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Experimental selection for calving ease and postnatal growth in seven cattle populations. II. Phenotypic differences

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Experimental selection for calving ease and postnatal growth in seven cattle populations. II. Phenotypic differences[1,2]

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ABSTRACT: Effects of selection for 2-yr-old heifer calving ease (reduced calving difficulty score) on phenotypic differences between select and control lines of cattle for birth, growth, yearling hip height, and pelvic measurements were estimated. The selection objective was to decrease calving difficulty score in 2-yr-old heifers, while either maintaining or increasing yearling weight. The control line objective was to maintain or increase yearling weight by the same amount as the select lines and to maintain or proportionally increase birth weight. Select and control lines were formed in 4 purebred and 3 composite populations. Selection began in 1992 and select (n = 6,926) and control (n = 2,043) line calves were born from 1993 through 1999. Selection was based on EBV calculated from a 4-trait BLUP with observations on 2-yr-old calving difficulty scores, birth weight, weaning weight, and postweaning gain. Calving difficulty was scored on a scale from 1 (unassisted) to 7 (caesarean). All birth traits in select lines differed significantly from control lines. Averaged over 7 yr, select lines calved 3.0 ± 0.5 d earlier, had 1.8 ± 0.5 d shorter gestations, were 2.99 ± 0.32 kg lighter at birth, had 5.6 ± 1.5% fewer calves assisted at birth (averaged across dam ages), and 2-yr-old heifers had 0.80 ± 0.08 lower calving difficulty score. Select lines averaged 19.8% lower 2-yr-old heifer calving assistance, but there was no difference in calving assistance of older cows, resulting in a highly significant interaction of selection and dam classification. Preweaning ADG was increased 15 ± 9 g/d (1.7%) in select lines. Increased preweaning gain offset decreased birth weights in select lines, resulting in weaning weights that did not differ ($P = 0.71$). Postweaning ADG ($P = 0.16$) and yearling weight ($P = 0.41$) also did not differ. Increased preweaning ADG in select lines was not maintained after weaning. Select line hip heights were 0.70 ± 0.21 cm shorter when measured as yearlings. Pelvic height, width, and area of select heifers measured 25 to 74 d after yearling weights were not significantly different. The differences between select and control lines significantly changed over the course of the experiment for some traits. In the final 2 yr of the experiment, select lines had 3.9 kg lower birth weight and 1.3 cm shorter hip heights. Selection can be used effectively to reduce 2-yr-old calving difficulty and calving assistance while maintaining or increasing yearling weight.

Key words: calving difficulty, cattle, gestation length, growth, pelvic area, selection response

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INTRODUCTION

Reducing calving difficulty and calving assistance rates in 2-yr-old dams is a desirable but complicated component of some breeders' selection objectives. Selection for a complex objective will produce changes in several traits that are correlated with the applied selection. Some changes are caused primarily by classical genetic correlations resulting from common physiological pathways or from close chromosomal linkage. Other changes result from directly selecting for an indicator trait (e.g., birth weight) intending to change a correlated trait (e.g., calving difficulty). When more than one trait is selected, the relative correlated responses can be modified by the amount of information available at the time of selection. Traits limited by age or sex or with low heritability will have less accuracy in prediction of genetic merit at any selection decision point than traits that are not limited in expression and have high heritability.

Bennett (2008) has reported direct and maternal breeding value trends resulting from experimental selection for improved calving ease while maintaining or increasing postnatal growth. Selection was based on breeding values estimated from 4-trait BLUP. Selec-

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tion for calving ease based on these estimated breeding values is expected to produce changes in the direct and indicator traits used for selection and other traits based on estimated genetic correlations (Bennett and Gregory, 2001a,b). Correlated genetic responses to selection for reduced heifer calving score while either maintaining or increasing weight might be expected for gestation length, birth date, calving difficulty in older cows, weights and growth at different ages, and skeletal measurements. The objective of this research is to estimate phenotypic differences and trends in differences for these traits resulting from selection for heifer calving ease.

MATERIALS AND METHODS

The US Meat Animal Research Center Animal Care and Use Committee approved the procedures used in this experiment.

Populations, Management, and Selection

A complete description of populations, management, and selection is given in Bennett (2008). Aspects of the experiment important for interpreting the present results are given below.

Populations. Four purebred (Angus, Charolais, Gelbvieh, and Hereford) and 3 composite (MARC I, MARC II, and MARC III) populations at the US Meat Animal Research Center (**USMARC**, Clay Center, NE) were used in this experiment. Select and control lines were formed in each of the 7 populations. Herd sizes were approximately 150 calving females (including 45 two-year-old heifers) for each select line and 42 calving females (including 12 two-year-old heifers) for each control line. The first selected parents were mated in 1992. Totals of 6,926 select and 2,043 control calves were born from 1993 through 1999.

Sires and semen originated from 3 sources: the original populations, bulls born within each line, and industry (purebreds only). Approximately 15 select and 6 control sires were bred to females each year. Select line sires were used until semen supplies were depleted or sires with lower heifer calving difficulty EBV became available. Numbers of unique bulls used were 351 (53 industry) in select lines and 235 (35 industry) in control lines.

Most females were bred by AI for about 21 d followed by natural service bulls in single sire pastures for about 42 d. Breeding of 2-yr-old and older cows began 3 wk after the beginning of yearling heifer AI. Gestation length was recorded for calves conceived by AI.

Management. Weaning age averaged 212 d for calves born to 2-yr-old heifers and 190 d for calves born to older cows. After an initial adjustment feeding period of about 42 d, females were fed diets composed of corn silage, alfalfa haylage, and protein-mineral-vitamin supplement in various proportions (2.2 to 2.3 Mcal of ME/kg of DM) and lengths of time, depending on weather conditions and weight gains, until they were placed on improved cool-season grass pasture from mid to late April. Hereford heifers born in 1998 and 1999 were managed differently and were fed for slaughter. After a 42-d adjustment period after weaning, males were fed a diet composed of corn silage, rolled corn, and protein-mineral-vitamin supplement (about 2.7 Mcal of ME/kg of DM). Calves were weighed at birth, at weaning, and at 148 d after weaning (birth year averages from 140 to 157 d). At that time, yearling hip height was measured while standing in a chute. Heifer pelvic width and height were measured with a Rice Pelvimeter (Lane Mfg., Denver, CO) 25 to 74 d after yearling weights. Pelvic area was approximated by the product of width and height. Heifers born in 1995 were not measured for pelvic width and height.

Calving difficulty was subjectively evaluated by field personnel trained each year for accuracy and consistency of calving difficulty scores. The subjective scores used and their descriptions are: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with a calf jack, 4 = slight difficulty with a calf jack, 5 = moderate difficulty with a calf jack, 6 = major difficulty with a calf jack, 7 = caesarean birth, and 8 = abnormal presentation. Calving assistance was defined by scores greater than 1 and reported as percentage assisted.

Data for Selection. Four traits were used in the EBV analysis: calving difficulty score for 2-yr-old heifers, birth weight, weaning weight adjusted to 200 d, and postweaning gain adjusted to 168 d. Actual weaning weights were adjusted to 200 d assuming linear growth from birth to weaning. Postweaning gain was adjusted to 168 d assuming linear growth from weaning to yearling weight measurement. Heifer calving difficulty scores were set to missing values for all calves born to 3-yr-old and older cows and for any calf scored an 8. All twin calf data and weaning weights and postweaning gains of fostered calves were set to missing values for analysis.

Estimated Breeding Values. Single trait analyses for EBV were used to make selections in 1992 and 1993. Subsequently, EBV were estimated from a 4-trait animal model using MTDFREML (Boldman et al., 1995). Direct genetic effects were modeled for all 4 traits: heifer calving difficulty score, birth weight, weaning weight, and postweaning gain. Maternal genetic effects were modeled for heifer calving difficulty score, birth weight, and weaning weight. Permanent environmental effects due to dams were modeled for birth and weaning weights. In purebred populations, genetic groups (USMARC source, industry source select, and industry source control) were used. Each population was analyzed independently including data from contributing experimental sources beginning in 1978. Each population was analyzed ignoring line (select or control) of the animal producing the record.

Selection Goals and Procedures. Two lines were selected within each population (see Bennett, 2008). The overall goals of selection were 2 lines with similar yearling weights, but one line with unchanged 2-yr-old calving difficulty (control) and the other having less calving difficulty (select). Within a population, select and control lines were selected for the same maternal genetic weaning weight and direct genetic yearling weight. Composite populations were selected for average weights and purebred populations were selected for increased maternal genetic weaning weight and direct genetic yearling weight values. Control lines were selected for average direct genetic birth weights in composite populations and for increased direct genetic birth weight proportional to increased yearling weight in purebred populations. Proportionality of birth and yearling weight increases in purebred control lines was achieved by setting birth and yearling weight EBV targets proportionally greater. The intention of this proportionality constraint was to leave heifer calving difficulty unchanged. Select lines were selected for lower heifer calving difficulty score EBV. Depending on the population, select lines were selected for lower direct genetic heifer calving difficulty score EBV, for equally weighted direct and maternal EBV, or for maternal EBV weighted twice as much as direct EBV.

Three stages of selection were done using updated EBV. In the first stage after weaning, male calves were selected as potential bull candidates, older cows were culled, and older bulls were culled. In the second stage after yearling weights, the final selection of young bulls was completed and yearling heifers were selected. The third stage of selection began 6 to 8 wk after the beginning of calving and was used to select semen and which live bulls were used for breeding.

Selection of heifers born in 1996 and 1997 was relaxed. Heifers retained for breeding were randomly selected within sire. Relaxation of selection allowed evaluation of 2-yr-old heifer calving difficulty in 1998 and 1999 unbiased by possible phenotypic effects of selection for EBV.

Statistical Analyses

The primary objectives of the statistical analyses were to estimate and test differences between select and control lines and year of birth trends in differences. Secondary objectives were to estimate and test whether selection responses in calves born to 2-yr-old dams were different than those born to older dams and also whether the age of older dams affected differences.

These objectives resulted in the following model of fixed effects:

$$Y_{ijklmno} = \mu + POP_i + LINE_j + YR_k + LINE \times YR_{ik} + HC_l + LINE \times HC_{jl} + AD(HC)_{lm} + LINE \times AD(HC)_{jlm} + LINE \times YR \times HC_{jkl} + F_{ijklmn} + R_{ijklmno},$$

where Y is the phenotype, POP is population, LINE is control or select, YR is year of calf birth (1993 through 1999), HC is dam classification (2-yr-old heifer; older cow), AD(HC) is dam age (3-yr-old; 4-yr-old; older than 4 yr) nested within the cow classification, F are additional fixed effects appropriate to the trait including interactions with POP, LINE, YR, HC, and AD(HC), and R corresponds to random effects appropriate to the animal. Interactions POP × LINE, POP × YR, POP × LINE × YR, and a residual were assumed random. This model reduces to

$$Y_{ijkno} = \mu + POP_i + LINE_j + YR_k + LINE \times YR_{jk} + F_{ijkn} + R_{ijkno}$$

for 2-yr-old heifer calving difficulty score. Linear trends in differences between select and control lines across years were tested using a contrast fitting coefficients −3, −2, −1, 0, 1, 2, and 3 to estimated select line means corresponding to birth years 1993 through 1999 and coefficients 3, 2, 1, 0, −1, −2, and −3 to the corresponding estimated 1993 through 1999 control line means.

Additional fixed effects and interactions appropriate to each trait including sex, birth location at USMARC nested within year, and the age of the animal at trait measurement were added to the analysis models. Male calves that were selection candidates for this and other projects remained intact at weaning and others were castrated resulting in 2 male sex classifications for postweaning traits. Table 1 summarizes the number of measurements in select and control lines and identifies additional fixed effects used for each trait.

The MIXED and GLIMMIX procedures (SAS Inst. Inc., Cary, NC) were used to implement the statistical models. The GLIMMIX procedure was used with a probit link function for calving assistance (dams of all ages) and with a cumulative probit link function for 2-yr-old heifer calving difficulty score (1 through 7). The df were determined by the containment method. This method resulted in a more conservative probability when one or more variance components were 0.

Trends in population means for yearling weight phenotypes were analyzed by comparing yearling weights for the 4 purebred populations with the average yearling weight for the 3 composite populations. The previous model for yearling weight was modified by making POP × YR and POP × YR × sex fixed instead of random. Least squares means for population and sex by birth year were averaged by year and sex for the 3 composites. These composite averages were subtracted from corresponding year × sex least squares means for each purebred population. Corresponding EBV means (sum of direct and maternal weaning weight and direct postweaning gain; Bennett, 2008) for purebred populations and differences from the average of the 3 composite EBV means were also calculated. Purebred population phenotypic and EBV deviations were regressed on birth year and the slopes were compared to evaluate whether EBV trends for yearling weight were similar to phenotypic trends.

Table 1. Number of observations in selection and control lines and additional fixed effects fitted for each trait analyzed

			Additional fixed effects analyzed[1]								
Trait	No. select	No. control	SX	HC × SX	HC × POP	LOC	AGE	AGE × YR	AGE × POP	AGE × HC	SX × YR
Julian birthday; birth wt	6,926	2,043	X	X							
Gestation length	4,227	1,149	X	X							
Calving assistance	6,729	1,960	X	X							
Heifer calving difficulty score	2,094	560	X								
Preweaning ADG; weaning wt	6,269	1,807	X	X	X	X	X	X	X	X	
Postweaning ADG; yearling wt	6,167	1,775	X	X	X	X	X	X	X	X	X
Yearling height	6,119	1,760	X	X	X	X	X	X	X	X	X
Female pelvic height; width; area	2,370	686			X	X	X	X	X	X	

[1]A base model consisting of mean, population (POP), selection goal (LINE), birth year (YR), 2-yr-old heifer vs. older dam classification (HC), 2-, 3-, 4-, or older than 4-yr-old dam age nested within HC [AD(HC)], LINE × YR, LINE × HC, LINE × AD(HC), and LINE × YR × HC was fitted to all traits except heifer calving difficulty score. The heifer calving difficulty score model consisted of mean, LINE, and LINE × YR. Sex (SX), measurement age (AGE), weaning management group and location nested within year [LOC(YR)], male weaning weight residual deviation (WWD), and interactions were fitted for specific traits in addition to the base model as indicated by an "X." For postweaning ADG, yearling weight, and yearling height, SX was defined by 2 effects: female or male; and steer or bull nested within male.

RESULTS

Birth Traits

Selection Differences. All birth traits in select lines differed significantly from control lines (Table 2). They calved 3.0 ± 0.5 d earlier, had 1.8 ± 0.5 d shorter gestations, were 2.99 ± 0.32 kg lighter at birth, had 5.6 ± 1.5% fewer calves assisted at birth, and 2-yr-old heifers had 0.80 ± 0.08 lower calving difficulty score (Table 3). These differences are similar to some important fixed effect differences discussed below (estimates not shown in tables). The average difference in birth weight was similar to the −2.74 ± 0.11 kg difference between female and male calves and approached the −3.73 ± 0.14 kg difference between 2-yr-old and older dams (Table 4). The birth weight difference of −4.01 kg between select and control lines in the final year (Table 5) was similar to differences between 2-yr-old dams and 4- and 5-yr-old dams (Table 4). The gestation length difference exceeded the 1.2 ± 0.1 d shorter gestation of female compared with male calves. The average difference in percentage of calves assisted at birth was about two-thirds of the −8.6 ± 0.9% difference between female and male calves, but the differences between select and control lines averaged across heifers and cows in the final years of the experiment (Table 5) exceeded 10%. The average difference in heifer calving difficulty score was similar to the −0.83 ± 0.07 score difference between female and male calves.

Dam Age Interactions. The 2-yr-old heifer calving assistance difference between select and control lines was much greater than in older dams, because there was little calving difficulty in older dams from either line (Table 4). The probit link function should account for interactions resulting from different incidences; however, the interaction was significant when analyzed with a probit link function. There was also a tendency ($P = 0.06$) for less calving assistance for 3-yr-old dams in select lines. The average difference between select and control lines was −21.2 ± 2.4% in 2-yr-old dams, similar to the difference of −20.6 ± 2.1% for female vs. male calves born to 2-yr-old dams (estimate not shown).

The significant interaction of line by heifer or cow classification (Table 2) for birth weight resulted from a 0.5-kg-greater difference between calves born to 2-yr-old heifers than those born to older dams in select lines compared with the same difference in control lines (Table 5). The significant interaction of line and age of cow for gestation length (Table 2) was the result of calves born to 4-yr-old dams with gestation lengths closer to 3-yr-old dams in select lines and closer to dams older than 4 yr in control lines (Table 5).

Birth Year Trends. Calving assistance differences between select and control lines in 2-yr-old heifers were greater at the end of the experiment, but there was no apparent trend in older dams (Table 5). In the observed scale, response in 2-yr-old heifer calving difficulty score appeared nonlinear, but in the probit scale, the trend in difficulty score differences was linear and select line heifers had increasingly lower transformed scores. Calving assistance cannot be less than 0%, which limits the observed differences between lines. Figure 1 shows estimated heifer calving difficulty scores transformed from the probit scale to the observed scale. There was an apparent phenotypic trend toward decreasing heifer calving assistance in the control lines. This resulted in a narrowing of the observed differences between select and control lines in later years, especially for higher difficulty scores. Supplemental quadratic birth year contrasts for heifer calving assistance and calving difficulty scores were not significant. Use of the probit link resulted in a simpler (linear) description of the trend in differences between lines similar to the removal of sex × age of dam interaction for dystocia scores with the (equivalent) threshold model (Quaas et al., 1988).

Table 2. Probabilities and *F*-values of the effects of selection vs. control line (LINE) and its interactions for birth traits

Effect	df	Ddf[1]	Julian birthday *F*-value	Julian birthday *P*	Gestation length *F*-value	Gestation length *P*	Birth weight *F*-value	Birth weight *P*	Calving assistance[2] *F*-value	Calving assistance[2] *P*	Heifer calving difficulty score[3] *F*-value	Heifer calving difficulty score[3] *P*
LINE	1	6	37.1	<0.001	13.8	0.01	85.1	<0.001	14.2	0.009	97.7	<0.001
LINE × year	6	72	3.76	0.03	0.69	0.66	5.56	<0.001	1.57	0.17	2.14	0.06
Linear	1	72	1.69	0.20	2.47	0.12	27.7	<0.001	1.80	0.18	7.70	0.007
LINE × HC[4]	1	>2,500	2.10	0.15	0.02	0.89	3.89	0.05	22.7	<0.001		
LINE × AD(HC)[5]	2	>2,500	1.14	0.32	3.72	0.02	0.15	0.86	2.79	0.06		
LINE × year × HC	6	>2,500	0.68	0.67	0.43	0.86	0.35	0.91	0.79	0.58		

[1]Denominator df (Ddf) were calculated by the containment method resulting in conservative df when a variance is estimated to be zero. The Ddf in the last 3 rows were 8,851 (birthday and birth weight), 5,258 (gestation length), 8,571 (calving assistance), and 2,550 (heifer calving difficulty score).

[2]Heifer and cow assistance at calving was analyzed with GLIMMIX (SAS Inst. Inc., Cary, NC) using a probit link function.

[3]Heifer calving difficulty scores (1 to 7) were assigned at birth and analyzed with GLIMMIX using a cumulative probit link function.

[4]Interaction of LINE and heifer (2-yr-old) or cow classification (HC).

[5]Interaction of LINE with age of dam (3-, 4-, or 5-yr of age and older; AD) nested within the cow class of HC.

Significant birth year trends in the differences between select and control lines for birth weight and heifer calving difficulty score resulted in larger differences in the final year than the first year.

Weaning and Yearling Weights and Gains

Selection Differences. Overall differences between select and control lines were small and not significantly different for weaning weight, postweaning ADG, and yearling weight (Table 6 and Table 7). One objective of the experimental selection was equal yearling weights for select and control lines. A highly significant lower birth weight in select lines (Table 3) was offset by significantly increased preweaning growth (Tables 6 and 7).

Dam Age Interactions. Interactions of dam ages of 3-, 4- or 5-yr-old and older with line were significant for preweaning ADG, weaning weight, and yearling weight. Calves born to 3-yr-old select line dams had increased weaning weight, yearling weight, and preweaning ADG compared with calves born to control line 3-yr-old dams, but older dams from both lines had calves with similar weights and ADG (Table 8).

Birth Year Trends. A decreasing linear trend in the select minus control line difference in yearling weight was the only significant birth year trend (Table 6 and Table 9). Even though the average difference in yearling weight was small, the difference in the final year was −8.7 kg. This trend also interacted with the 2-yr-old vs. older dam classification. A significant interaction of line × birth year × dam classification for yearling weight (Table 6) seemed to be caused by a much larger select minus control line difference in calves born in 1999 to 2-yr-old dams than those born to older dams (−14.1 vs. −3.3 kg; estimates not shown).

Yearling Hip Height and Pelvic Measurements

Selection Differences. Select lines were 0.70 ± 0.21cm shorter ($P = 0.02$) when measured for hip height as yearlings (Table 10 and Table 11). Differences between select and control lines for pelvic measurements of heifers were small and not significant.

Dam Age Interactions. Control lines were taller than select lines regardless of age of dam, but the difference was smaller when dams were 3-yr-old and larger when dams were more than 4-yr-old (Table 12). Although there were no overall differences between select and control lines for pelvic measurements, the differences interacted with dam classification. Select line heifers born to 2-yr-old dams had smaller pelvic width, height, and area, but heifers born to select and control older dams had similar measurements (Table 12).

Birth Year Trends. The difference between select and control lines in yearling height increased with birth year (Table 13). Similar to yearling weight, the select minus control line difference in calves born in 1999 to

Table 3. Selection and control line least squares means of birth traits and square roots of estimated variance components[1]

Item	Julian birthday	Gestation length, d	Birth weight, kg	Calving assistance,[2] %	Heifer calving difficulty score[3]
Least squares means					
Control	87.7	285.2	39.86	14.2	2.64
Select	84.6	283.5	36.87	8.6	1.84
Select − Control	−3.0	−1.8	−2.99	−5.6	−0.80
Square root of estimated variance components					
POP × LINE[4]	0.4	0.8	0.51		
POP × year	0.0	0.5	0.67		
POP × LINE × year	1.2	0.0	0.48		
Residual	15.6	4.7	4.93		

[1]See Table 2 for significance tests.
[2]Means transformed from analysis with a probit link function. Square roots of variance components are not reported.
[3]Means transformed from analysis of heifer calving difficulty scores (1 to 7) with a cumulative probit link function. Square roots of variance components are not reported.
[4]Interaction of population (POP) and selection lines (LINE).

Table 4. Selection and control line least squares means of birth traits by age of dam[1]

Line	Dam age, yr	Julian birthday	Gestation length, d	Birth weight, kg	Calving assistance,[2] %
Control	2	76.4	285.2	38.13	47.3
	3	99.5	284.7	40.60	5.2
	4	98.8	285.9	41.90	1.1
	>4	98.6	285.4	42.28	1.1
Select	2	74.0	283.4	34.87	26.0
	3	96.8	283.1	37.95	2.8
	4	94.2	283.4	39.23	1.8
	>4	95.0	284.3	39.45	1.2

[1]See Table 2 for significance tests.
[2]Means transformed from analysis with a probit link function.

Table 5. Trend in differences (select minus control least-squares means) of birth traits by year of calves' birth[1]

Year	Julian birthday, d	Gestation length, d	Birth weight, kg	Calving assistance,[2] %		Heifer calving difficulty score[3]
				Heifer	Cow	
1993	−7.3	−1.2	−1.11	−6.4	1.7	−0.37
1994	−1.4	−1.9	−2.70	−18.5	−0.4	−0.75
1995	−1.8	−1.3	−2.47	−20.1	−1.2	−1.05
1996	−2.0	−1.8	−3.08	−26.6	−0.8	−1.00
1997	−1.4	−1.9	−3.60	−21.9	−0.4	−0.97
1998	−5.8	−2.1	−3.94	−22.2	0.5	−0.67
1999	−1.6	−2.1	−4.01	−22.6	0.6	−0.77
Trend estimates[4]						
Linear	0.32 ± 0.24	−0.13 ± 0.09	−0.44 ± 0.08	−0.091 ± 0.032	0.018 ± 0.044	−0.08 ± 0.03

[1]See Table 2 for significance tests.
[2]Differences of means transformed from analysis with a probit link function. Linear trend estimates are not transformed.
[3]Differences of means transformed from analysis of heifer calving difficult scores (1 to 7) with a cumulative probit link function. Linear trend estimates are not transformed.
[4]Linear trend estimates were evaluated using coefficients −3, −2, −1, 0, 1, 2, and 3 for 1993 through 1999.

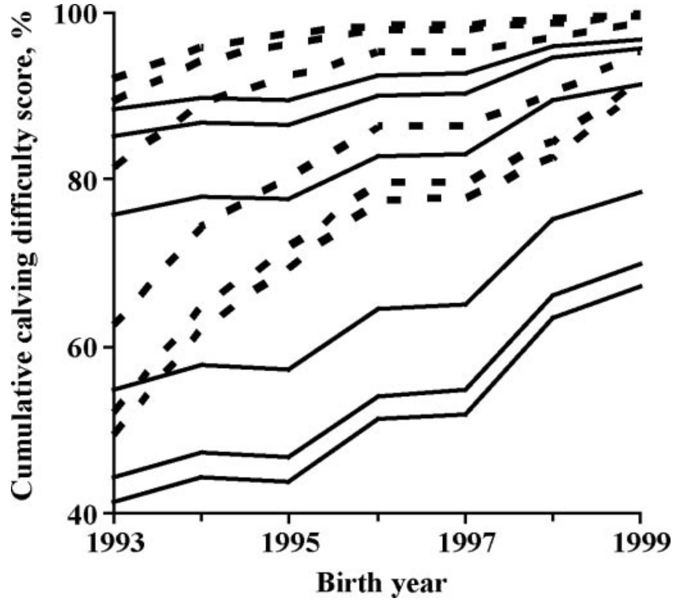

Figure 1. Birth year trends in cumulative select (dashed lines) and control (solid lines) 2-yr-old heifer calving difficulty scores estimated from an analysis with a cumulative probit link function. The lowest solid line represents percentage of score 1 (no assistance) in the control lines. The lowest dashed line represents percentage of score 1 in the select lines. The next highest line represents the cumulative percentage of scores 1 and 2 combined, and so on. The difference between 100% and the highest dashed or solid line represents the percentage caesarean births in select and control lines, respectively.

2-yr-old dams was much larger than in those born to older dams (−2.5 vs. −1.0 cm; estimates not shown).

Population Trends in Yearling Weight

One experimental goal was to increase genetic values for yearling weight in some of the purebred populations and to maintain yearling weight EBV in the composite populations. Figure 2 plots the birth year differences in male average phenotypic yearling weight for each purebred population from the male average yearling weight of the 3 composite populations. Yearling weight phenotypic differences between each purebred population and the average of the 3 composite populations were calculated. These phenotypic differences were regressed on the sum of purebred population EBV means for direct yearling weight and maternal weaning weight. Purebred population EBV means were also adjusted by subtracting the average EBV of the 3 composite populations. Table 14 shows that phenotypic changes in purebred population yearling weights tended to be greater than those estimated from EBV, especially when adjusted for the composite average.

Table 6. Probabilities and *F*-values of the effects of selection vs. control line (LINE) and its interactions for postnatal weights and growth rates

			Preweaning ADG		Weaning weight		Postweaning ADG		Yearling weight	
Effect	df	Ddf[1]	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*
LINE	1	6	9.57	0.02	0.15	0.71	2.62	0.16	0.79	0.41
LINE × year	6	36	1.02	0.43	0.67	0.67	0.79	0.58	1.38	0.25
Linear	1	36	1.85	0.18	0.01	0.92	3.00	0.09	4.33	0.04
LINE × HC[2]	1	>7,770	0.36	0.55	0.73	0.39	2.17	0.14	2.53	0.11
LINE × AD(HC)[3]	2	>7,770	6.04	0.002	4.86	0.008	2.27	0.10	5.88	0.003
LINE × year × HC[4]	6	>7,770	0.99	0.43	0.92	0.48	0.80	0.66	3.68	<0.001

[1]Denominator df (Ddf) were calculated by the containment method resulting in conservative df when a variance is estimated to be zero. The Ddf in the last 3 rows were 7,915 (preweaning ADG and weaning weight) and 7,774 (postweaning ADG and yearling weight).
[2]Interaction of LINE and heifer (2-yr-old) or cow classification (HC).
[3]Interaction of LINE with age of dam (3-, 4-, or 5-yr of age or older; AD) nested within the cow class of HC.
[4]Numerator df were 12 for postweaning ADG and yearling weight.

Table 7. Selection and control least squares means of postnatal weights and growth rates and square roots of estimated variance components[1]

Item	Preweaning ADG, g/d	Weaning weight, kg	Postweaning ADG, g/d	Yearling weight, kg
Least squares means				
Control	882	214.0	963	358.2
Select	897	214.2	953	356.7
Select − Control	15	0.3	−10	−1.5
Square root of estimated variance components				
POP × LINE[2]	7	1.3	7	1.5
POP × year	36	7.1	54	11.1
POP × LINE × year	7	1.2	11	2.6
Residual	105	21.8	134	31.4

[1]See Table 6 for significance tests.
[2]Interaction of population (POP) and selection lines (LINE).

DISCUSSION

Selection Experiments

MacNeil et al. (1998) applied 16 yr of mass selection using either independent culling levels for below-average birth weights and increased yearling weights or single-trait selection for increased yearling weight in 2 lines of an inbred Hereford population. Direct genetic breeding values for birth weight and yearling weight diverged over the course of the experiment. In the final 2 yr of the experiment, birth weights were 2.4 kg lighter and yearling weights were 13.2 kg lighter in the independent culling line. Although there was an average direct genetic breeding value difference in heifer calving assistance favoring the line with lower birth weight, the difference did not increase with year. MacNeil et al. (1999) progeny tested sires from the third to fourth generation of the experiment. Based on crossbred progeny, the breeding values of sires from the line selected by independent culling levels were 2.5 kg less birth weight, 2.0 d longer gestation, and 5.9 kg lighter at 180 d than breeding values for sires from the single-trait line.

MacNeil (2003) selected a composite population using an index of birth weight and yearling weight developed by Dickerson et al. (1974) with the goal of controlling the rate of increase in birth weight, while still allowing substantial change in yearling weight. Comparisons of breeding value trends for birth weight and yearling weight in the index line and a randomly selected control line showed differences of 0.27 kg/generation for birth weight and 6.0 kg/generation for yearling weight for approximately 3 generations.

Meijering and Postma (1985) experimentally evaluated the hypothesis that sires producing progeny with low risk of dystocia also produced heifers with a greater risk of dystocia in their calves. Sires from 3 dairy breeds with high or low risk of progeny dystocia were used to produce purebred progeny. Female progeny were then assigned within sire to high and low risk dystocia sires. Results suggested that the hypothesis was not true.

Arnold et al. (1990) selected Angus bulls with EPD for birth weight either >3.0 kg or <1.5 kg. All sires were selected for yearling weight EPD >20 kg regardless of their birth weight EPD. Sires were randomly bred to Angus cows to produce 170 progeny. Progeny from low birth weight EPD sires were 3.7 ± 1.1 kg and 6.6 ± 7.8 kg lighter for birth and yearling weight, respectively, compared with EPD differences of 2.9 kg for birth weight and 6.3 kg for yearling weight. Low birth

Table 8. Selection and control least squares means of postnatal weights and growth rates by age of dam[1]

Selection	Dam age, yr	Preweaning ADG, g/d	Weaning weight, kg	Postweaning ADG, g/d	Yearling weight, kg
Control	2	823	201.1	966	346.7
	3	904	219.2	956	361.6
	4	960	230.8	964	373.3
	>4	956	230.5	965	374.2
Select	2	837	200.8	949	343.7
	3	937	222.7	961	365.4
	4	973	231.2	961	373.9
	>4	962	229.0	949	370.1

[1]See Table 6 for significance tests.

Table 9. Trend in differences (select minus control least squares means) of postnatal weights and growth rates by year of calves' birth[1]

Year	Preweaning ADG, g/d	Weaning weight, kg	Postweaning ADG, g/d	Yearling weight, kg
1993	8	0.8	5	2.2
1994	0	−2.2	−8	−1.5
1995	18	0.6	−11	−0.8
1996	26	2.3	−8	0.7
1997	17	−0.1	−6	−0.7
1998	27	1.7	−12	−1.3
1999	13	−1.3	−32	−8.7
Trend estimates[2]				
Linear	2.4 ± 1.8	0.0 ± 0.4	−4.0 ± 2.3	−1.1 ± 0.5

[1]See Table 6 for significance tests.
[2]Linear trend estimates were evaluated using coefficients −3, −2, −1, 0, 1, 2, and 3 for 1993 through 1999.

Table 10. Probabilities and *F*-values of the effects of selection vs. control line (LINE) and its interactions for yearling linear and area measurements

			Yearling height		Pelvic height[2]		Pelvic width[2]		Pelvic area[2]	
Effect	df	Ddf[1]	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*
LINE	1	6	10.74	0.02	0.25	0.64	1.75	0.23	0.90	0.38
LINE × year	5	36	2.73	0.03	1.90	0.12	0.24	0.94	0.94	0.47
Linear	1	36	11.80	0.002	0.04	0.83	0.01	0.91	0.08	0.77
LINE × HC[3]	1	>2,900	1.43	0.23	5.49	0.02	4.1	0.04	6.44	0.01
LINE × AD(HC)[4]	2	>2,900	3.21	0.04	0.72	0.49	0.05	0.95	0.26	0.77
LINE × year × HC[5]	5	>2,900	2.57	0.002	1.95	0.08	0.49	0.79	0.99	0.42

[1]Denominator df (Ddf) were calculated by the containment method resulting in conservative df when a variance is estimated to be zero. The Ddf in the last 3 rows were 7,711 (yearling height) and 2,923 (female pelvic height, width, and area).
[2]Measured only on females.
[3]Interaction of LINE and heifer (2-yr-old) or cow classification (HC).
[4]Interaction of LINE with age of dam (3-, 4-, or 5-yr of age and older; AD) nested within the cow class of HC.
[5]Numerator df was 10 for yearling height.

weight sires had nonsignificant but shorter (0.6 ± 0.8 d) gestations. Progeny of low birth weight EPD sires had slightly larger pelvic areas (2.7 ± 3.7 cm^2).

Generally, these selection experiments were limited in actual or effective numbers and in the number of populations. None of the reported experiments had the objective of entirely eliminating yearling weight differences between selected lines or progeny of selected sires. The power of these experiments to detect differences in heifer calving difficulty or other traits with low heritability, low to moderate genetic correlations, or measured on only a portion of the progeny was low. In spite of these limitations, expected reductions in birth weight change relative to yearling weight change in the beef cattle experiments were substantially achieved. A strength of the present experiment is the combination of elements found in the cited experiments: inference to many populations, size of the responses achieved through using EPD based on information from progeny-tested sires used within herds and across the industry (e.g., 4.0 kg birth weight difference in the final 2 yr), and the multigeneration application of selection. In addition, this experiment nearly orthogonalizes the calving ease response and the yearling weight response and has large numbers of observations to estimate differences for heifer calving difficulty scores and weakly correlated traits. The experiment does not readily allow estimation of realized heritabilities or genetic correlations, because selection was complex and information from both external and within herd sources was used.

Differences between select and control lines were tested for average differences and for trends in differences. Average differences reported in Tables 3, 7, and 11 need to be interpreted in light of trends reported in Tables 5, 9, and 13. Line differences were generally much larger at the end of the experiment when there were strong line × year interactions.

Phenotypic Trend in Calving Assistance

There was a strong phenotypic trend in control lines for calving assistance and calving difficulty scores for 2-yr-old dams resulting in a change from 41% unassisted in 1993 to 67% unassisted in 1999 (Figure 1). Control lines were not randomly selected, but the intended result of selecting for birth weight EBV changes that were proportional to yearling weight EBV changes was to leave genetic change in heifer calving assistance

Table 11. Selection and control least squares means of yearling linear measurements and square roots of estimated variance components[1]

Item	Yearling hip height, cm	Pelvic height,[2] cm	Pelvic width,[2] cm	Pelvic area,[2] cm^2
Least squares means				
Control	122.85	14.31	12.49	179.5
Select	122.15	14.26	12.43	177.9
Select − Control	−0.70	−0.05	−0.06	−1.6
Square root of estimated variance components				
POP × LINE[3]	0.33	0.10	0.03	1.9
POP × year	0.47	0.27	0.33	7.4
POP × LINE × year	0.23	0.00	0.06	0.8
Residual	3.36	0.75	0.66	16.3

[1]See Table 10 for significance tests.
[2]Measured only on females.
[3]Interaction of population (POP) and selection lines (LINE).

Table 12. Selection and control least squares means of yearling linear measurements by age of dam[1]

Selection	Dam age, yr	Yearling hip height, cm	Pelvic height,[2] cm	Pelvic width,[2] cm	Pelvic area,[2] cm^2
Control	2	121.9	14.21	12.43	177.4
	3	123.3	14.34	12.52	180.2
	4	124.0	14.36	12.57	181.2
	>4	124.2	14.48	12.60	183.1
Select	2	121.0	14.08	12.30	173.8
	3	123.0	14.41	12.53	181.1
	4	123.6	14.44	12.57	182.1
	>4	123.3	14.46	12.59	182.7

[1]See Table 10 for significance tests.
[2]Measured only on females.

and difficulty scores unchanged. Trends in control line direct EBV for 2-yr-old calving difficulty score were positive but offset by a similar sized negative trend in maternal EBV (Bennett, 2008). Several individuals assigned the subjective calving difficulty scores throughout the experiment, but all were trained in scoring before each calving period. A change in scorer interpretation of calving difficulty scores cannot be ruled out, but the yearly training was intended to standardize the scoring.

In a study done in Nebraska from 1993 through 1995 (Colburn et al., 1997), the authors noted a 3-yr trend toward increasing temperatures for the period corresponding to the month when calving began (February) and the 2 preceding months (December and January) and suggested that the temperature trend could be a partial explanation of observed decreases in calving assistance. The basis for this suggestion was research showing that cold weather leads to an increase in blood flow to the uterus (Ferrell, 1991) and that the 3 mo preceding birth is a period of rapid fetal growth (Ferrell et al., 1976). Burns et al. (1979) exchanged lines of cattle developed in Florida and Montana and compared performance in the 2 environments. They found that birth weights in Florida were 6.5 and 8.8 kg lighter in 2 phases of the experiment. One environmental factor that differs between the 2 environments is warmer temperatures in Florida. In the present study, the average temperatures (average of high and low) for January were −10.7, −8.8, −6.9, −10.0, −11.1, −5.2, and −6.8°C, and for February were −6.8, −6.4, 1.3, −0.7, −3.4, 2.0, and 2.9°C for 1993 through 1999, respectively. Temperatures in January and especially February increased over the course of the experiment. The average birth date for calves born to heifers was mid-March; January and February would be a period of high fetal growth. Average birth weights for calves born to control line heifers were 39.1, 39.2, 37.8, 38.4, 37.5, 37.8, and 37.0 kg for 1993 through 1999 despite control line increases in direct and maternal EBV totaling 1.6 kg (Bennett, 2008). It is possible that the warmer late-gestation temperatures contributed to the control line trend of declining 2-yr-old calving assistance.

Dam Age and Calving Assistance

The highly significant interaction (Table 2) of line × dam classification (2-yr-old vs. 3-yr and older) and the calving assistance trends (Table 5) show little support for a moderate or stronger relationship between 2-yr-old dams vs. older dam for calving assistance. Select line cows were culled each year based on EBV for heifer calving difficulty score, which might have affected the results. However, if there was a strong relationship between 2-yr-old and older calving assistance, then culling select line cows might have been expected to result in lower calving assistance in older select line cows.

The conclusion drawn from this study is different than those drawn from several studies that estimated high genetic correlations between calving assistance or

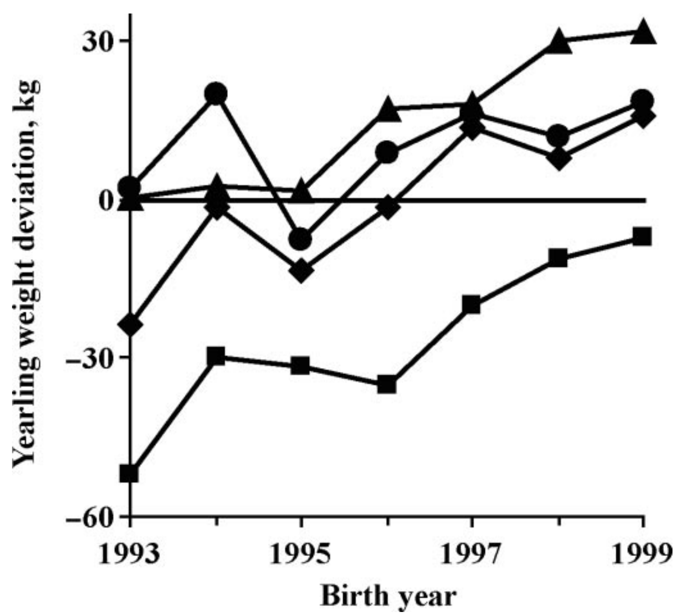

Figure 2. Birth year trends in male yearling weight deviations of 4 purebred populations from the average of the 3 composite populations. Angus, Charolais, Gelbvieh, and Hereford deviations are indicated by solid diamonds, triangles, circles, and squares, respectively.

Table 13. Trend in differences (select minus control least squares means) of yearling linear measurements by year of calves' birth[1]

Year	Yearling hip height, cm	Pelvic height,[2] cm	Pelvic width,[2] cm	Pelvic area,[2] cm^2
1993	−0.05	−0.03	−0.10	−1.8
1994	−0.51	−0.08	−0.02	−1.3
1995	−0.63	NA	NA	NA
1996	−0.64	−0.13	−0.06	−2.5
1997	−0.56	0.18	−0.00	2.0
1998	−0.77	−0.13	−0.11	−3.2
1999	−1.75	−0.11	−0.08	−2.8
Trend estimates[3]				
Linear	−0.20 ± 0.06	−0.01 ± 0.01	−0.00 ± 0.04	−0.17 ± 0.60

[1]See Table 10 for significance tests.

[2]Measured only on females. Pelvic traits not measured in heifers born in 1995.

[3]Linear trend estimates were evaluated using coefficients −3, −2, −1, 0, 1, 2, and 3 for 1993 through 1999.

calving difficulty measured in heifers or older cows in dairy and beef cattle (e.g., Eriksson et al., 2004; Jamrozik et al., 2005). Large selection responses realized for 2-yr-old dam calving assistance were not seen in 4-yr-old and older dams. Part of the reason could be the low incidences of calving assistance for older dams (Table 4), although analysis with a probit link function should have eliminated the scaling effect from the differences (Quaas et al., 1988).

Pelvic Measurements

Pelvic measurements made before pregnancy were not different between select and control lines. Bellows et al. (1971) and others have identified precalving pelvic area as a significant contributor to dystocia in primiparous heifers. Bennett and Gregory (2001b) estimated a genetic correlation of −0.35 between pelvic area of heifers before pregnancy and maternal genetic heifer calving difficulty scores. This was similar to correlations of maternal genetic heifer calving difficulty scores with hip height and yearling scrotal circumference of bulls. The present experiment does not provide evidence for whether pelvic area has an important role in maternal genetic effects, because there was not a difference in maternal EBV for calving difficulty score. Although pelvic areas did not differ, birth weights did differ between select and control lines. Therefore, pelvic area was larger relative to birth weight in the select lines.

Comparisons with EBV Differences

Phenotypic comparisons of select and control lines are not as dependent as EBV on the assumed genetic model and parameters. Phenotypic differences for 2-yr-old heifer calving difficulty of calves born in 1998 and 1999 (Table 5) were less than their EBV difference of −1.11 (Bennett, 2008). This was likely due to the nongenetic trend of decreasing calving assistance as discussed above. Phenotypic differences (1998 and 1999) for birth weight (Table 5) and weaning weight (Table 9) were similar to EBV differences of −3.7 kg and 0.6 kg, respectively. Select lines were somewhat smaller than control lines for yearling weight phenotype (Table 9), although EBV were similar. Phenotypic and EBV

Table 14. Slopes of purebred yearling weight EBV, EBV deviation from average of 3 composite population EBV, or male and female phenotypic deviations in yearling weight from the average of 3 composite populations regressed on birth years 1993 through 1999

Population	EBV slope,[1] kg/yr	Adjusted EBV slope,[2] kg/yr	Male slope,[3] kg/yr	Female slope,[3] kg/yr
Angus	4.6 ± 0.5	3.3 ± 0.6	5.9 ± 1.4	3.7 ± 0.9
Charolais	2.9 ± 0.8	1.6 ± 0.9	6.0 ± 0.8	3.8 ± 1.3
Gelbvieh	1.0 ± 0.4	−0.3 ± 0.4	2.0 ± 1.9	−1.9 ± 1.5
Hereford	3.5 ± 0.6	2.1 ± 0.7	6.6 ± 1.2	3.2 ± 1.3[4]

[1]Yearling weight EBV is the sum of direct and maternal genetic weaning weight and direct genetic postweaning gain.

[2]Deviation from the average EBV of the 3 composite populations (MARC I, MARC II, and MARC III).

[3]Deviation of sex × population × birth year least squares mean for yearling weight from the average of least squares means for the 3 composite populations.

[4]Estimate based on 1993 through 1997, because Hereford heifers were managed differently from other heifer populations in 1998 and 1999.

yearling weight trends for purebred and composite populations show that the intended increase in yearling weights for some purebreds relative to composites (Table 14, Figure 2) was achieved, but that EBV increases were somewhat less than phenotypic increases. Qualitatively, yearling weight trends were similar to long-term trends in industry with yearling weight plus milk increasing the most for Angus and Hereford, and the least for Gelbvieh with differences among many breeds narrowing over time (Cundiff et al., 2007).

Conclusions

When selection is applied in multiple stages and based on information that is updated with measurements collected at different times and from an increasing number of relatives, correlated responses to selection can differ from those predicted solely by genetic correlations. Using a specific multi-stage selection scheme, selection for improved calving ease while either maintaining or increasing yearling weight resulted in earlier calving, shorter gestations, lower birth weights, fewer 2-yr-old dams assisted at calving, lower levels of difficulty among those assisted, faster preweaning growth, and shorter yearling hip heights. Calving assistance in older cows, weaning weight, postweaning gain, yearling weight, and pelvic measurements did not differ when compared with controls selected for the same yearling weights, while either maintaining or proportionally increasing birth weight. For cattle populations that are at or near optimal yearling weights, selection for improved calving ease while restricting changes in yearling weight is one potential method for reducing labor and veterinary costs, while likely increasing calf survival and cow productivity (Laster et al., 1973).

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