

Effects of Inbreeding and Heterozygosity on Preweaning Traits in a Closed Population of Herefords Under Selection¹

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ABSTRACT: Records of five inbred lines at the Livestock and Range Research Laboratory were used to evaluate effects of inbreeding and heterozygosity on preweaning traits. Members of each line were descendants of a single founder Hereford bull. A total of 8,065 records of birth weight and 7,380 records of preweaning daily gain and weaning weight were analyzed by derivative-free REML using a model that included fixed effects of sex, combination of year and month of birth and parity of dam, with covariates for direct and maternal genetic fractions of inheritance from the genetic groups, inbreeding, and heterozygosity fractions. Heterozygosity fractions were computed for crosses between lines. The random model effects were direct and maternal genetic and uncorrelated maternal permanent environmental and temporary environmental. Direct inbreeding and heterozygosity

fractions averaged .098 and .343, and maternal inbreeding and heterozygosity fractions averaged .075 and .294. Regression coefficients of traits on direct and maternal inbreeding fractions were -5.8 ± 1.1 and -4.7 ± 1.3 for birth weight, $-.189 \pm .031$ and $-.252 \pm .039$ for preweaning daily gain, and -44.5 ± 6.6 and -56.1 ± 8.4 kg for weaning weight. Estimates for direct heritability, maternal heritability, and direct-maternal genetic correlations were .37, .12, and $-.01$ for birth weight; .16, .25, and $-.27$ for daily gain; and .17, .26, and $-.21$ for weaning weight. Results suggest that heterosis represents recovery of accumulated inbreeding depression. Results also indicate that selection can overcome inbreeding depression and antagonism exists between direct and maternal genetic effects for preweaning traits.

Key Words: Beef Cattle, Inbreeding, Heterosis

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Introduction

The usual plan in formation of inbred lines has been to make genetic relationships to a desired animal as large as possible. Unfortunately, increased homozygosity, the primary genetic consequence of formation of inbred lines, has been associated with a decline in performance (Burrow, 1993).

Inbred lines have also been formed to create specific crosses that can take advantage of nonadditive genetic effects, under the hypothesis that heterosis is recovery of accumulated inbreeding depression that has occurred with the formation of inbred lines (Gregory et al., 1994). The bioeconomic importance of heterosis and the systems to take advantage of heterosis from generation to generation have been discussed by many

authors (e.g., Cundiff et al., 1992; Gregory et al., 1992a,b; Núñez-Domínguez et al., 1992; Newman et al., 1993; Davis et al., 1994). Within an environment, heterosis in a given trait seems to be a function of the genetic differences among inbred lines or groups being crossed. The goal of this study was to estimate the effects of inbreeding and effects of heterozygosity of line crosses on preweaning traits in a closed population of Hereford cattle under selection.

Materials and Methods

By the late 1920s, corn breeders had achieved success in developing hybrid varieties that out-produced their inbred parents based on the pioneering work of Shull (1908). Formation of the inbred lines in the initial phase of this research was apparently motivated by this success. Development of inbred lines of beef cattle received much emphasis in the research programs of several western states as reviewed by Brinks and Knapp (1975). Fourteen of these inbred

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lines were located at Fort Keogh Livestock and Range Research Laboratory (LARRL), Miles City, Montana. Throughout their development, these lines were selected for postweaning growth and structural soundness. Five of the highest performing lines at LARRL were subsequently used in line crossing experiments (Brinks et al., 1967, 1972; Urick et al., 1968, 1983) that comprised the second phase of this research. In the third and final phase of this research, selection was relaxed and the line cross progenies were mated at random (Nelsen et al., 1984, 1986; Reynolds et al., 1991). The preceding reports and Urick et al. (1966), MacNeil et al. (1992), and Ferreira (1996) provide detail regarding climatic conditions and livestock husbandry at LARRL.

Five inbred lines, each founded by a single Hereford bull, were identified as Line 1, Line 4, Line 6, Line 9, and Line 10. Each inbred line was composed of all descendants of a given founder bull, whether descendants came from mating the founder bull or descendants of the founder bull with the base population or from matings within the line. Line 1 remained closed to outside breeding from 1934 to 1971, Line 4 from 1947 to 1975, Line 6 from 1949 to 1975, Line 9 from 1951 to 1970, and Line 10 from 1950 to 1975. The base population, common to all lines, was defined as foundation males and females that did not have performance information of their own as well as other individuals from matings within that group. Five males and 306 females did not have performance records of their own. A total of seven genetic groups was formed, with groups 1 to 5 being Lines 1, 4, 6, 9, 10 and groups 6 and 7 being immigrants and the base population, respectively. Any individual not related to the inbred lines or the base population was considered an immigrant. Individuals with a composite genotype were considered to be line crosses (Table 1).

The genetic fraction contributed by an inbred line to an individual (I_{gi}) was derived from the corresponding genetic line fractions of its parents, except in situations when an individual from a known inbred line was mated to an individual of the base population (Table 1). For example, $I_{gi} = \frac{1}{2}(S_{gi} + D_{gi})$, where S_{gi} and D_{gi} represent the fractional genetic contributions of line i to the sire and dam, respectively, with $\Sigma I_{gi} = 1$ and $i = 1, \dots, 7$. Total heterozygosity was estimated as $1 - \Sigma(S_{gi}D_{gi})$ for $i = 1, \dots, 6$, with the base population excluded. Inbreeding coefficients were computed with the MTDFNRM program of the MTDFREML package (Boldman et al., 1995). Descriptions of traits and covariates for direct and maternal genetic contributions are given in Table 2. Summary statistics for life span of groups and average inbreeding by group are in Table 3.

Traits were birth weight, preweaning daily gain, and weaning weight adjusted to 205 d of age. Single- and two-trait analyses were conducted with the MTDFREML program (Boldman et al., 1995) assum-

Table 1. Criteria for assignment to groups and number of individuals by group

Mating	Group formed	n
Base population $\times$ base population	Base population	191
Line 1		
$\times$ base population	Line 1	252
$\times$ Line 1	Line 1	2,321
Line 4		
$\times$ base population	Line 4	114
$\times$ Line 4	Line 4	398
Line 6		
$\times$ base population	Line 6	101
$\times$ Line 6	Line 6	325
Line 9		
$\times$ base population	Line 9	136
$\times$ Line 9	Line 9	231
Line 10		
$\times$ base population	Line 10	122
$\times$ Line 10	Line 10	283
Immigrants		
$\times$ base population	Immigrants	43
Line		
$\times$ different line	Line cross	747
Line cross		
$\times$ line cross	Line cross	2,299

ing the model $\mathbf{y} = \mathbf{XB} + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{Z}_3\mathbf{u}_3 + \mathbf{e}$; where $\mathbf{y}$ = the vector of observations, $\mathbf{B}$ = vector of unobservable fixed effects, $\mathbf{u}_1$ = vector of random additive direct (as animal) genetic effects, $\mathbf{u}_2$ = vector of random additive maternal (as dam) genetic effects, $\mathbf{u}_3$ = vector of random uncorrelated maternal permanent environmental effects, $\mathbf{X}$ = matrix that relates elements of $\mathbf{y}$ to fixed effects, $\mathbf{Z}_1$ = matrix that relates elements of $\mathbf{y}$ to direct genetic effects, $\mathbf{Z}_2$ = matrix that relates elements of $\mathbf{y}$ to maternal genetic effects, $\mathbf{Z}_3$ = matrix that relates elements of $\mathbf{y}$ to random uncorrelated maternal effects, and $\mathbf{e}$ = vector of residual effects.

All numerator relationships and inbreeding were included in calculation of the inverse of the numerator relationship matrix. Covariance between direct and maternal genetic effects was included in the covariance matrix for the random effects ($\mathbf{u}_1$ and $\mathbf{u}_2$).

The vector of fixed effects included sex (bull, heifer, steer), combination of year of birth (1934 to 1988) with month of birth (March to June), parity of dam (1 through 10), and covariates for the linear effects of direct and maternal genetic fractions from genetic groups and direct and maternal inbreeding and heterozygosity fractions.

Average merit of lines was calculated as $\Sigma(l_i b_i) / \Sigma l_i$, where l_i represents the mean genetic fraction of the population from line i , b_i is the regression coefficient of trait on genetic fraction from line i , for $i = \text{Line 1}, \dots, \text{Line 10}$. The average inbreeding depression (**AID**) was calculated as $b_F * F$, where b_F represents the regression coefficient of trait on inbreeding fraction and F is the average inbreeding fraction across lines.

Table 2. Description of traits and covariates

Variable	n	Mean	SD	CV	Minimum	Maximum
a) Prewaning traits, kg						
Birth weight	8,065	34.5	4.7	13.7	10.4	56.2
Daily gain	7,380	.8	.1	17.7	.2	1.2
Weaning weight	7,380	192.0	29.9	15.6	67.6	287.6
b) Covariates, fractions						
Direct genetic contributions						
Line 1		.426	.427	100.3	.0	1.000
Line 4		.161	.269	166.7	.0	1.000
Line 6		.156	.257	165.3	.0	1.000
Line 9		.066	.227	342.6	.0	1.000
Line 10		.133	.246	184.0	.0	1.000
Immigrants		.035	.106	307.2	.0	1.000
Base population		.024	.152	642.1	.0	1.000
Inbreeding		.098	.080	81.8	.0	.458
Heterozygosity		.343	.401	117.2	.0	1.000
Maternal genetic contributions						
Line 1		.396	.437	110.4	.0	1.000
Line 4		.146	.269	183.4	.0	1.000
Line 6		.147	.260	177.6	.0	1.000
Line 9		.050	.209	420.7	.0	1.000
Line 10		.123	.247	201.2	.0	1.000
Immigrants		.021	.075	361.6	.0	1.000
Base population		.119	.323	272.7	.0	1.000
Inbreeding		.075	.076	101.1	.0	.458
Heterozygosity		.294	.400	136.3	.0	1.000

The effect of heterosis was calculated as $b_H * H - AID$, where b_H represents the regression coefficient of trait on heterozygosity fraction and H represents the average heterozygosity fraction.

To estimate trends for genetic merit and inbreeding effect, breeding values and inbreeding depression were estimated for each individual in the population, with inbreeding depression calculated as the product of inbreeding fraction and the across-line coefficient of regression on inbreeding fraction. Regressions of breeding value and inbreeding depression on year of birth for direct and maternal genetic contributions were calculated within each line for the time period

the lines were closed (all lines included) and within the line cross group.

Results and Discussion

Line Effects. The analysis constrained the solution for the base population to be zero. Partial regression coefficients in Table 4 associated with genetic fractions of inbred lines indicate the phenotypic change in the trait when the proportion of genes from an inbred line changes from none to all. This change measures

Table 3. Life span of groups, and number of individuals and averages of direct and maternal inbreeding coefficients (fraction) by group and trait

Group	Life span ^a	n	Birth weight		n	Weaning weight ^b	
			Direct	Maternal		Direct	Maternal
Line 1	1931–73	2,553	.143	.104	2,432	.142	.104
Line 4	1947–75	514	.139	.072	476	.139	.072
Line 6	1949–75	427	.135	.076	406	.135	.075
Line 9	1951–70	367	.085	.030	336	.081	.026
Line 10	1950–75	406	.118	.075	379	.117	.073
Immigrants	—	43	.000	.000	41	.000	.000
Base population	1923–38	191	.001	.000	184	.001	.000
Line cross	1958–88	3,564	.061	.064	3,126	.058	.062
Population	1923–88	8,065	.080	.075	7,380	.097	.074

^aEarliest and latest year of birth for members within a group. Recording of performance started in 1934.

^bSame for preweaning daily gain.

Table 4. Partial regression coefficients (b) and standard errors (SE) of preweaning traits on direct and maternal line fractions, inbreeding, and heterozygosity fractions

Covariate	Preweaning traits, kg		
	Birth weight b ^a ± SE	Daily gain b ^a ± SE	Weaning weight b ^a ± SE
a) Direct genetic contribution			
Base population	.00 ± .00 ^f	.000 ± .000	.00 ± .00
Line 1	1.21 ± .95	.012 ± .020	4.12 ± 4.41
Line 4	-.21 ± 1.47 ^a	-.025 ± .030 ^a	-4.56 ± 6.71 ^a
Line 6	-.64 ± 1.45 ^{bc}	-.024 ± .030 ^b	-5.57 ± 6.70 ^b
Line 9	-.55 ± 1.45 ^{de}	.009 ± .030	1.80 ± 6.65
Line 10	2.63 ± 1.46 ^{bd}	-.014 ± .030 ^c	-.40 ± 6.63 ^c
Immigrant	2.73 ± 1.30 ^{acef}	.041 ± .028 ^{abc}	11.19 ± .61 ^{abc}
Average ^b	.49 ± 1.00	-.008 ± .020	-.92 ± 4.69
Inbreeding	-5.80 ± 1.14	-.189 ± .031	-44.52 ± 6.59
Heterozygosity	.03 ± .32	.004 ± .008	.80 ± 1.77
b) Maternal genetic contribution			
Base population	.00 ± .00 ^b	.000 ± .000 ^{cd}	.00 ± .00 ^{bc}
Line 1	.02 ± .70	.065 ± .022 ^{abc}	13.78 ± 4.70 ^{ab}
Line 4	.88 ± .77	-.002 ± .024 ^a	.41 ± 5.36
Line 6	-.65 ± .81 ^a	.049 ± .026	9.28 ± 5.71
Line 9	.19 ± .78	-.007 ± .025 ^b	-1.21 ± 5.48 ^a
Line 10	1.86 ± .77 ^{ab}	.029 ± .025	8.22 ± 5.36
Immigrant	1.15 ± 1.21	.044 ± .037	10.08 ± 8.19
Average ^b	.46 ± 1.00	.027 ± .010 ^d	6.10 ± 2.69 ^c
Inbreeding	-4.67 ± 1.31	-.252 ± .039	-56.10 ± 8.41
Heterozygosity	.02 ± .37	-.011 ± .011	-2.26 ± 2.30

^aSolutions with a common letter within a) or within b) are significantly different ($P < .05$).

^bAverage for Lines 1, 4, 6, 9, and 10.

the average difference in phenotypic merit of a line from the base population.

The average of the regression coefficients on direct fractions of genes of Lines 1, 4, 6, 9, and 10 was not significantly different from zero ($P > .05$) for all traits (Section a of Table 4). Only the regression coefficient of birth weight on the direct immigrant gene fraction was different from that of the base population ($P < .05$). For the maternal genetic contribution (Section b of Table 4), the averages of the regression coefficients of preweaning daily gain and weaning weight on fractions of genes of Lines 1, 4, 6, 9, and 10 were different from those of the base population ($P < .05$). Line 1 dams produced calves with greater preweaning daily gains and heavier weaning weights than the base population, despite not producing the heaviest calves at birth. Other differences in maternal line effects were close to zero, except for birth weight on the fraction of genes of Line 10. Of the total difference between the average merit of lines and the base population (Table 5), the direct genetic contribution accounted for .7 of change in birth weight, whereas for weaning weight, more than .9 of the change was due to the maternal genetic contribution. The ratio of more than 1.0 for the average merit of inbred lines to average inbreeding depression (Table 5) indicates that selection can overcome inbreeding depression, at least for the range of inbreeding of the lines studied.

Means and coefficients of regression of breeding value and inbreeding depression on year of birth for direct and maternal genetic contributions are shown in Table 6. The trends for direct and maternal inbreeding depression and for direct and maternal

Table 5. Average merit of lines, absolute and relative effects of inbreeding and heterozygosity, and amount of inbreeding depression recovered by heterosis for all groups

Trait	Average effect of			As % of raw mean		Heterosis/ Inbreeding
	Lines ^a	Inbreeding ^b	Heterosis ^c	Inbreeding	Heterosis	
	kg					
a) Direct genetic contribution						
Birth weight	.74	-.57	.58	-1.65	1.68	-1.02
Daily gain	-.00	-.02	.02	-2.40	2.58	-1.07
Weaning weight	.31	-4.33	4.60	-2.25	2.39	-1.06
b) Maternal genetic contribution						
Birth weight	.32	-.35	.35	-1.01	1.02	-1.01
Daily gain	.04	-.02	.02	-2.42	2.03	-.83
Weaning weight	9.18	-4.14	3.51	-2.16	1.83	-.84
c) Total						
Birth weight	1.06	-.92	.93	-2.66	2.70	-1.02
Daily gain	.04	-.04	.04	-4.83	4.61	-.95
Weaning weight	9.49	-8.47	8.11	-4.41	4.22	-.95

^aAverage merit for inbred lines = $\Sigma(l_i b_i) / \Sigma l_i$, where l_i represents the mean genetic fraction from line, i , b_i is the regression coefficient of trait on line fraction, and i = Line 1, ..., Line 10.

^bAverage inbreeding depression (AID) = $b_F * F$; where b_F represents the regression coefficient of trait on inbreeding coefficient, and F represents the average inbreeding.

^cHeterosis = $b_H * H - AID$, where b_H represents the regression coefficient of trait on heterozygosity fraction, and H represents average heterozygosity.

Table 6. Means and regression coefficients with standard errors (SE) of direct and maternal breeding values (b_{BV}) and direct and maternal inbreeding depression (b_{ID}) on calf year of birth within group (lines or line cross) by trait

Groups	Birth weight, kg								Weaning weight, kg							
	Breeding value				Inbreeding depression				Breeding value				Inbreeding depression			
	Mean $\pm$ SE	$b_{BV} \pm$ SE			Mean $\pm$ SE	$b_{ID} \pm$ SE			Mean $\pm$ SE	$b_{BV} \pm$ SE			Mean $\pm$ SE	$b_{ID} \pm$ SE		
a) Direct genetic contribution																
Line 1	1.25	.03	.11	.00	-.83	.01	-.03	.00	5.09	.11	.39	.01	-6.35	.06	-.23	.01
Line 4	1.90	.08	.16	.01	-.80	.03	-.06	.00	4.05	.25	.54	.02	-6.14	.20	-.46	.02
Line 6	-.38	.07	.04	.01	-.78	.03	-.06	.00	.68	.15	.10	.02	-5.95	.21	-.45	.02
Line 9	-.09	.07	-.03	.01	-.49	.02	-.04	.00	-3.25	.19	.24	.03	-3.75	.18	-.33	.03
Line 10	.05	.07	-.03	.01	-.68	.03	-.06	.00	2.15	.17	.02	.02	-5.21	.21	-.43	.02
All lines	.94	.03	.05	.00	-.78	.01	-.03	.00	3.53	.09	.17	.01	-5.95	.06	-.22	.00
Line cross	1.16	.03	.02	.00	-.35	.00	-.02	.00	4.78	.08	.03	.01	-2.71	.04	-.11	.00
b) Maternal genetic contribution																
Line 1	.91	.01	.04	.00	-.48	.01	-.03	.00	4.43	.15	.56	.02	-5.81	.09	-.38	.01
Line 4	-.05	.03	-.01	.00	-.33	.02	-.04	.00	5.44	.26	.41	.03	-4.01	.23	-.53	.02
Line 6	-.07	.02	.00	.00	-.35	.02	-.04	.00	6.90	.24	.10	.03	-4.24	.25	-.52	.02
Line 9	.72	.03	.00	.01	-.14	.01	-.03	.00	10.38	.27	.32	.05	-1.68	.16	-.32	.03
Line 10	-.08	.02	-.01	.00	-.34	.02	-.05	.00	6.08	.27	.21	.04	-4.13	.26	-.55	.02
All lines	.59	.01	.01	.00	-.41	.01	-.02	.00	5.46	.11	.34	.01	-4.92	.07	-.25	.01
Line cross	.02	.01	-.04	.00	-.30	.00	.00	.00	4.66	.12	-.55	.01	-3.57	.06	-.01	.01

breeding values for individuals combined are shown in Figure 1.

For the period the lines were closed (1934 to 1975), maternal breeding value for weaning weight increased more than direct breeding value (Figure 1b). For birth weight the opposite happened: the increase over years in direct breeding value was larger than the increase in maternal breeding value (Figure 1a). The within-line regression coefficients for direct and maternal breeding values on year of birth (Table 6) show that the yearly increase in maternal genetic merit was twice the yearly increase in direct genetic merit for weaning weight (.34 vs .17 kg/yr). For birth weight the yearly increase in direct genetic merit was five times larger than the yearly increase in maternal genetic merit (.05 vs .01 kg/yr).

Formation of lines resulted in increased weaning weight due to improvement of the maternal genetic potential. Straight line dams had calves with greater preweaning daily gain and weaning weight than dams from the base population. Selection for maternal performance will improve weaning weight in addition to gain from selection for direct performance (e.g., Van Vleck et al., 1977). The unbalanced relationship observed between the direct and maternal genetic contributions indicates that part of the phenotypic gain expected for preweaning traits from selecting either for direct or for maternal additive genetic potential will be offset by loss in the other, and that the total selection response will be less than that expected from heritability of either of the two effects.

Within lines, the ratios of the yearly increase for birth and weaning weight in direct breeding values to the yearly direct inbreeding depression were 1.7 and

.8 and for maternal breeding values were .5 and 1.4, respectively. These ratios indicate that selection response for direct genetic merit overcame the inbreeding depression only for birth weight, and that selection response to maternal genetic contribution overcame accumulated inbreeding depression only for weaning weight. This result agrees with the phenotypic merit of lines described previously shown in Table 5. Within the line cross group, a downward trend was evident in the direct and maternal genetic merit for weaning weight.

Differences Among Lines. The regressions of traits on fractions of genes from the lines were not homogenous across lines. Differences among lines can be due to differential selection response or fixation of genes coming from founders. Each founder bull came from a different population. Only the Line 1 founder came from the base population (e.g., Urick et al., 1966). The fact that Line 1 differed from the base population only for daily gain and weaning weight suggests that birth and weaning weight are influenced by some genes with effects not common to both traits. This result is consistent with previous reports (MacNeil et al., 1992).

Means and regression coefficients associated with inbreeding depression were similar for all lines, but means and regression coefficients for year of birth associated with direct and maternal breeding values varied among lines (Table 6). The rankings of lines for direct and maternal genetic merits changed for birth and weaning weight, as well as for yearly increases in breeding values. Lines 4 and 1 averaged the largest direct genetic merit, and Lines 1 and 9 averaged the largest maternal genetic merit for birth

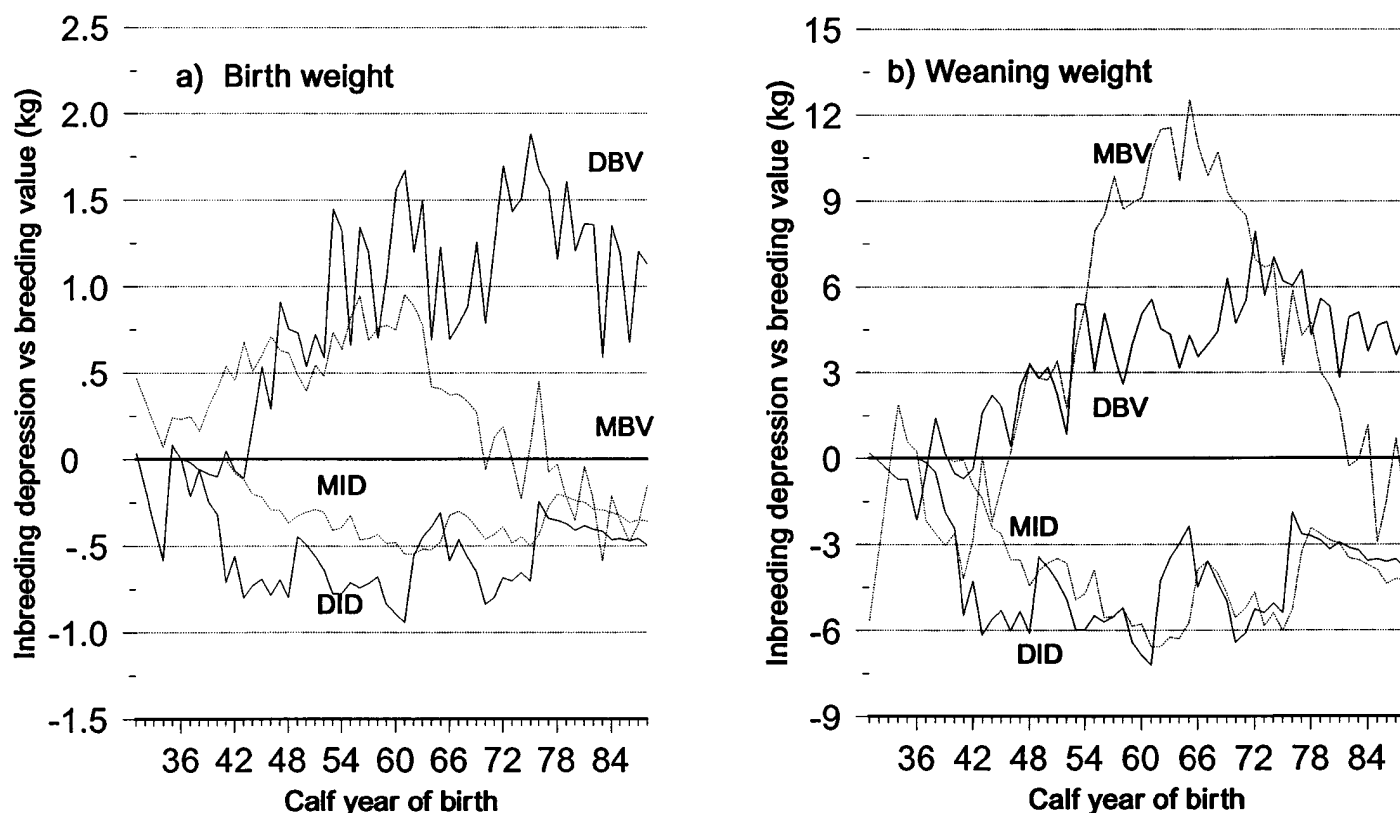


Figure 1. Trends for effects of direct (DID) and maternal (MID) inbreeding depression and direct (DBV) and maternal (MBV) breeding values for birth and weaning weight for all individuals combined.

and weaning weight, respectively. For birth weight, a yearly decrease in breeding value was observed for direct genetic merit in Lines 9 and 10 and for maternal genetic breeding value in Lines 4 and 10. However, for all lines combined, breeding values for direct and maternal genetic contributions to weaning weight increased over the years.

On the average, the increase in direct and maternal breeding values for birth weight was also expressed in weaning weight. Line 4 had the largest yearly increase in direct breeding value for birth and weaning weights. Similarly, Line 1 had the largest yearly increase in maternal breeding value for birth and weaning weights.

Differences between the largest and smallest means for direct breeding values were 2.3 and 8.3 and for maternal breeding values were 1 and 6 kg for birth and weaning weight, respectively. The differences among lines are consistent with previous reports (Brinks et al., 1965, 1967, 1972) and show that real additive genetic differences existed among the lines that might be associated with fixation of some founder genes.

Inbreeding Effects. The pooled across-line regression coefficients of performance on direct and maternal inbreeding fractions (Table 4) differed from zero for all traits ($P < .05$). These partial regression coefficients are within the range reported by Burrow

(1993), except for the regression coefficient of birth weight on maternal inbreeding fraction. The observed significant and negative effect of maternal inbreeding on birth weight is contrary to some previous reports. Brinks et al. (1965) and MacNeil et al. (1988) reported regression coefficients of birth weight on maternal inbreeding that were slightly positive, although not significantly different from zero. However, Snelling et al. (1996) in an across-environment analysis reported the same pattern as in this study. The inconsistency of the effect of maternal inbreeding on birth weight might be associated with an interaction between levels of maternal inbreeding and direct inbreeding.

Table 5 shows the average depression across lines due to increase in direct and maternal inbreeding in the population. Of the total accumulated inbreeding depression, direct inbreeding accounted for about 62% of the depression for birth and 51% for weaning weight, which agree with previous reports (Burrow, 1993).

Heterozygosity. Much as expected, the regression coefficients associated with direct and maternal heterozygosity did not differ significantly from zero (Table 4a,b). Under the hypothesis of dominance, which seems to be the case for growth traits in beef cattle (Kress et al., 1992; Gregory et al., 1994), heterozygosity has an effect opposite to that of inbreeding. Thus,

Table 7. Fractions of phenotypic variances^a associated with, and correlations among, random effects

		Birth weight				Weaning weight				Daily gain			
Random effects		a ₁	m ₁	c ₁	e ₁	a ₂	m ₂	c ₂	e ₂	a ₃	m ₃	c ₃	e ₃
a) Single trait analysis													
Direct genetic	(a _i)	.37	-.01	—	—	.17	-.21	—	—	.16	-.27	—	—
Maternal genetic	(m _i)		.12	—	—		.26	—	—		.25	—	—
Maternal environmental	(c _i)			.06	—			.14	—			.15	—
Residual	(e _i)				.45				.48				.14
b) Two-trait analysis													
Direct genetic	(a ₁)	.36	.03	—	—	.50	.10	—	—				
Maternal genetic	(m ₁)		.13	—	—	.22	.41	—	—				
Maternal environmental	(c ₁)			.06	—			.36	—				
Residual	(e ₁)				.45				.35				
Direct genetic	(a ₂)					.15	.00	—	—				
Maternal genetic	(m ₂)						.21	—	—				
Maternal environmental	(c ₂)							.16	—				
Residual	(e ₂)								.48				

^aPhenotypic variances (kg)² were as follows: birth weight, 17.7; weaning weight, 530.4; and daily gain, 0.011.

the theoretical expectation is for heterosis to recover effects of inbreeding depression. This expectation implies that inbreeding is required in order for heterosis to be expressed in line crosses. In this study, the expectation was that the regression coefficient of a trait on heterozygosity would be zero because it measures the effect of heterozygosity given zero inbreeding. A negative regression coefficient associated with heterozygosity would indicate incomplete recovery for inbreeding depression, and a positive value would indicate recovery above expectation.

Mean effects of direct and maternal heterosis for all groups (Table 5) were estimated as deviations of the corresponding average effect of heterozygosity from the absolute average of inbreeding depression. The results agree with previous reports (Flower et al., 1963; Brinks et al., 1967; Brinks et al., 1972; Urick et al., 1981; MacNeil et al., 1982; Urick et al., 1983). Crossing lines recovered nearly all of the effects of inbreeding depression with ratios of 1.01, .95, and .95, for birth weight, daily gain, and weaning weight, respectively (Table 5c). Effects of direct heterosis were greater than maternal heterosis for all traits. These results support the hypothesis that inbreeding depression on preweaning growth traits in beef cattle is due to a loss in heterozygosity that occurs in formation of lines and that heterosis is basically recovery of that depression.

Heritability Estimates. Estimates of heritability, shown in Table 7, are within the range reported in the literature for these traits (e.g., MacNeil et al., 1992; Mohiuddin, 1993; Koots et al., 1994; Ferreira, 1996; Van Vleck et al., 1996). The improvement observed for direct and maternal performance agrees with the moderate negative correlation found between additive direct and maternal effects for weaning traits (Table 7). Estimates of genetic correlation between birth and weaning weight were .50 for the direct genetic effects,

.41 for the maternal genetic effects, and .16 on the average between maternal and direct genetic effects of the two traits (Table 7).

Implications

In the populations of Hereford cattle that were developed under selected mating and with moderate increases in inbreeding, selection seemed to overcome accumulated inbreeding depression for preweaning traits. Crosses between lines recovered nearly all the inbreeding depression but seemed to dilute the differentiated genetic progress achieved among the lines. Selection for maternal performance would improve weaning traits in addition to gain from selecting for direct performance. A successful selection program seems possible even in small closed populations with moderate inbreeding.

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