in the linecross population. The dissimilar patterns of response in the two populations are attributed to high rates and levels of inbreeding. Although variable, the actual progress was below prediction in most of the traits studied.

INTRODUCTION

Experience has shown that most traits of economic importance in beef cattle have moderate to high heritabilities and can be improved by selection. In practical as well as experimental animal breeding it is frequently of interest to know what genetic progress is being made and whether this is in agreement with prediction based on the knowledge of heritability and selection applied. However, previous investigations point out that selection progress frequently falls short of expectation (Lush, 1951; Pirchner, 1969).

Evidence from the literature has shown that when selection is practised, inbreeding followed by crossing of the lines in a large population can be a potent means of changing the population means (Flower *et al.*, 1963; Harwin, 1963; Brinks *et al.*, 1967; Urick *et al.*, 1968; Ray *et al.*,

1970; Brinks *et al.*, 1971; Brinks *et al.*, 1972; Lasley, 1972; Nwakalor *et al.*, 1976).

In the first paper of this series (Nwakalor, Brinks and Richardson, 1982)

the selection applied and the generation intervals were studied in inbred and linecross populations of a Hereford cattle herd. The purpose of this paper is to evaluate the expected genetic progress as well as the genetic response actually realized in the same herd. Agreement between expected and actual response is examined. The applicability of results to beef cattle breeding in Nigeria is discussed.

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MATERIALS AND METHODS

The data were the same as those used in the first paper of this series (Nwakalor, *et al*, 1981) to study the intensity of selection; 14 inbred lines and 14 corresponding (by line of inbred sire) linecross groups of Hereford cattle at San Juan Basin Research Centre, Hesperus, Colorado. The conditions under which the animals were kept have been described in the first paper. The performance characteristics studied were weaning weight and post-weaning traits of males and females described in the first paper (Nwakalor, *et al*, 1981), in addition to birth weight, heart girth circumference at birth, weaning score and weaning age. Weaning score was measured on a scale of 6 points in which 6 represents prime; 5, choice; 4, good; 3, medium; 2, common; and 1, cull. Adjustments of data were as given previously.

Expected Genetic Progress. Genetic progress (ΔG_i) in each of the traits considered in the index was calculated directly from the relative weights in standard measure (a_j), the genetic correlations (r_{gij}) and square roots of heritability (g_i) as $\Delta G_i = (a_j)(r_{gij})(g_i)(g_j)$ (Harvey and Bearden, 1962). This is equivalent to the matrix multiplication $A'G$, where A' is the transpose of A (the row vector of the relative weights in standard measure) and G the genetic variance-covariance matrix in standard measure. In the G matrix the diagonal elements amount to the heritabilities (genetic variances) and the off diagonal elements are the products of $r_{gij} \cdot g_i g_j$ multiplications (genetic covariances).

The genetic correlations and square roots of heritability values were taken from previous studies of Petty and Cartwright (1966), Armstrong (1964), Brinks *et al*. (1964) and Preston and Willis (1974). The ΔG_i values were obtained for inbred

male, inbred female and linecross female selection. The expected genetic progress per generation in standard measure resulting from selection of bulls was converted into actual units by multiplying by the respective standard deviations (table 1) and then averaged with that from selection among females or halved, as the case may be, to estimate the overall genetic progress expected from selection. Improvements expected in initial and final weights on test of bulls were calculated in actual units from weaning weight and average daily gain information. In female selection the expected genetic progress in actual units in the gain periods was obtained as the difference between the two weights concerned.

Realized Genetic Progress. The actual genetic progress resulting from selection was estimated by within-line regression of offspring deviations from annual trait means on generation numbers, after making the necessary adjustments for known causes of environmental variations. Generation numbers were calculated for all animals as $G_0 = (G_s + G_d)/2$, where G_0 is the generation of offspring; G_s , the generation of sire; and G_d , the generation of dam (Brinks *et al*, 1961). The generation numbers measure the average number of segregations back to foundation animals (Koch, *et al*, 1974). All foundation animals and all parents which came from the control line in the herd were assigned generation zero. As Koch *et al*, 1974 noted, this procedure provides a direct estimate of response per generation that is independent of maternal effects or selection bias. Estimates of genetic change resulting from within line selection were calculated for the inbred and linecross populations as the average of regressions by line of inbred sire. In addition, estimates of genetic change due to between line selection as a result of culling of six of the original 14 lines and their corresponding linecross groups were obtain-

ed as the difference between the pooled phenotypic regressions of performance records on years and the average of within line phenotypic regressions on years.

slightly more efficient feed conversion of inbreds. Linecross bulls, on the other hand, gain faster and consume more feed and therefore would be expected to be

TABLE I
Overall Means and Variations of Performance Traits for inbred and linecross Populations

Trait	Inbreds				Linecrosses			
	N	Mean	Std. Dev.	Coeff. of Variation(%)	N	Mean	Std. Dev.	Coeff. of Variation(%)
Calves:								
Birth wt. ..(kg)	345	32.8	4.3	13.0	483	34.5	4.1	11.8
HGC at birth..(cm)	1491	182.3	11.2	6.1	1955	186.2	10.7	5.7
Adjusted wn. wt. (unadj. for Fx) .. (kg)	1580	184	27.9	15.0	—	—	—	—
Adjusted wn. wt. (kg)	1580	198	27.8	14.0	2070	205	26.2	12.9
Weaning score .. (pts.)	1455	4.5	.74	16.4	1901	4.8	.70	14.6
Weaning age .. (days)	1833	201	24.0	11.9	2313	203	23.0	11.3
Bulls:								
Initial test wt. .. (kg)	515	195	34.9	17.9	735	215	33.5	15.6
Final wt. .. (kg.)	329	343	46.0	13.4	580	379	46.6	12.3
Feed consumption .. (kg)	479	924	201.2	21.7	670	1056	191.3	18.1
Feed efficiency (unadj.).. (values)	478	6.51	.917	14.1	668	6.71	.785	11.6
Feed efficiency (adj.).. (values)	478	6.46	.960	14.9	668	6.75	.833	12.3
140-day ave. daily gain.. (kg.)	512	1.11	.191	17.1	729	1.17	.173	14.7
Females:								
Gain wn. - 12 mo .. (kg)	357	29.5	8.7	29.4	322	33.1	10.3	31.1
12-months wt. .. (kg)	357	218	29.4	32.2	33.1	10.3	31.1	
Gain 12-18 mo. .. (kg)	342	68	13.2	19.2	314	72	12.5	17.6
18-months wt. .. (kg)	436	284	30.1	10.6	399	309	28.7	9.2
Mature spring wt. .. (kg)	441	447	43.4	9.7	388	471	42.5	9.1
Mature summer wt. .. (kg)	446	502	48.4	9.6	393	528	44.2	8.3
Mature fall wt. .. (kg)	443	491	47.3	9.6	390	517	44.6	8.6

RESULTS AND DISCUSSION

Means and Variations. The overall means and variations of performance characteristics are shown in table 1. The means manifest heterosis for the linecrosses and inbreeding depression for the inbreds where the average inbreeding had risen to 36.3 percent by 1973. However, since lower feed consumption per unit of gain is desirable, slightly higher values for the linecross population of 6.71 and 6.75 respectively for unadjusted and adjusted feed efficiency as compared with corresponding values of 6.51 and 6.46 for the inbred group suggest

more efficient. Koch *et al.* (1963) pointed out that increases in feed consumption may not result in proportional increase in gain; a curvilinear trend could result from increased losses through heat increment of feeding and/or changes in composition of gain at the higher levels of intake.

The standard deviations of the traits show that opportunity was considerable for selection. Higher variations in the inbred population result from an increase in genetic variance between individual lines.

Expected Genetic Progress. The genetic

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correlations and square roots of heritability used to estimate expected genetic progress are given in table 2 (Petty and Carwright, 1966; Armstrong, 1964;

With weaning weight unadjusted for inbreeding:

$A'G [(.3945 \quad -.0061 \quad .6219)] G$
The results of these multiplications

TABLE 2.
Genetic Correlations and Square Roots of Heritability used to estimate expected genetic Progress

Inbred Males						
Trait	WW	FE	ADG			Sq. Rt. of $h^2 (g_i)$
Weaning weight (WW)	1.00	.08	.58			.55
Feed efficiency (FE)		1.00	-.17			.60
Average daily gain (ADG)			1.00			.42
Females						
	WW	12W	18W	SPW	FAW	Sq. Rt. of $h^2 (g_i)$
Weaning weight (WW)	1.00	.71	.67	.59	.51	.55
12-mo. weight (12W)		1.00	.90	.66	.62	.64
18-mo. weight (18W)			1.00	.84	.74	.71
Mature spring weight (SPW)				1.00	.93	.72
Mature fall weight (FAW)					1.00	.75

Brinks *et al.*, 1964; Preston and Willis, 1974). Except for correlation between feed efficiency and average daily gain, there is no genetic antagonism between traits to retard improvement. Using the matrix multiplication procedure described before and setting

$$G = \begin{bmatrix} .3000 & .0264 & .2297 \\ .0264 & .3600 & -.0734 \\ .2297 & -.0734 & .5200 \end{bmatrix}$$

the expected genetic progress from sire selection ($A'G_S$) was obtained as:

With weaning weight adjusted for inbreeding:

$$A'G [(.4461 \quad -.0092 \quad .6126)] G$$

(table 3) show that genetic progress was expected from sire selection for all traits under study. Most of the expected genetic progress in weaning weight of 4.07 and 4.02 kg resulted from sire selection. Expected genetic progress in the two cases amounted to 4.62 and 4.43 kg for initial weight and 10.27 and 10.00 kg for final weight. Progress expected per generation in actual units was fairly large for average daily gain (.040 kg) but smaller for feed efficiency (-.018). Even though selection pressure was relatively mild on postweaning traits in females, a fair amount of additional improvement should be expected in initial weight, final weight, feed efficiency and average daily gain from selection among females. Therefore, expected progress indicated for these traits (table 3) are likely to be biased somewhat downward.

TABLE 3.
Expected genetic Progress per Generation in Standard and Actual Units from Selection among Males and Females

	Progress in Standard Measure		Progress in Actual Measure ^b					
	With WW Adj. for Fx	With WW Unadj. for Fx	With WW Adj. for Fx		With WW Unadj. for Fx			
Males								
Trait	ΔG_S	ΔG_S	ΔG_S	Ave. ^a	ΔG_S	Ave. ^a		
Weaning wt.	.2743	.2611	7.62	4.07	7.27	4.02		
* Initial test wt.	—	—	9.23	4.62	8.86	4.43		
** Final wt. off test	—	—	20.50	10.27	19.97	10.00		
Feed efficiency	-.0365	-.0374	-.035	-.018	-.036	-.018		
Ave. daily gain	.4218	.4144	.081	.040	.079	.040		
Inbred Females								
	ΔG_D	ΔG_D	ΔG_S	ΔG_D	Ave. ^a	ΔG_S	ΔG_D	Ave. ^a
Weaning wt.	.0182	.0277	7.63	.51	4.07	7.27	.77	4.02
+ Gain WN-12 mo.	—	—	-2.93	-.55	-1.74	-2.58	-.95	-1.76
12-month wt.	-.0019	-.0072	4.69	-.05	2.33	4.69	-.18	2.26
+ Gain 12-18 mo.	—	—	2.22	-.48	.88	2.22	-.49	.87
18-month wt.	-.0174	-.0225	6.92	-.52	3.20	6.92	-.68	3.12
Mature spring wt.	-.0465	-.0480	8.57	-2.02	3.28	8.57	-2.08	3.25
Mature fall wt.	-.0587	-.0613	8.58	-2.78	2.90	8.58	-2.90	2.84
Linecross Females ^c								
Weaning wt.		.0309				7.63	.81	4.22
+ Gain WN-12 mo.		—				-2.75	-1.40	-2.08
12-month wt.		-.0226				4.87	-.59	2.15
+ Gain 12-18 mo.		—				1.73	.40	1.07
18-month wt.		-.0064				6.60	-.19	4.68
Mature spring wt.		.0230				8.39	.98	3.21
Mature fall wt.		.0137				8.08	.61	4.35

^aAve. = $\frac{1}{2}(\Delta G_S + \Delta G_D)$ for weaning weight in males and females and postweaning traits in females
= $\frac{1}{2} \Delta G_S$ for postweaning traits in males

where ΔG_S and ΔG_D are expected genetic progress from selection among bulls and females respectively.

^bUnit in kg. except for feed efficiency

* Progress = Progress in WW + 20 (Progress in ADG)

**Progress = Progress in WW + 160 (Progress in ADG)

+ Progress = Difference between the two weights concerned

^cWeaning weight = adjusted weaning weight.

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The results in standard and actual units show that except for weaning weight, genetic progress expected from selection of inbred females was negative in all traits (table 3). On the contrary, positive progress was expected from linecross female selection in weaning weight and mature spring and fall weights. For 12- and 18-month weights genetic progress expected from linecross female selection was as well negative.

As demonstrated earlier (Nwakalor *et al*, 1981) most of the selection pressure for increased weights and gains was on the sires. Therefore, sire contribution to progress in the postweaning traits of females has to be taken into account. The 18-month weight in heifers was considered nearly equivalent to the final weight in bulls and one standard deviation of selection pressure in final weight of bulls was equated to one standard deviation of selection pressure in 18-month weight of heifers (Brinks *et al*, 1965). Considering that the genetic correlation between weights of bulls and heifers is not unity, the expected genetic improvement obtained is probably biased upward but represents a reasonable maximum estimate. The standardized selection differential of .46 for final weight of bulls was set equal to .46 standard deviations of 18-month weight of heifers, and the expected direct response in 18-month weight calculated. The correlated response in

other postweaning traits in females were then computed.

The results in actual units from selection among sires and females for postweaning traits in females together with their averages (table 3) show that genetic improvement was expected in weaning weight and all postweaning traits in females studied except gain from weaning to 12 months. To the extent that the phenotypic correlations and the genetic parameters used to estimate expected genetic progress were derived from studies in other herds, the results are likely to be biased somehow either way.

Realized Response to Selection

Phenotypic time trends. The Phenotypic regressions of the means of performance traits on years together with the averages of within line regressions for the inbred and linecross populations are shown in table 4. Estimate of the total phenotypic change was obtained for each trait. The regressions contain both the genetic and the environmental trends; the genetic trend is due to both within and between line selections since six of the 14 lines developed were culled from the herd for lower performance during the selection period. The averages of within line regressions contain the environmental trend and the genetic change due to selection within culling of poor lines.

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Expected genetic progress per generation in standard measure resulting from female selection (ΔG_D) was obtained by matrix multiplications shown below, setting $G =$

.3000	.2499	.2616	.2336	.2104
.2499	.4100	.4090	.3041	.2976
.2626	.4090	.5000	.4294	.3941
.2336	.3041	.4294	.5200	.5022
.2104	.2976	.3941	.5022	.5700

Inbred Females: with weaning weight

adjusted for inbreeding.

$$A'G = [(.2690 \ .0826 \ .0636 \ -.1105 \ -.1105)] G$$

Inbred Females: with weaning weight
unadjusted for inbreeding

$$A'G = [(.2690 \ .0826 \ .0636 \ -.1105 \ -.1105)] G$$

Linecross Females:

$$A'G = [(.2693 \ -.2960 \ .0147 \ .1185 \ -.0354)] G$$

TABLE 4
Regressions of Means of Performance Traits on Years for the inbred and linecross Populations

Inbreds					Linecrosses			
Trait	N	Pooled Reg. (bP)	Ave. of Within Line Regs. (bP _w)	(bP-bP _w)	N	Pooled Reg. (bP)	Ave. of Within Line Regs. (bP _w)	(bP-bP _w)
Calves:								
Birth wt. .. (kg)	5	-.080	.061	-.141	5	-.086	.033	-.119
Heart grith circum. at birth (cm)	25	.152	-.150	.302	24	.340	.892	-.551
Adj. wn. wt. (unadj. for Fx) .. (kg).	28	-.351	-.492	.141	—	—	—	—
Adjusted wn. wt. .. (kg)	28	.327	.094	.233	28	.432	.917	-.485
Weaning score .. (X10 ⁻² p ₈) 6 8 3	27	2.184	2.184	2.554	-.370	27	3.369	7.052
Weaning age .. (days)	28	-.368	-1.041	.763	28	-.011	.967	-.978
Bulls:								
Initial test wt. .. (kg)	25	-.364	-.482	.118	25	-.390	.912	-1.301
Final wt. .. (kg).	17	2.738	2.284	.454	17	4.023	5.036	1.013 *
Feed consumption .. (kg)	23	16.129	25.601	9.472	23	18.351	24.011	6.149
Feed Eff. (unadj.) .. (X10 ⁻² values)	23	5.096	17.490	-12.394	23	1.809	-3.307	5.116
Feed Eff. (adj.) .. (X10 ⁻² values)	23	4.994	19.283	-14.289	23	1.488	-2.888	4.376
140-days ave. daily gain (X10 ⁻² kg).	25	-.559	-.996	.437	25	.155	2.100	-1.945
Females:								
Gain wn. -12 mo. .. (kg)	24	.376	.139	.236	22	.178	.110	.068
12-mo. wt. .. (kg).	24	.605	.196	.410	22	.949	.591	-.224
Gain 12-18 mo. .. (kg.)	27	.183	.178	.050	21	.367	.591	-.224
18-mo. wt. .. (kg).	27	.781	.161	.620	26	1.390	-1.260	2.650
Mature spring wt. .. (kg)	27	-.454	-.238	-.216	27	1.264	.588	.676
Mature summer wt. .. (kg)	27	-.587	-.906	.318	27	1.365	.800	.565
Mature fall wt. .. (kg)	27	-.618	-.824	.205	27	1.589	.836	.753

The average phenotype trend in birth weight was negative for both inbred and linecross calves, being $-.080$ and $-.086$ kg per year and resulting each in a decline of about .4kg over five years. However, large increases in birth weight are not desirable because of problems of dystocia. Heart girth circumference at birth increased by .152 cm and .340 cm per year or 3.8 and 8.1 cm over the years in the two populations. The regression of adjusted weaning weight (unadjusted for inbreeding) showed a downward trend of $-.351$ kg per year or a decrease of 9.8 kg over 28 years in the inbred group. After

correcting the data for inbreeding effects, a positive trend was obtained for the inbreds as for the linecrosses, resulting in .327 and .432 kg per year or 9.2 and 12.1 kg, respectively, over 28 years. The regressions for weaning score of 2.184×10^{-2} and 369×10^{-2} points per year represent increases of 59.0×10^{-2} and 91.0×10^{-2} points over the years for the two groups. To the extent that part of this phenotypic change is genetic, an improvement should be expected in body conformation at weaning due to selection. Weaning age

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declined by .368 and .011 days per year or 10.3 and .3 days over the years for the inbred and linecross calves. The difference in trend probably indicates a tendency for the linecross to calve earlier than the inbred animals in the season.

Phenotypic regressions of postweaning traits of bulls on years yielded negative average trends of $-.364$ and $-.390$ kg per year for initial test weight, amounting to declines of 9.1 and 9.8 in 25 years, respectively, for inbreds and linecrosses. Regressions of 2.738 and 4.023 kg per year or total increase of 46.5 and 68.4 kg in 17 years for final weight and 16.129 and 18.351 kg per year or 371 and 422 kg in 23 years for feed consumption, respectively, in the two populations indicate strong upward trends for the traits. These regressions appear extremely large and probably overestimate the actual genetic improvement.

Positive regressions for feed efficiency of 5.096×10^{-2} and 1.809×10^{-2} values per year or 117.2×10^{-2} and 41.6×10^{-2} values over 23 years, respectively, for inbred and linecross bulls for unadjusted data, and 4.994×10^{-2} and 1.488×10^{-2} values per year or 114.9×10^{-2} and 34.2×10^{-2} values over the same period, respectively, for the two groups for adjusted data, represent average phenotypic declines in feed efficiency. Linecross bulls appear to have been less adversely affected than their inbred contemporaries. Whereas 140-day average daily gain decreased by $-.559 \times 10^{-2}$ kg per year or 14.0×10^{-2} kg in 25 years for inbred bulls, it increased by corresponding values of $.155 \times 10^{-2}$ and 3.9×10^{-2} kg for linecross bulls.

The regressions of postweaning traits of females on years indicate substantial phenotypic improvements for yearling weights and gains and were respectively for inbreds and linecrosses: .376 and .178 kg for gain from weaning to 12 months, .605 and .949 kg for 12-month weight, .183 and .367 kg for 12 to 18 months gain

and .781 and 1.390 kg for 18-month weight. The corresponding total increases over the years were: 9.2 and 3.9, 14.5 and 20.9, 4.2 and 7.7, and 21.1 and 36.2 kg. The average change per year was negative for the inbreds and positive for the linecrosses for all three mature weights and were $-.454$ and 1.264 kg for mature spring weight, $-.587$ and 1.365 kg for mature summer weight, and $-.618$ and 1.589 for mature fall weight. Over 27 years these amounted respectively to decreases and increases of 12.0 and 34.1, 15.9 and 36.9, and 16.7 and 42.9 kg.

Armstrong (1964) reported negative phenotypic trends for initial weight, final weight, average daily gain, and feed efficiency for inbred bulls in the same herd over the years. Brinks *et al* (1965) and Brinks and Knapp (1975) demonstrated that in addition to a marked detrimental effect on birth and weanling traits, inbreeding of calf and dam also had a sizeable detrimental effect on postweaning gain and final weight off test in bulls and a large detrimental effect on postweaning weights and gains in females.

Genetic Progress. The estimated genetic changes per generation in the inbred and the linecross populations due to within line selection are shown in table 5. Results show that by 1973, 5.5 and 5.4 generations of selection had been practised respectively in the inbred and linecross populations. Inspection of generation numbers by line and year showed lack of variability in the early years thus making intra year regression on generation numbers statistically impossible. Possibly, some confounded year effects and insufficient overlap of generations could bias the estimated genetic changes. However, the use of within line offspring deviation from annual means of traits should remove a large part of the year to year environmental variations.

TABLE 5

Estimated of genetic Changes in Performance Traits per Generation and Year^a for the inbred and linecross

Trait	Inbreds			Linecrosses		
	N	bG per gen.	bG per yr.	N	bG per gen.	bG per yr.
Calves:						
Birth wt. .. (kg)	345	-.153	-.024	483	.262	.042
Heart girth circum. at birth .. (cm)	1494	-.5.220	-.833	1955	-.028	-.005
Adj. wn. wt. (unadj. for .. (kg)	1583	-.097	-.015	—	—	—
Adjusted wn. wt. .. (kg)	1583	3.478	.556	2070	2.648	.423
Weaning score .. (X10 ⁻² pts.)	1457	-4.990	-.797	1901	-.542	-.086
Bulls:						
Initial test wt. .. (kg)	510	-.324	-.047	738	4.190	.661
Final wt. .. (kg)	329	-2.200	-.320	583	.591	.092
Feed consumption .. (kg)	474	3.142	.457	672	7.645	1.206
Feed off. (unadj.) .. (X10 ⁻² values)	473	-15.020	-2.186	670	2.633	.415
Feed off. (adj.) .. (X10 ⁻² values)	473	-17.003	-2.475	670	3.970	.626
140-day ave. daily gain .. (X10 ⁻² kg)	507	2.052	.298	732	1.242	.196
Females:						
Gain wn-12 mo. .. (kg)	343	-.381	-.058	319	1.628	.245
12-month wt. .. (kg)	343	1.039	.158	319	6.595	.995
Gain 12-18 mo. .. (kg)	328	-1.640	-.250	311	.844	.127
18-month wt. .. (kg)	421	-1.728	-.264	195	4.556	.687
Mature spring wt. .. (kg)	428	-.868	-.150	388	.447	.074
Mature summer wt. .. (kg)	433	-4.783	-.826	393	5.169	.854
Mature fall wt. .. (kg)	431	-4.926	-.851	390	2.919	.483

^aBy dividing the regression of trait on generation by the number of years within generation.

Estimates of genetic changes (table 5) show that except for adjusted weaning weight (adjusted for inbreeding) all birth and weanling traits studied declined genetically over the years in the inbred population. During the period there were decline of .7 kg in birth weight, 23.4 cm in heart girth circumference at birth, .5 kg in adjusted weaning weight (unadjusted for inbreeding), and .223 points in weaning score. Genetic improvement of 15.6 kg is indicated for adjusted weaning weight (adjusted for inbreeding). The total genetic changes of -.5 and 15.6 kg in weaning weight of inbred calves are greater than the total phenotypic changes of -9.8 and 9.2 kg, suggesting that the environmental trend was negative. In the linecross population, genetic regression

per generation yielded total genetic increase of 1.2 kg in birth weight over the period. Genetic change amounted essentially to zero for heart girth circumference at birth and showed a slight decrease of .024 points for weaning score during the selection period. About equal phenotypic and genetic changes of .432 and .423 kg per year in weaning weight would imply that the environment was fairly stable so that virtually all the phenotypic improvement was genetic; the results obtained for the inbreds and those from previous study (Nwakalor *et al*, 1981) make this seem unlikely.

The genetic regressions for postweaning traits of males show that there were declines of 1.3 and 8.7 kg in initial and final weights of inbred bulls over the

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years, equivalents of .04 and .19 standard deviations. However, genetic progress was indicated for them in feed consumption, feed efficiency (adjusted and unadjusted) and average daily gain, amounting to 12.3 kg, .668 and .590 values and .08 kg, respectively, over the period. In linecross bulls, there were genetic improvements of 17.9, 2.5 and 32.6 kg, respectively, in initial weight, final weight, and feed consumption. Even though there was greater genetic improvement in feed consumption in the linecrosses than the inbreds, the former declined with time in feed efficiency, reaching .169 and .112 values for adjusted and unadjusted data over the entire period. The total improvement of .05 kg in average daily gain for the linecross bulls was less than that in the inbred population. The reasons for lower feed efficiency among linecross bulls are not clear. It seems likely that increased losses through heat increment of feeding and/or changes in composition of gain at the higher levels of intake may be implicated (Koch *et al.*, 1963).

In postweaning traits inbred females showed negative genetic changes for gain from weaning to 12 months, 12 to 18 months gain, 18-month weight of heifers, and mature spring, summer and fall weights of cows, yielding overall declines of 1.6, 7.0, 7.4, 4.0, 22.3 and 23.0 kg, respectively over the generations. Regression for 12-month weight suggests improvement of 4.4 kg in genetic merit during the same period. On the contrary, response to selection in linecross females was positive in all yearling weights and gains and mature weights. Total genetic increases were 6.8, 27.9, 3.6 and 19.2 kg for gain from weaning to 12 months, 12-month weight, gain from 12 to 18 months and 18-month weight; in standard deviation units these correspond to .67, 1.1, .28 and .67. Genetic improvements amounted to 2.0, 23.0 and 13.0 kg for mature spring, summer and fall weights.

the equivalent standard deviations of improvement were .05, .52 and .29.

It seems clear that these results have been influenced by the effects of inbreeding. Whereas response to selection was confounded with cumulative inbreeding of dam and offspring in the inbred lines, inbreeding effect was apparently negligible in the linecrosses where linecross females were used as dams. Inbreeding also could have contributed error from random genetic drift among different lines subjected to the same type of selection (Dickerson *et al.*, 1974). It seems plausible to postulate that high rates and levels of inbreeding are responsible for the dissimilar patterns of genetic response observed for the inbred and the linecross groups. Armstrong (1964) reached a similar conclusion in his study where selection in inbred lines generally failed to improve genetic merit in all traits studied.

Genetic Progress from Between Line Selection

Of the 14 lines and their linecross counterparts that were developed over the years, six have been discarded and eight still remain in the herd. Lines 6, 7 and 8 were culled in 1955 and lines 1 and 15 in 1958 and 1967 for lower productivity. Line 2 was discontinued in 1964 because of dwarfism which was also observed in line 8. The line culling provided opportunity to enlarge more promising lines and start new ones and also should lead to faster genetic progress in the overall herd. Previous analysis of weaning weight data demonstrated that the discontinued lines had in fact below average genetic merit (Nwakalor *et al.*, 1976).

The pooled phenotypic regressions given in table 4 contain the environmental and the genetic changes due to within and between line selections. The averages of within line phenotypic regressions (table

4) are both the environmental and within line selection effects. The difference between two regressions estimates the approximate genetic progress resulting from **culling of poorer lines**. The phenotypic regressions in the pooled analysis would be greater than the average within line regressions due to smaller number of records contributed by the poorer lines and effects of between line selection. The average of within line regressions should give an indication of what is expected from a population of inbred lines without culling of poor lines.

The results show that in the inbred population, except for birth weight, weaning score, feed consumption and mature spring weight, genetic improvement was made in all other traits, due to culling of poorer lines. Improvements were as much as .2, .5, .4 and .6 kg per year respectively for adjusted weaning weight (adjusted for inbreeding), final weight in bulls, and 12- and 18-month weights in females. In the linecross population negative genetic progress was indicated in all birth and weanling traits, postweaning traits in males and 12 to 18 months gain in females. Improvements per year were .1, .9, 2.7, .7, .6, and .8 kg,

In the inbred population genetic progress was expected in weaning weight and all postweaning traits in males and females studied except gain from weaning to 12 months. Actual genetic improvement in these traits was generally not as rapid as expected, and was negative in most cases. In feed efficiency much more progress was realized than expected. In the linecross group genetic progress was expected in weaning weight and all postweaning traits in males and females studied except gain from weaning to 12 months in females. Although mostly positive, the estimated genetic response was again smaller than expected in all traits except gain from weaning to 12 months, and 12-and 18-month weights.

The average phenotypic change in the inbred group was less than the expected genetic response in several traits including weaning weight, initial weight, feed efficiency, average daily gain, 12 to 18 months gain, mature spring and mature fall weights and was negative in almost all cases. However, this was greater than the expected genetic progress in final weight, gain from weaning to 12 months, and respectively, for gain from weaning to 12 months, 12-month, 18-month, mature spring, summer, and fall weights in linecross females. Thus, as expected, the culling of poorer lines yielded greater genetic improvement in the inbred than linecross population because heterosis from crossing of higher performing lines would be less than that from more extreme lines. Between line selection resulted in additional genetic progress over that achieved by restricting selection within lines.

Expected vs. Actual Response. Table 6 summarizes the expected genetic response and estimates of the actual genetic and phenotypic responses per generation. The phenotypic response per generation was obtained by multiplying the regression on years by the generation interval. For those traits where the expected genetic response was not calculated only the estimated genetic and the average phenotypic responses are listed for direct comparison. The expected genetic response in weaning weight and postweaning traits in linecross males was obtained as the average of the expected responses in linecross females and inbred males when weaning weight was adjusted for inbreeding.

12-and 18-month weights. In the linecross group the average phenotypic change was greater than the expected genetic change in most of the traits for which the latter was computed, including final weight in bulls and all postweaning traits in females studied. Generally, the ratio of the

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average phenotypic response to the expected genetic response in these traits was much greater than unity, indicating that even though the phenotypic regressions may overestimate the actual genetic response, there was apparently considerable positive response in the traits. Similar to the estimated genetic response, the average phenotypic response was far below the predicted genetic progress for weaning weight, initial weight, feed efficiency and average daily gain.

Although variable, the results from this study are not in harmony with expectations. Apparently, the actual progress was below prediction in most of the traits

studied. Lack of agreement may be attributed perhaps to errors in estimates of actual genetic change as evidenced by large standard errors of regressions which characterize within line estimates and low correlations of selection intensity and genetic response. In their study, Brinks, *et al*, (1965) reported that actual progress was greater than expected in birth and weanling traits and was as great as or greater than expected for all postweaning traits studied in a mildly inbred line. However, our results agree closely with those of Armstrong (1964) from the data of inbred lines of the same herd and those of Dickerson *et al* (1954) from swine data, where selection apparently failed to im-

TABLE 6

Comparison of expected and estimated average genetic and phenotypic Responses per Generation in weanling and postweaning Traits.

Traits	Inbreds					Linecrosses				
	Exp. Gen. Resp.	Est. Gen. Res.	Ratio Est. to Exp.	Ave. Phen. Res.	Ratio Phen. to Exp. Gen.	Exp. Gen. Resp.	Est. Gen. Res.	Ratio Est. to Exp.	Ave. Phen. Res.	Ratio Phen. to Exp. Gen.
Calves:										
Birth wt. . . . (kg)		-.15	-	-.33	-		.26	-	-.36	-
Heart girth circum. at birth . . . (cm)		-5.23	-	.64	-		-.03	-	1.42	-
Adj. WW (unadj. for Fk. . . (kg)	4.02	-.10	-.02	1.45	-.36	4.14	2.65	.64	1.82	.44
Adj. WW . . . (kg)		3.48	-	1.35	-					
Weaning score . . . (X10 ² pts.)		-4.99	-	9.02	-		-.54	-	14.18	-
Bulls:										
Initial test wt. . . . (kg)	4.43	-.33	-.07	-1.57	-.36	4.62	4.19	.91	-1.68	-.36
Final wt. offtest . . . (kg)	9.99	-2.20	-.22	12.27	1.21	10.27	.59	.06	18.03	1.75
Feed consum. . . . (kg)		3.14	-	69.52	-		7.64	-	79.09	-
Feed eff. (unadj.) . . . (X10 ²)		-15.02	-	21.91	-		2.63	-	7.78	-
Feed eff. (Adj.) . . . (X10 ²)	-1.80	-17.00	9.44	21.47	-11.93	-1.80	3.97	-2.21	6.40	-3.56
140-day ave. daily gain . . . (X10 ²)	3.99	2.05	.51	-2.40	-.60	4.04	1.24	.30	.66	.16
Females:										
Gain wt-12 mo. . . . (kg)	-1.76	-.36	.22	1.70	-.96	-2.08	1.63	-.78	.82	-.39
12-month wt. . . . (kg)	2.26	1.04	.46	2.49	1.19	2.15	6.60	3.07	4.36	2.03
Gain 12-18 mo. . . . (kg)	.87	-1.64	-1.90	.82	-.94	1.07	.84	.79	1.69	1.96
18-month wt. . . . (kg)	3.12	-1.73	-.55	3.43	1.10	3.21	4.55	1.42	6.10	1.90
Mature spring wt. . . . (kg)	3.25	-.87	-.27	-1.95	-.60	4.68		.10	5.46	1.17
Mature summer wt. . . . (kg)		-4.79	-	-2.53	-		5.17	-	5.88	-
Mature fall wt. . . . (kg)	2.84	-4.93	-1.73	-2.65	-.93	4.35	2.92	.67	6.86	1.56

prove measurably the genetic merit for traits studied. Dickerson *et al* (1974), also from swine data, demonstrated that improvement from selection was at least as rapid as expected in all lines and crosses for postweaning growth, but was far below postweaning growth, but was far below prediction for sow productivity in parental lines selected for cross performance. Possibly, the discrepancy involved can be resolved by improvements in design and scale of experiments, more accurate estimates of genetic and phenotypic parameters, more dependable methods of estimating genetic progress and a reappraisal of the effects of inbreeding on selection within inbred lines and their crosses.

The results presented could be of practical interest to animal breeders in Nigeria, especially those engaged in the genetic improvement of beef cattle. They should be able to keep accurate records of performance of animals in their herds and use these records in making decisions as to which animals should be selected on the basis of superiority for the production of the next generation. Over time, the performances of the populations could be evaluated to know if they are making any progress. Based on their knowledge of heritabilities and selection applied breeders can compare realized and expected response.

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