

Comparison of Selection by Independent Culling Levels for Below-Average Birth Weight and High Yearling Weight with Mass Selection for High Yearling Weight in Line 1 Hereford Cattle¹

M. D. MacNeil², J. J. Urick, and W. M. Snelling

Fort Keogh Livestock and Range Research Laboratory, USDA,
Agricultural Research Service, Miles City, MT 59301

ABSTRACT: Mass selection by independent culling levels (YB subline) for below-average birth weight (BWT) and high yearling weight (YWT) was compared with single-trait mass selection (YW subline) for high YWT in the inbred population of Line 1 Hereford cattle at Miles City, Montana. There were 4.2 generations of selection in YB and YW. Heritability estimates for the base population derived from multiple-trait REML were .28 and .31 for direct effects and .16 and .06 for maternal effects on BWT and YWT, respectively. Mid-parent cumulative selection

differentials for BWT of YB and YW diverged (-2.9 vs 8.2 kg, respectively), as did the associated genetic trends for direct effects (-0.014 kg/yr vs .105 kg/yr, respectively). Mid-parent cumulative selection differential for YWT of YB (102.1 kg) was 64% of that attained in YW (160.7 kg). Likewise, response in YWT of YB (.91 kg/yr) was 61% of response attained in YW (1.5 kg/yr). For BWT and YWT, maternal genetic trends were similar across selection lines. Assistance at parturition of first-parity 2-yr-old heifers was consistently less frequent in YB than in YW.

Key Words: Beef Cattle, Selection, Genetic Trend, Growth Factors, Calving

©1998 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 1998. 76:458-467

Introduction

Selection for increased production tends to decrease fitness (Meuwissen et al., 1995). Simultaneous improvement of antagonistically correlated traits poses a significant challenge for beef cattle breeders. Reducing calf mortality by controlling birth weight while increasing subsequent growth is an important applied illustration of this problem (Dickerson et al., 1974). Excessive calf birth weight was shown to be an important causative agent affecting the incidence and severity of dystocia (Bellows et al., 1971; Laster et al., 1973). Because birth weight has a positive genetic correlation with weights at subsequent ages (e.g., Brinks et al., 1964; Smith et al., 1976), selection for reduced birth weight may compromise production

efficiency through prolonged feeding to reach market weight. Thus, we hypothesized that a selection strategy with negative emphasis on birth weight and positive emphasis on subsequent growth might be effective in reducing the incidence and severity of dystocia while minimally reducing the rate of genetic progress for subsequent growth. The objective of this research was to compare mass selection, by independent culling levels, for below-average birth weight and high yearling weight with single-trait mass selection for high yearling weight. Here, attention is focused on selection applied, and genetic responses in birth weight, yearling weight, and calving ease of 2-yr-old heifers.

Materials and Methods

Formation of Selection Lines. In 1977, females comprising the Miles City Line 1 Hereford herd were randomly divided into two sublines. Sires for one subline, hereafter designated **YB**, were selected for below-average birth weight and high yearling weight. Sires for the second subline, hereafter designated **YW**, were selected for high yearling weight alone. Sires used in both lines to produce calves in 1978 and 1979 were born from 1973 to 1977 and were identified based on their own performance and in some cases on

¹This research was conducted under a cooperative agreement between USDA, ARS and the Montana Agric. Exp. Sta. and is published as contribution No. J-5096 from the Montana Agric. Exp. Sta. USDA, Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer. All agency services are available without discrimination.

²To whom correspondence should be addressed: Rt. 1, Box 2021 (phone 406/232-8213; fax: 406/232-8209; E-mail: mike@larrl.ars.usda.gov).

Received December 13, 1996.

Accepted September 20, 1997.

progeny performance to meet the intent of the respective selection lines. This selection of sires from the base population contributes to a founder effect resulting in genetic divergence between lines at the start of the experiment. Generation 0 of this experiment was composed of the parents of calves born in the project in 1978 or thereafter that themselves were born before 1978 and their herd-year contemporaries. For calves born in 1978 and after, generation number was the average generation number of their parents plus one (Brinks et al., 1961). Data from all Line 1 Hereford contemporaries of the members of Generation 0 were used in computing selection differentials.

Management and Data Recording. Management of the Line 1 population at Fort Keogh Livestock and Range Research Laboratory from 1935 to 1989 has been chronicled by MacNeil et al. (1992). Management of the cattle through the conclusion of this experiment was similar to the protocol in place in 1989.

Calving commenced in late March and continued until late May of each year. At calving, first-parity heifers were observed periodically throughout the day and night in lots of about 8 ha. Observers were instructed to assist any heifer that had not made significant progress toward calving within the 1st h after being initially observed in labor. This directive led to an atypically high rate of assistance for heifers in this experiment. Until 1989, cows were calved on range with observation only during daylight hours. In 1989 and thereafter, the cows and heifers were calved together at the same facility. Calves born during the previous 24-h period were weighed each morning. Calving difficulty was determined by the level of assistance needed for successful parturition and scored: 1 = none, 2 = easy pull, 3 = hard pull, and 4 = Caesarian section. Observed abnormal presentations of the calf were also recorded. Cow-calf pairs were moved to native range spring pasture a few days after birth.

Mating assignments were made to minimize the inbreeding coefficient of the resulting progeny as much as possible while maintaining an approximately equal cow-to-bull ratio. In early June the cow-calf pairs were moved to smaller breeding pastures of 222 to 549 ha. Heifers were exposed for breeding to the same bulls, in the same pastures, and at the same time as the older cows. A 45-d breeding season commenced on approximately June 15. Technicians rode horseback through the breeding pastures three or more times per week to diagnose and treat any health problems, ensure assigned matings, and group cows together with the bull when scattered. Bulls that were injured during the breeding season were replaced with an alternate bull equipped with a chin-ball marker and parentage was determined through observed breedings and use of blood-typing (Stormont, 1959).

After the breeding season, cow-calf pairs were moved to rangeland summer pasture, where they

remained until weaning in mid-October. Calves received a preweaning vaccination for stress-induced diseases at a late summer working 4 to 6 wk before weaning. At weaning, calves were removed from their dams and allowed a period of 2 to 4 wk for adaptation to postweaning conditions.

Until 1987, weaned heifer calves were wintered on pasture and supplemented as needed to gain approximately 454 g/d. Subsequently, the heifer calves were wintered in a feedlot and fed a corn silage-based diet sufficient to gain approximately 568 g/d. The heifers were weighed every 28 d during the wintering period after adjustment to being weaned. With the onset of green grass the following spring the heifers were turned out on crested wheatgrass pasture, where they remained until they were moved to the breeding pastures.

After acclimation to feedlot conditions, bull calves were weighed two or three times within a 1-wk period to initiate a 168-d postweaning gain test. During the postweaning gain test they were fed a diet containing approximately 15% corn, 10% oats, 5% of a 33% CP supplement, and 70% corn silage and weighed every 28 d. Feed levels were adjusted as conditions warranted to maintain an average rate of gain between 1.1 and 1.25 kg/d. This level of average performance was thought sufficient to allow for expression of genetic differences in growth potential among candidates for selection without compromising structural soundness. Upon completion of the 168-d test period, the bulls were again weighed two or three times within a 1-wk period and postweaning gain was calculated from averages of the initial and final weights.

Selection Criteria. Selection decisions were based on performance within year of birth and sex subclasses after adjustment of phenotype for age of dam effects. Age of dam for cows greater than 5 yr old was coded as 5. Adjustment factors used were initially calculated from data collected between 1972, when calving of 2-yr-old heifers was initiated, and 1978. They were updated periodically throughout the experiment using all the accumulated data available to that time due to the relatively small number of records from 2-yr-old females. Multiplicative adjustment factors for age of dam effects on birth weight and gain from birth to weaning were used from 1978 to 1988. Subsequently, additive adjustment factors were used to adjust for age of dam effects. Yearling weight was calculated as birth weight + (average daily gain from birth to weaning \times 180) + (average daily gain during the postweaning gain test \times 185).

In the YB subline, sires were selected for high yearling weight from among all calves with below-average birth weight. In the YW subline sires were mass-selected for high yearling weight. Sires were selected based on their individual phenotypic performance without consideration of the growth performance of relatives. In both sublines, the selection of

sires was restricted such that no sire left more than three sons that subsequently became sires and no dam left more than two sons that became sires. Beginning in 1985, there was an intentional effort to select a future sire from within each current sire family to control accumulation of inbreeding. Bulls were also required to pass a breeding soundness exam as yearlings before being used for breeding. Sires were used as yearlings and 2-yr-olds for either 1 or 2 yr. Most of the available heifers were exposed for breeding as yearlings. In the fall, nonpregnant and phenotypically undesirable heifers were culled. Thereafter, selected females remained in the herd until they failed to conceive twice, became unsound, or reached 10 yr of age.

Analyses of Data. Cumulative selection differentials were calculated following the methodology of Newman et al. (1973) as modified by Koch et al. (1994) to assess differences in selection applied between sires and dams. Following Koch et al. (1994): Total cumulative selection = $ID + (CS + CD)/2$, with $CS = (\text{sum of(sire IDs)} + \text{sum of(SCS + DCS)})/2/n$ and $CD = (\text{sum of(dam IDs)} + \text{sum of(SCD + DCD)})/2/n$. In these formulas, ID = the deviation of phenotype from contemporary group mean, CS = cumulative sire differential, CD = cumulative dam differential, SCD = sire's cumulative dam differential, SCS = sire's cumulative sire differential, DCD = dam's cumulative dam differential, DCS = dam's cumulative sire differential, and n = number in a contemporary group.

Results from preliminary analyses of variance indicated that year of birth, sex of calf, age of dam, and a variety of two-factor interactions among these effects significantly affected birth weight and yearling weight. Hence, contemporary groups were formed as year, sex of calf, age of dam subclasses for further analyses. Hypotheses of homogeneity of intracontemporary group variance were tested. There was a tendency for male calves to have slightly higher within-sex phenotypic variance, as was previously observed by Koch et al. (1994). This tendency approached significance ($P < .2$) only for yearling weight in the YW selection line. Therefore, the analyses and results described hereafter are in their original units of measure. Arithmetic average birth weight and yearling weight were 37.3 and 380 kg, respectively.

Derivative-free, multiple-trait REML (Meyer, 1991) methods as implemented by Boldman et al. (1993) were used to predict breeding values simultaneously with estimation of (co)variance components for birth weight and yearling weight. Fixed effects assumed for birth weight were contemporary groups, linear and quadratic regressions on Julian day of birth, and linear regressions on inbreeding of the calf and its dam. Yearling weight was modeled with similar fixed effects, except that the regressions on

Julian day of birth were not included. Random effects assumed for both traits were direct and maternal additive genetic effects, their covariance, and residual nongenetic effects. Including maternal permanent environmental effects for both traits was attempted in a preliminary analysis that failed to converge. Hence, separate analyses were conducted with maternal permanent environmental effects on one trait included in each analysis. Results from the better-fitting model, that including maternal permanent environmental effects on yearling weight, are presented here. The criterion used to determine convergence of the derivative-free search procedure was variance of twice the log-likelihood in the simplex less than 10^{-8} . Several analyses were started with different initial values for the (co)variance components and the presumably converged analysis was restarted after reaching this criterion to increase the chance of attaining a global maximum. Significance of random effects was evaluated using likelihood ratio tests for individual (co)variance components.

Incidence of dystocia experienced by 2-yr-old heifers at their first calving was analyzed using animal model marginal maximum-likelihood (MML) methods (Hoeschele et al., 1987) to predict breeding values for calving ability on the underlying continuous scale based on the binary observations. There were 500 observations of calving by 2-yr-old heifers with an average assistance rate of 50% (calving difficulty score 1 vs scores 2, 3, and 4). The paucity of data and present computing capabilities precluded obtaining multiple-trait MML estimates of breeding values and parameters associated with calving ability. Thus, results from single-trait MML analyses are reported here. However, including the records on which selection decisions were based would have removed potential bias in the parameter estimates and genetic trends (Pollak et al., 1984). Contemporary groups formed as year and sex-of-calf subclasses and regressions on inbreeding of calf and dam were included in the analysis as fixed effects. Correlated direct breeding values due to the genotype of the calf and maternal breeding values due to the genotype of the dam were included as random effects. The analysis was assumed to have converged when changes in the estimated genetic (co)variances were all less than 10^{-5} between rounds of iteration.

Genetic trends were estimated by partitioning the solution vectors for direct and maternal additive genetic effects into sub-vectors corresponding to the YB and YW sublimes. Elements of the resulting sub-vectors of breeding values corresponding to animals within sublimes were averaged for each birth-year and the resulting birth-year averages were then regressed on birth-year. Resulting regression coefficients for each subline have been interpreted here as estimates of genetic trend for the respective subline.

Results and Discussion

Generation intervals attained in this experiment (Table 1) were less than those typically attained in other beef cattle selection experiments reviewed by Mrode (1988). Shorter generation intervals associated with sire paths of selection as opposed to dam paths result from the extensive use of yearling and 2-yr-old bulls and the use of individual sires for not more than 2 yr. The difference between generation intervals for dams of sire and dams of dams may indicate some bias toward selection of bulls from older cows. This bias may result from a tendency to desire phenotypically larger bulls to be used in natural service on mature cows under extensive conditions. Given two male candidates for selection with nearly equal performance records, the larger bull tended to be the one that was selected. The difference in generation intervals may have also resulted from some under-adjustment of performance records made by male progeny of young cows. This latter source of bias could arise from the lack of sufficient prior within-herd information on the performance of progeny from 2-yr-old dams at the start of the experiment and the larger-than-usual age of dam effects associated with 2-yr-old dams in the Line 1 population (MacNeil and Snelling, 1996).

Results pertaining to family sizes (Table 1) for sires and dams document the expansion of both selection lines from four-sire lines at the beginning of the experiment to five-sire lines. Over the course of the experiment, there were 37 sires and 239 dams that produced 944 progeny in YB and 39 sires and 287 dams that produced 1,058 progeny in YW. Recruitment of new sires and dams was slightly less in YB than in YW, both stemming from and resulting in the marginally smaller size of the YB subline. Family sizes, their variances and covariances, and generation intervals (Table 1) provide the basis for comparing effective population sizes of the sublines. Average effective population sizes per generation were 28.4 and 32.5 for YB and YW, respectively. Primary determinants of the larger effective population size of YW were the greater numbers of sires and dams per generation moderated by the larger variance in size of maternal half-sib families relative to YB.

This experiment was initiated using an inbred herd of cattle with the most distantly related potential mates having an additive relationship of approximately .5, and experimental resources were not sufficient for replication necessary to account for genetic drift. However, accrual of inbreeding during the experiment was only about 5% (Table 1). Despite the slightly smaller effective population size and similar number of elapsed generations in YB, inbreeding did not accrue more rapidly than in YW. Principal effects of inbreeding likely were 1) reducing the number of candidates available for selection resulting from inbreeding depression of fitness traits and 2)

Table 1. Demographic structure of lines selected by independent culling levels for below-average birth weight and high yearling weight (YB) and for high yearling weight (YW)

Statistic	YB	YW
Average age of parents, all calves born, yr		
Sires	2.76	2.77
Dams	4.39	4.28
Generation intervals, yr		
Sires of sires	2.95	2.97
Sires of dams	2.83	2.81
Dams of sires	4.97	4.86
Dams of dams	4.35	4.30
Family size, no.		
Sires/yr	2.64	2.79
Dams/yr	17.07	20.50
Progeny/sire	20.52	22.51
Progeny/dam	2.87	2.86
Sires/sire	1.06	1.03
Dams/sire	6.45	7.56
Sires/dam	.14	.12
Dams/dam	.88	.90
(Co) Variance		
Var (sires/sire)	1.26	.93
Var (dam/sire)	12.39	13.29
Cov (sires, dams/sire)	1.74	.60
Var (sires/dam)	.13	.17
Var (dams/dam)	1.04	1.28
Cov (sires, dams/dam)	.10	.05
Inbreeding, (F_x), %		
Base population		25.11
ΔF_x /yr	.29	.37
F_x in 1993	29.84	30.94

reducing heritabilities due the proportionate decrease in additive genetic variance.

Estimates of genetic and nongenetic variances and covariances together with associated estimates of heritability and genetic correlation for birth weight and yearling weight are presented in Table 2. These estimates were derived simultaneously using derivative-free REML (Meyer, 1991) and data from a population with a long prior history of selection for postweaning growth (MacNeil et al., 1992). The direct heritability of birth weight was approximately twice its maternal counterpart, and the direct-maternal covariance was negligible. Comparable recent estimates from other Hereford populations have been .41, .24, and .46 for direct heritability; .08, .11, and .08 for maternal heritability; and .04, .37, and .13 for direct-maternal genetic correlation (Meyer, 1992; Waldron et al., 1993; and Koch et al., 1994, respectively). The direct heritability of yearling weight was more than fivefold greater than its maternal counterpart, with the direct maternal covariance again negligible. Koch et al. (1994) observed direct and maternal heritabilities for yearling weight of .44 and .06 with a direct-maternal genetic correlation of .08. Consistent with genetic theory of long-term selection and inbreeding, heritabilities from the present study seem modestly

Table 2. Restricted maximum likelihood estimates of genetic and nongenetic variances (Var, kg²) and covariances (Cov, kg²) and associated estimates of heritability and genetic correlation (parentetical) for birth weight (BW) and yearling weight (YW)

Genetic effects	BW _d	YW _d	BW _m	YW _m
BW, direct (BW _d)	6.00 (.28)	29.03 (.58)	.07 (.02)	-4.90 (-.22)
YW, direct (YW _d)		418.65 (.31)	13.15 (.35)	-.33 (-.00)
BW, maternal (BW _m)			3.30 (.16)	10.37 (.64)
YW, maternal (YW _m)				79.36 (.06)
Nongenetic effects	Var (BW)	Var (YW)	Cov	
Maternal PE ^a	—	124.71	—	
Residual	11.72	717.83	18.08	
Phenotypic	21.09	1,340.22	61.60	

^aPE = Permanent environment.

reduced relative to the average of the preceding literature estimates from other Hereford cattle populations. However, the ability to definitively reach such a conclusion is beyond the design, scope, and resources of the present study. In the present study, the permanent environmental effect on yearling weight due to dams accounted for 9% of the phenotypic variance, compared to 5% in Koch et al. (1994). The uncommonly estimated covariances between direct genetic effects on yearling weight and maternal genetic effects on birth weight and between maternal genetic effects on birth weight and yearling weight were of moderate magnitude ($P < .01$). A plausible biological explanation for these latter two observations is illusive. However, in a diallel crossing experiment with inbred lines of Hereford cattle that included progenitors of the base population for this study (Brinks et al., 1967; Urick et al., 1968), small positive correlations were observed for line-specific direct effects on yearling weight and maternal effects on birth weight and for line-specific maternal effects on birth and yearling weights.

Shown in Table 3 are average generation numbers, numbers of calves born, and cumulative selection differentials for birth weight arrayed by birth year of progeny from the YB and YW selection lines, respectively. The progression of generations through time was consistent between lines with only small intra-year discrepancies. Both selection lines were approximately 5.2 generations removed from the base population at the conclusion of the experiment. Thus, the experiment itself was similar in duration to most of the other selection experiments conducted with beef cattle and contained in the review of Mrode (1988).

The negative birth weight sire selection differentials in the YB line result from the purposeful selection of sires with below-average birth weight. The positive birth weight sire selection differentials in the YW line result not from purposeful selection for high birth weight, but from the phenotypic correlation of birth weight and yearling weight (.37) and the selection of sires in YW for high yearling weight. In

YB and YW the modest positive dam selection differentials for birth weight reflect mortality of heifer calves with very light birth weight and the joint effects of the phenotypic correlation of birth weight with yearling weight and a tendency for the lightest heifers to be culled from both lines at 12 to 18 mo of age. Fewer heifers were culled during the final years of the experiment than were culled earlier in an attempt to increase herd size. Total selection applied to birth weight in the YB selection line, averaged over sex of progeny, was -5.8 kg. In contrast, the birth weight secondary selection differential in the YW line was +16.5 kg. These selection differentials provide the basis for anticipating genetic divergence in birth weight between the YB and YW selection lines.

Shown in Table 4 are numbers of calves alive at 1 yr of age and the cumulative selection differentials for yearling weight of the YW and YB selection lines, respectively. Total selection applied to yearling weight was +321 kg in the YW selection line vs +204 kg in the YB selection line.

Genetic trends in birth weight obtained over the course of this experiment as estimated from the converged solutions of the animal model equations are shown in Figure 1. The initial difference in breeding values between YB and YW (total of direct and maternal: $1.65 \pm .12$ kg vs $2.61 \pm .16$ kg, respectively) represents a founder effect attributable to the nonrandom selection of sires from within the base population for use as parents of the 1978 and 1979 calf crops. Virtually all the differential response in birth weight between the YB and YW sublines was found in the direct effects. Direct genetic effects on birth weight diverged as a result of the differential selection practiced in the YB and YW sublines. In the YB line direct breeding value for birth weight trended slightly negative, whereas in the YW line they trended upward as a correlated response to selection for yearling weight. Regressions of average direct breeding value for birth weight on birth year were $-.01 \pm .02$ kg and $.10 \pm .01$ kg for YB and YW, respectively. Maternal genetic effects on birth weight increased slowly and

Table 3. Average generation number, numbers of male and female calves born, and birth weight cumulative selection differentials^a by progeny birth year for the independent culling levels (below-average birth weight and high yearling weight) and single-trait (yearling weight) selection lines

Birth year	Independent culling levels selection line						Single-trait (yearling weight) selection line						
	Males calves			Female calves			Male calves			Female calves			
	Generation number	n	CSD	CDD	n	CSD	CDD	n	CSD	CDD	n	CSD	CDD
78	1.00	22	-0.05	1.64	26	-0.73	.51	22	2.27	.29	17	1.73	-.27
79	1.38	23	-1.36	.79	32	-1.99	1.56	26	4.47	.81	31	5.01	.21
80	1.80	27	-.69	2.04	19	-1.31	1.99	23	5.00	.69	26	3.98	-.07
81	1.95	25	.57	2.03	27	-.07	2.57	24	9.05	1.28	31	8.00	-.08
82	2.30	30	-1.20	2.37	21	-.82	1.21	22	7.06	1.75	29	7.00	.90
83	2.63	29	-.48	1.87	22	-.16	1.27	27	7.03	1.99	36	6.05	.25
84	2.74	33	-3.37	2.80	28	-3.96	1.24	28	9.05	2.38	34	7.97	.86
85	2.89	28	-3.62	2.99	27	-4.15	1.66	22	8.21	1.89	37	6.91	.83
86	3.28	22	-5.50	2.18	20	-5.69	2.45	20	5.96	2.56	28	6.88	-.08
87	3.58	26	-4.61	2.62	23	-5.48	1.63	28	9.18	2.20	29	8.18	1.22
88	3.69	28	-4.86	2.99	27	-5.58	1.74	27	9.82	1.40	41	10.63	1.52
89	4.04	25	-6.30	1.66	29	-6.96	1.95	33	12.22	2.89	31	12.98	.32
90	4.36	25	-5.86	2.88	32	-6.55	1.71	34	7.20	2.97	35	8.07	1.13
91	4.71	36	-7.35	2.60	36	-8.14	1.77	44	15.23	2.72	45	14.30	1.44
92	4.96	23	-6.42	2.34	33	-7.50	1.38	34	16.31	3.73	35	16.11	1.36
93	5.17	41	-6.90	2.56	34	-8.36	1.07	47	13.48	2.92	45	14.38	2.12

^aCSD = cumulative sire selection differential, kg; CDD = cumulative dam selection differential, kg.

Table 4. Numbers of male and female calves alive at 1 year of age and yearling weight selection differentials^a for the independent culling levels (below-average birth weight and high yearling weight) and single-trait (yearling weight) selection lines

Birth year	Independent culling levels selection line						Single-trait (yearling weight) selection line					
	Male calves			Female calves			Male calves			Female calves		
	n	CSD	CDD	n	CSD	CDD	n	CSD	CDD	n	CSD	CDD
78	17	67.28	18.35	22	60.64	7.80	18	51.21	8.49	15	63.40	-1.75
79	19	91.94	6.30	24	73.15	8.89	20	70.38	10.44	23	63.05	4.99
80	25	70.39	18.98	16	65.48	3.88	20	71.56	14.40	24	71.06	3.94
81	24	89.67	10.63	25	90.58	21.05	23	95.75	22.11	31	107.56	8.12
82	26	86.02	16.62	20	93.81	4.42	21	121.34	29.42	24	120.92	13.23
83	25	105.13	17.40	21	102.78	10.10	22	137.26	20.69	30	144.09	21.61
84	27	112.13	20.65	24	120.87	4.28	25	128.31	31.82	32	137.31	11.10
85	24	123.27	20.85	22	134.51	16.25	18	148.15	25.97	28	156.60	19.66
86	21	138.40	31.08	18	140.40	25.06	19	157.90	45.70	25	168.23	8.64
87	26	161.95	30.08	21	163.43	19.65	22	160.46	37.85	28	167.52	12.36
88	26	160.52	32.54	27	172.00	25.64	23	171.18	38.50	39	179.80	14.48
89	20	173.42	35.71	27	172.61	25.14	28	182.78	58.58	26	194.68	12.64
90	23	185.12	33.83	30	195.73	30.48	31	202.73	47.83	30	213.88	13.14
91	33	185.19	32.93	35	198.50	33.85	41	223.55	54.79	43	239.07	23.72
92	21	183.10	37.44	32	181.22	27.41	28	243.23	58.84	34	251.15	27.53
93	36	150.96	36.66	32	185.30	35.12	42	274.36	54.56	41	284.64	29.36

^aCSD = cumulative sire selection differential, kg; CDD = cumulative dam selection differential, kg.

similarly across lines in response to the selection practiced. Regressions of average maternal breeding value for birth weight on birth year were $.05 \pm .01$ kg and $.06 \pm .01$ kg for YB and YW, respectively. In the YB line, the total of direct and maternal genetic effects

on birth weight ($.50 \pm .21$) indicates that imposition of an independent culling level for below-average birth weight in sire selection was nearly sufficient to offset the genotypic increase in birth weight resulting from selection for increased yearling weight, whereas the

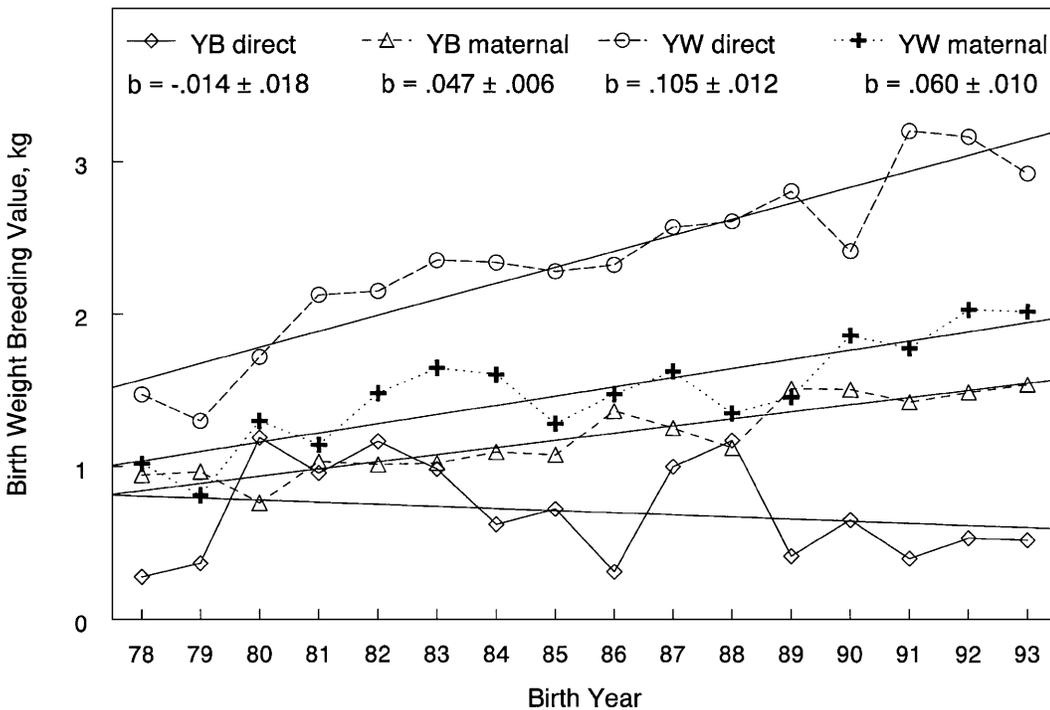


Figure 1. Trends in direct and maternal breeding values for birth weight of a line selected by independent culling levels for below-average birth weight and high yearling weight (YB) and a line selected for high yearling weight alone (YW).

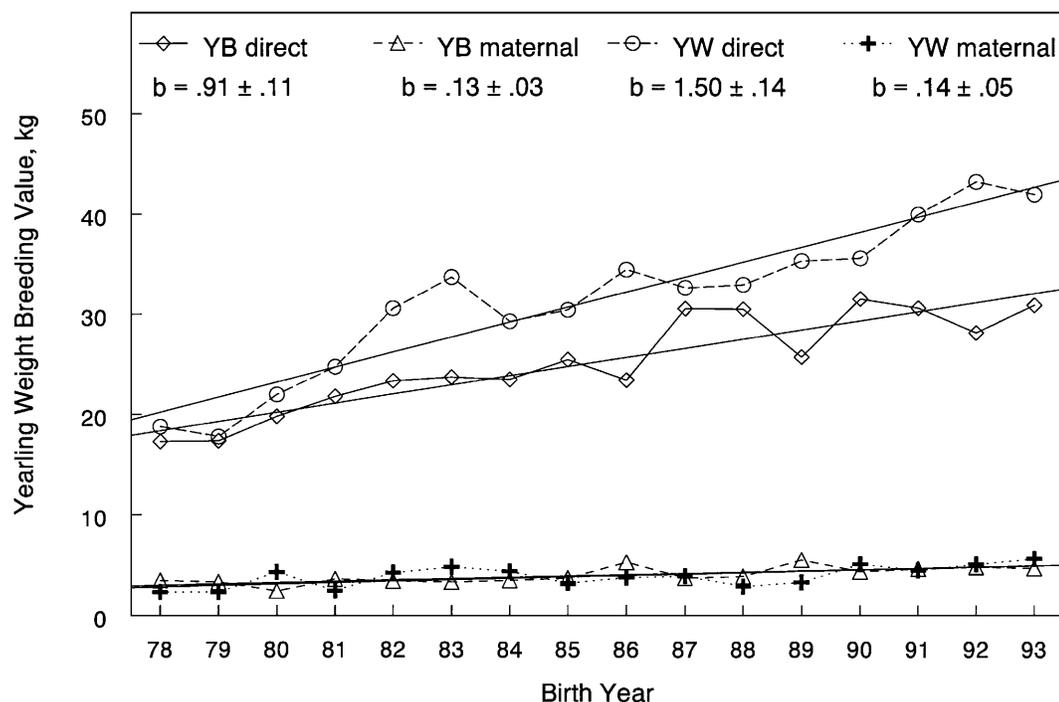


Figure 2. Trends in direct and maternal breeding values for yearling weight of a line selected by independent culling levels for below-average birth weight and high yearling weight (YB) and a line selected for high yearling weight alone (YW).

total genetic correlated response of birth weight in YW was $2.48 \pm .27$ kg. Phenotypically, calves born in YB during the final 2 yr of this study were 2.4 kg (6%) lighter than those in YW.

Genetic trends in 365-d weight during this experiment as estimated from the converged solutions of the animal model mixed-model equations are shown in Figure 2. Direct genetic effects on 365-d weight increased more slowly in YB than in YW, as would be expected from the difference between lines in 365-d weight selection differential. Regressions of average direct breeding value for 365-d weight on birth year were $.91 \pm .11$ and $1.50 \pm .14$ for YB and YW, respectively. Maternal genetic effects were similar and essentially unchanged in YB and YW throughout the course of this experiment. Regressions of average maternal breeding value for birth weight on birth year were $.13 \pm .03$ and $.14 \pm .04$ kg for YB and YW, respectively. The 36% reduction in genetic response in 365-d weight of YB relative to YW (15.6 ± 1.5 vs 24.5 ± 2.6 kg, respectively) represents the cost of limiting genetic increase in birth weight through the imposed independent culling level for below-average birth weight applied in sire selection in this experiment. The genetic difference between YB and YW resulted in a corresponding phenotypic difference of 13.2 kg (3%) between lines during the final 2 yr of the study.

The benefit anticipated to result from the independent culling levels selection strategy was a reduction

in the incidence of dystocia experienced by 2-yr-old heifers in the YB line relative to the YW line. With a similar objective of controlling the genetic increase in birth weight while increasing yearling weight, Dickerson et al. (1974) proposed a selection index: yearling weight - $(3.2 \times \text{birth weight})$. Doornbos et al. (1994) observed total genetic increases of .011 kg/yr in birth weight and 1.97 kg/yr in yearling weight as a result of sire selection based on this index. Further experimental validation of this index was considered as a potential objective for the present experiment. To avoid redundancy with other planned experiments, the heuristic independent culling level was used in this experiment. In the YB subline, total genetic increases comparable to those observed by Doornbos et al. (1994) were .04 kg/yr and 1.04 kg/yr, respectively.

Arnold et al. (1990) examined a similar strategy of selection by independent culling levels for low birth weight and high yearling weight on a breed-wide basis using national cattle evaluation. Their results seem promising for breaking the genetic antagonism between direct effects on birth weight and subsequent growth. However, calving ability is the outcome of interaction between dam and fetus (Hanset, 1981). By examining only one round of sire selection, Arnold et al. (1990) ignored maternal effects and correlations between direct and maternal effects that may affect calving ability.

In the present experiment, estimated direct and maternal heritabilities for calving ability were .31 and

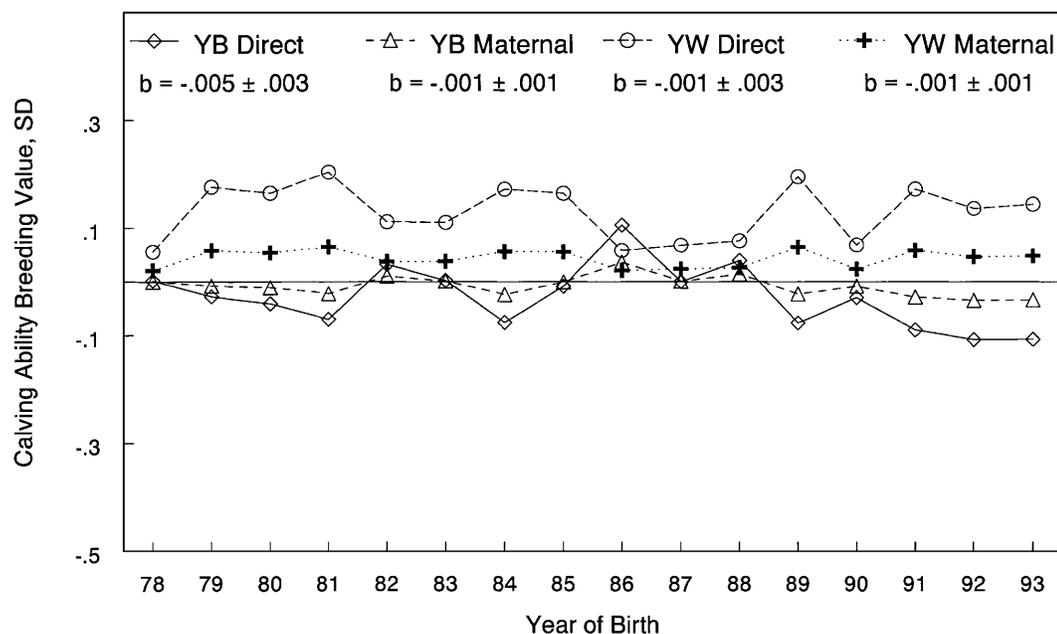


Figure 3. Trends in direct and maternal breeding values for calving ability of a line selected by independent culling levels for below-average birth weight and high yearling weight (YB) and a line selected for high yearling weight alone (YW).

.04, respectively. Thus, in this population, it would seem that the additive genetic contribution to calving ability as a trait of the calf was more important than as a trait of the dam. However, these results must be considered with caution, because of the paucity of data contributing to them, because the direct and maternal effects were highly correlated (.9), and because they may be biased by selection on correlated traits. Genetic trends in calving ability at first parturition are shown in Figure 3. Genetic potential of the YW subline resulted in more frequent assistance consistently being required at parturition relative to YB. Thus, selection of sires for below-average birth weight in conjunction with high subsequent growth resulted in a reduced need for assistance at parturition. This result was primarily due to the genotype of the calf and is consistent with the common recommendation that primiparous heifers be bred to bulls with low birth weight EPD (Bellows et al., 1982). However, the strategy of selecting bulls by independent culling levels for below-average birth weight and high yearling weight did not result in any divergence through time of calving ability relative to selecting bulls for high yearling weight alone. Thus, selection for low-birth-weight and high genetic potential for subsequent growth simultaneously seems to be a valid management strategy for controlling the incidence of calving difficulty in 2-yr-old heifers, but not a strategy that will result in genetically improved calving ability.

In France, Charolais cattle were selected by a more elaborate system of independent culling levels to improve the level of calving ability and meat produc-

tion concurrently (Menissier et al., 1981). Direct and maternal paths of selection were considered. The observed improvement in calving ability seemed to be related to size of the pelvic opening of heifers in relation to weight, rather than to a limitation in the increase in birth weight. However, there is conflicting evidence that single-trait selection of sires based on greater yearling pelvic area may yield negligible improvement in either the severity or incidence of dystocia in their daughters (Kriese et al., 1994). Favorable selection responses have also resulted from selection on expected progeny differences for calving ease from multiple-trait evaluations that included birth weight, 200-d weight, and postweaning gain (Bennett, 1997). Concurrent with improved calving ability, birth weight has been reduced and selected lines have continued to diverge from control lines over 4 yr.

The efficacy of using only growth traits as selection criteria for improvement of calving ability has been called into question, a conclusion that is supported by results from the present research. Questions concerning correlated responses in 1) mature size and maturing rate of cows and 2) direct effects on growth and carcass traits of crossbred progeny will be addressed in future publications.

Implications

This research has demonstrated the feasibility of increasing genetic potential for yearling weight

without also increasing genetic potential for birth weight, despite the positive genetic correlation between these traits. However, selection based on these growth traits did not establish a favorable genetic trend in calving ability. Direct selection may be more effective in reducing dystocia than pressure applied to indicator traits. Appropriately chosen selection criteria may also be effective in managing other genetic antagonisms that limit the efficiency of beef production.

Literature Cited

- Arnold, J. W., J. K. Bertrand, L. L. Benyshek, J. W. Comerford, and T. E. Kiser. 1990. Selection for low birth weight and high yearling weight in Angus beef cattle. *Livest. Prod. Sci.* 25: 31-41.
- Bellows, R. A., R. E. Short, D. C. Anderson, B. W. Knapp, and O. F. Pahnish. 1971. Cause and effect relationships associated with calving difficulty and calf birth weight. *J. Anim. Sci.* 33: 407-415.
- Bellows, R. A., R. E. Short, and G. V. Richardson. 1982. Effects of sire, age of dam, and gestation feed level on dystocia and postpartum reproduction. *J. Anim. Sci.* 55:18-27.
- Bennett, G. L. 1997. Selection for calving ease. *Proc. Beef Improv. Fed. 29th Annu. Mtg. Res. Symp.*, May 14-17, Dickenson, ND. (In press).
- Boldman, K. G., L. A. Kriese, L. D. Van Vleck, and S. D. Kachman. 1993. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances (draft). USDA, ARS, Lincoln, NE.
- Brinks, J. S., R. T. Clark, N. M. Kieffer, and J. J. Urlick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. *J. Anim. Sci.* 23:711.
- Brinks, J. S., R. T. Clark, and F. J. Rice. 1961. Estimation of genetic trends in beef cattle. *J. Anim. Sci.* 20:903 (Abstr.).
- Brinks, J. S., J. J. Urlick, O. F. Pahnish, B. W. Knapp, and T. J. Riley. 1967. Heterosis in preweaning and weaning traits among lines of Hereford cattle. *J. Anim. Sci.* 26:278.
- Dickerson, G. E., N. Künzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. *J. Anim. Sci.* 39:659.
- Doornbos, D. E., D. D. Kress, D. C. Anderson, and K. C. Davis. 1994. Genetic trends for a selection index and growth traits in Herefords selected for light birth weight and greater growth rate. *J. Anim. Sci.* (Suppl. 1)72:203. (Abstr.).
- Hanset, R. 1981. Selection problems when antagonistic effects exist between production characteristics and calving difficulties. *Livest. Prod. Sci.* 8:291.
- Hoeschele, I., D. Gianola, and J. L. Foulley. 1987. Estimation of variance components with quasi-continuous data using Bayesian methods. *J. Anim. Breed. Genet.* 104:334.
- Koch, R. M., L. V. Cundiff, and K. E. Gregory. 1994. Cumulative selection and genetic change for weaning or yearling weight or for yearling weight plus muscle score in Hereford cattle. *J. Anim. Sci.* 72:864.
- Kriese, L. A., L. D. Van Vleck, K. E. Gregory, K. G. Boldman, L. V. Cundiff, and R. M. Koch. 1994. Estimates of genetic parameters for 320-day pelvic measurements of males and females and calving ease of 2-year-old females. *J. Anim. Sci.* 72:1954.
- Laster, D. B., H. A. Glimp, L. V. Cundiff, and K. E. Gregory. 1973. Factors affecting dystocia and the effects of dystocia on subsequent reproduction in beef cattle. *J. Anim. Sci.* 36:695.
- MacNeil, M. D., and W. M. Snelling. 1996. Systematic error in genetic evaluation of Miles City Line 1 Hereford cattle resulting from preadjustment for age of dam. *J. Anim. Sci.* 74:1794.
- MacNeil, M. D., J. J. Urlick, S. Newman, and B. W. Knapp. 1992. Selection for postweaning growth in inbred Hereford cattle: the Fort Keogh, Montana Line 1 example. *J. Anim. Sci.* 70:723.
- Meunier, F., J. L. Foulley, and W. A. Pattie. 1981. The calving ability of the Charolais breed in France and its possibilities for genetic improvement. III. Genetic improvement of calving ability in the Charolais as a maternal breed. *Ir. Vet. J.* 35:128.
- Meuwissen, T.H.E., J. P. Gibson, and M. Quinton. 1995. Genetic improvement of production while maintaining fitness. *Theor. Appl. Genet.* 90:627.
- Meyer, K. 1991. Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. *Genet. Sel. Evol.* 23:67.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179.
- Mrode, R. A. 1988. Selection experiments in beef cattle. Part 2: A review of responses and correlated responses. *Anim. Breed. Abstr.* 56:155.
- Newman, J. A., G. W. Rahnefeld, and H. T. Fredeen. 1973. Selection intensity and response to selection for yearling weight in beef cattle. *Can. J. Anim. Sci.* 53:1.
- Pollak, E. J., J. van der Werf, and R. L. Quaas. 1984. Selection bias and multiple trait evaluation. *J. Dairy Sci.* 67:1590.
- Smith, G. M., H. A. Fitzhugh, Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Short-horn cattle. *J. Anim. Sci.* 43:389.
- Stormont, C. 1959. On the applications of blood groups in animal breeding. *Proc. Xth Int. Congr. Genet.* 1:206.
- Urlick, J. J., J. S. Brinks, O. F. Pahnish, B. W. Knapp, and T. M. Riley. 1968. Heterosis in postweaning traits among lines of Hereford cattle. *J. Anim. Sci.* 27:323.
- Waldron, D. F., C. A. Morris, R. L. Baker, and D. L. Johnson. 1993. Maternal effects for growth traits in beef cattle. *Livest. Prod. Sci.* 34:57.