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ABSTRACT: One approach to reducing calving difficulty is to select heifers with higher breeding value for calving ease. Calving ease is often associated with lower birth weight and that may result in other possible effects on lifetime productivity. Females from experimental select and control calving ease lines within each of the seven populations were compared. Random samples of 720 heifers from lines selected for better calving ease breeding values and 190 heifers from control lines selected for average birth weights were followed through four parities. Select and control lines within the same population were selected to achieve similar yearling weight breeding values. Weights of sampled heifers in select lines were 2.6 kg ($P < 0.01$) lighter at birth but not different from control lines at weaning. Select lines had significantly shorter hip height, lighter mature weight, and greater calving success at second parity. Their calves were born significantly earlier with lighter weights and less assistance. Significant interactions with parity showed fewer calves assisted and greater calf survival to weaning as heifers but negligible differences with control lines in later parities. Steer progeny sampled from these dams in select lines (n = 204) were not different from steers in control lines (n = 91) for hot carcass weight but had significantly greater fat depth. Two production systems were compared considering the seven populations as replicates. The systems differed in selection history of females (select and control lines) and the use of bulls within their lines as young cows, but used the same bulls in both lines as older cows. Cows were culled after single unsuccessful breeding and kept for up to four parities. Select line cows tended ($P \le 0.10$) to wean more calves and stay in the herd longer. They were assisted significantly fewer times at calving and had greater calf weight gain to weaning when evaluated over their herd life. Mature weights were lighter in select lines, but marketable cow weight from the systems was nearly identical. Control lines did have more marketable young cow weight and select lines older cow weight. Weaned calf weight per heifer starting the system was significantly greater for the select heifer system due to greater survival of calves from heifers and greater calving success at second parity. No important unfavorable effects of genetic differences in calving ease were identified in this experiment.

Key words: beef cattle, calving difficulty, cow productivity, mature size, production systems

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INTRODUCTION

Traits targeted for selection are expected to change in intended and beneficial directions based on intensity, heritabilities, and genetic correlations. Other traits also can change depending on correlations with selection criteria, but these changes may not be beneficial. One approach to predicting changes in other traits is to estimate genetic correlations with selection criteria. This works well when all combinations of traits have been measured in structured populations, relationships

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among traits are linear, and heritabilities are at least moderate. Alternatively, selecting and then measuring responses in targeted and nontargeted traits can estimate responses in low heritability traits and identify nonlinear associations if enough change is made.

Improved calving ease in heifers combined with selection for postnatal growth is a selection strategy used by beef cattle breeders. This strategy has resulted in breed trends over the last 25 years of large increases in yearling weight EPD and modest to moderate decreases in birth weight EPD (highly correlated to calving difficulty) thus achieving anticipated changes in targeted and closely correlated traits (Kuehn and Thallman, 2017). The potential effects of these changes on cow productivity raise two areas of concern. One is the negative direct−maternal genetic correlation for calving ease and birth weight (Bennett and Gregory, 2001). Direct and maternal calving ease were negatively correlated in Simmental sired crossbred calves, Piedmontese, Asturiana de los Valles beef cattle, and Angus ranging from −0.93 to −0.22 (Burfening et al., 1981; Cubas et al., 1991; Carnier et al., 2000; Gutiérrez et al., 2007). Another possible change is increased calf mortality of calves born with both higher and lower birth weights (Morris et al., 1986; Azzam et al., 1993).

The objective of this experiment was to estimate differences in cow traits and productivity between lines selected for improved heifer calving ease and growth and their control lines (Bennett, 2008; Bennett et al., 2008). These control lines were selected so that they had the same yearling weights as their corresponding select lines. The hypothesis tested was that genetically improving heifer calving ease in the absence of differences in yearling weights affects cow productivity.

MATERIALS AND METHODS

Research protocols were approved and monitored by the USDA, ARS, U.S. Meat Animal Research Center Institutional and Animal Care Committee in accordance with the 1988 Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching.

Experimental Design

The experiment was conducted at the U.S. Meat Animal Research Center, Clay Center, NE. Experimental design, selection methods, management of cows and calves, and breeding value trends for traits measured up to yearling age were described by Bennett (2008). Briefly, four purebreds (Angus, Charolais, Gelbvieh, and Hereford) and three composite populations (MARC I, MARC II, and MARC III) of cattle were each split into a select line (about 135 cows) and a control line (about 35 cows). Cattle in both lines were selected based on multitrait EBV calculated from calving difficulty score in heifers, birth weight, weaning weight, and postweaning gain to yearling age measured at the research center within each population. An exception was industry sires initially screened into the four purebred populations using industry EPD for birth and yearling weights. Birth weight EPD was used as a proxy for calving difficulty in industry sires from Angus, Charolais, and Hereford breeds because these breeds did not calculate EPD for calving ease at that time. Select lines were selected for lower calving difficulty score EBV and control lines for birth weight EBV change proportional to yearling weight EBV change. Both lines were selected so that yearling weights were not expected to change (composite populations) or select and control lines would increase by the same amount (purebred populations). Calves were born from 1993 through 1999 and the selection goals were achieved (Bennett et al., 2008). Select lines had reduced calving difficulty scores and similar growth to yearling age compared to control lines.

Heifers born in 1996 and 1997 were randomly sampled within sire (Table 1) and retained in the experimental herd until weaning their fourth calf at

Table 1. Number of heifers sampled

Population	Select	Control	1996	1997
Angus	100	30	65	65
Charolais	99	31	64	66
Gelbvieh	108	21	63	66
Hereford	100	30	66	64
MARC I	106	25	67	64
MARC II	107	23	65	65
MARC III	100	30	64	66
Total	720	190	454	456

about 5.5 yr of age unless culled sooner. Cows were culled after being open one time, were unhealthy, or were otherwise unlikely to have and wean another calf. Heifers remained in the selection herd through 1999 and thus heifers and cows in select lines were bred to selected bulls and those in control lines were bred to control bulls. Select and control line cows were bred to the same bulls beginning in 1999 for calves born in 2000. Heifers born in 1996 and 1997 completed the experiment in 2001 and 2002, respectively. Within populations and parity groupings, select and control lines were managed as a single group except when separated into similar breeding pastures. Hereford cows born in 1997 were used for other purposes following weaning in 2001 resulting in a maximum of three calvings for that replicate.

Steers born in 1998 and 1999 to the females sampled in 1996 and 1997 were randomly sampled within sire and dam and fed for slaughter. All steers within a population and year were slaughtered on the same day.

Cow and Calf Management

Matings were made within select and control lines to produce calves born in the last 2 yr of selection (1998 and 1999) and managed as described by Bennett (2008). Cows from both lines within a population were bred by natural service or AI to the same bulls for calves born in 2000, 2001, and 2002. Breeding lasted for 9 wk by natural service or for 3 wk of AI followed by 6 wk natural service in individual sire pastures, beginning May 27, 1999; May 30, 2000; and June 11, 2001, respectively. Bulls were selected from within a population for use across both lines in the population. The selection of these bulls used the same criteria as select lines. Hereford population calves born in 2000 and 2001 were an exception. All cows were bred by AI to a single MARC II bull each year followed by natural service to Angus bulls.

After 1999, cow and calf management were similar to pre-1999 management as described by Bennett (2008). Cows were maintained on pasture with limited additional corn silage and alfalfa haylage fed from November until April to offset reduced forage availability and winter weather conditions. Cows were measured three times each year. Cow weights, hip heights, and cow condition scores (1 to 10) were recorded in January or February before calving began (precalving), in May or June before breeding started (prebreeding), and in October up to 3 wk after weaning when palpated for pregnancy (palpation).

Weights of calves were recorded at birth on pasture and upon entering the feedlot at weaning. Calving difficulty was subjectively assessed by trained field staff and given scores with increasing difficulty from 1 (no assistance) to 7 (cesarean birth). Abnormal presentations were given a score of 8 but were considered separate from the 1 to 7 continuum of difficulty. Calf data for this experiment were considered complete at weaning, except for sampled steers born in 1998 and 1999 which were fed a diet based on corn and corn silage until slaughter at about 15 mo of age. Carcass weight, fat depth, longissimus area, estimated internal (kidney, heart, and pelvic) fat %, and marbling score were recorded at a commercial abattoir, and Yield Grade was calculated.

Statistical Analyses

Individual animal analyses. Three types of statistical analyses were used on individual animal traits. A nonlinear procedure PROC NLMIXED in SAS (Version 9.4, SAS Institute Inc., Cary, NC) was used to fit modified Brody curves (Brody, 1945) to herd-life weights and hip heights of cows and test for selection differences. Other individual traits were fitted to linear models using PROC GLIMMIX in SAS with an identity link for continuous traits and a logit link for binary traits. Only selection and control means or differences and their significant interactions are reported for cow and calf measurements.

Cow measurement analyses. The Brody equation for postinflection growth was modified with multiplicative factors (ME_d) to account for the differences in nutritional and physiological status at precalving (ME_2) and prebreeding (ME_3) weights from those at pregnancy palpation ($ME_1 = 1.0$). The remaining Brody curve parameters for mature value (A), equation extrapolated proportion of A remaining at 0 wk of age (B) and maturing rate (k) were augmented to allow differences in cow's birth year (BY_c = 1996, 1997), selection goal (SC_f = control or select), population (PO_g = 1 to 7), age of cow at each measurement in weeks (AW_z), a random effect of the cow for the A parameter (cow_j), and a random residual (e_z). The resulting nonlinear model for cow weight was

$$\text{Cow weight}_{c,d,f,g,j,z} = (A_{c,f,g} + \text{cow}_j) \times [1 - \text{ME}_d \times B_{c,f,g} \times \exp(-k_{c,f,g} \times \text{AW}_z)] + e_z.$$

The model used for cow hip heights was reduced because the temporal effects of ME on bone growth are not expected. The nonlinear model for hip height was

$$\text{Cow height}_{c,f,g,j,z} = (A_{c,f,g} + \text{cow}_j) \times [1 - B_{c,f,g} \times \exp(-k_{c,f,g} \times \text{AW}_z)] \times + e_z.$$

A linear model for 8,949 cow condition scores across 13 herd-life measurement events (HE_h; precalving, prebreeding, and palpation from the first palpation through the fifth palpation) included random effects for cow (cow_j), sire of cow (sire_i), and residual (e_z) and interactions including selection goal with HE. Thus, the linear model for cow condition score was

$$\text{Condition score}_{c,f,g,h,i,j,z} = \mu + \text{BY}_c + \text{SC}_f + \text{PO}_g + \text{HE}_h + \text{SC}_f \times \text{HE}_h + \text{BY}_c \times \text{HE}_h + \text{PO}_g \times \text{HE}_h + \text{sire}_i + \text{cow}_j + e_z.$$

Reproductive success or failure within each parity was fitted to a linear model using a logit link function. Data consisted of either heifers that began the experiment or cows present at the previous pregnancy palpation. The model used for reproductive success was

$$\text{Success}_{c,f,g} = \mu + \text{BY}_c + \text{SC}_f + \text{PO}_g.$$

Calf measurement analyses. Calf birth date was analyzed with the following linear model including differences in sire lines (SB_n) nested within the Hereford population and interaction of selection with cow's birth year, population, parity (PA_o, 1 to 4), and sex of calf (MF_p):

$$\text{Birth date}_{c,f,g,i,j,n,o,p,z} = \mu + \text{BY}_c + \text{SC}_f + \text{PO}_g + \text{SB}_n(\text{PO}_g) + \text{PA}_o + \text{MF}_p + \text{SC}_f \times \text{BY}_c + \text{SC}_f \times \text{PO}_g + \text{SC}_f \times \text{PA}_o + \text{SC}_f \times \text{MF}_p + \text{BY}_c \times \text{PA}_o + \text{PO}_g \times \text{PA}_o + \text{sire}_i + \text{cow}_j + e_z.$$

The following model was used for calf birth weight:

$$\text{Birth weight}_{c,f,g,i,j,n,o,p,z} = \mu + \text{BY}_c + \text{SC}_f + \text{PO}_g + \text{SB}_n(\text{PO}_g) + \text{PA}_o + \text{MF}_p + \text{PO}_g \times \text{BY}_c + \text{SC}_f \times \text{PO}_g + \text{SC}_f \times \text{PA}_o + \text{SC}_f \times \text{MF}_p + \text{BY}_c \times \text{PA}_o + \text{PO}_g \times \text{PA}_o + \text{PO}_g \times \text{MF}_p + \text{sire}_i + \text{cow}_j + e_z.$$

Calf weaning weight used the same model as the birth weight with the addition of a covariate for weaning age and interaction of parity with sex. Binary calf traits of weaning survival, calving assistance (calving difficulty score > 1), and incidence of difficult calving (moderate difficulty with a calf jack through cesarean with scores of 5, 6, or 7) were analyzed with a logit link. In this model parity (PA_o) was defined as two classes, heifer (first parity) or cow, because of high survival and low calving assistance rates in calves born to cows. The logit-link model for binary calf traits was

$$\text{Binary calf trait}_{c,f,g,j,o,p,z} = \mu + \text{BY}_c + \text{SC}_f + \text{PO}_g + \text{PA}_o + MF_p + \text{SC}_f \times \text{PO}_g + \text{SC}_f \times \text{PA}_o + \text{SC}_f \times \text{MF}_p + \text{cow}_j + e_z.$$

Carcass traits for steers born in 1998 and 1999 were analyzed with a linear model including calf birth year (CY_q), dam parity nested within a year (first parity in both years and second parity in the second year), and slaughter age (SA_z) as a covariate, resulting in

$$\text{Carcass trait}_{f,g,o,q,z} = \mu + \text{SC}_f + \text{PO}_g + \text{CY}_q + \text{PA}_o(CY_q) + \text{MF}_p + \text{SC}_f \times \text{CY}_q + b \cdot \text{SA}_z + e_z.$$

System-level analyses. System traits were accumulated across the four parities for the 28 combinations of select and control lines sampled in 1996 or 1997 in the seven populations. No adjustments were made to data but select and control lines within a sampling year and population were managed the same except for the sires of calves born in 1998 and 1999. System traits for each of the 28 combinations were standardized by dividing by the original number of heifers sampled. Differences in standardized traits between select and control lines were calculated within populations and sampling years. Differences for the two sampling years were weighted by expected variances of the differences based on the original numbers of heifers sampled to calculate a weighted average of differences within each population. A *t*-test was used on the resulting seven population values to determine whether select and control lines were significantly different. Herefords sampled in 1997 only completed three parities. The Hereford difference used was a weighted average of traits accumulated through four parities for heifers sampled in 1996 and through three parities for heifers sampled in 1997.

RESULTS AND DISCUSSION

Heifer Sampling

Heifers in select lines sampled for this experiment (Table 1) were the progeny of 172 sires and 629 dams. Those in control lines were the progeny of 93 sires and 177 dams. They reflected differences in the overall selection experiment (Bennett et al., 2008). Birth weights of control lines exceeded those of select lines but weaning weights did not differ (Table 2). Population differences are not reported for these or any other traits because small numbers in each control line result in unreliable within-population differences. However, the combined statistical power of seven small control lines is adequate to estimate overall differences between select and control lines.

Cow Measurements

Modified Brody curves showed substantial and significant differences between select and control lines for mature measurements. Control lines exceeded select lines by 3.3% for mature weight and 1.6% for mature height (Table 3). Control lines already exceeded select lines for height as yearlings (Bennett et al., 2008) and that is reflected in a significantly greater proportion of mature height extrapolated to 0 weeks of age (parameter B). These patterns are illustrated in Figs. 1 and 2. Condition score had repeatability of 0.34 and did not differ between lines nor did line differences interact with measurement events ($P = 0.28$). The differences in the development of height and weight may indicate that the smaller frame size of select line cows limit weight at maturity but not earlier growth.

Estimates of genetic correlations between mature weight and other weights from birth through maturity are usually positive and moderate to high. Bullock et al. (1993) reported mature weight genetic correlations increasing from 0.64 for birth weight to 0.89 for yearling weight with corresponding heritabilities of 0.49 and 0.30. Portes et al. (2020) estimated somewhat greater genetic correlations between yearling weights and 5-yr-old weights but higher heritabilities of birth and 5-yr-old weights. Meyer (1995) analyzed herds of Hereford and Wokalup cattle and concluded that genetic correlations between cannon bone length measured at birth and mature weight were 0.6 to 0.7. Further, animals with shorter bone length at birth tended to approach mature weights more quickly.

In the select lines described here, breeding values for calving ease (strongly influenced by birth weight breeding values) and yearling weight were selected against their genetic correlation (Cockrem, 1959) with the same genetic goal as a constrained phenotypic index (Brascamp, 1984). The −3.3% difference in observed mature weight is between the −7% difference in birth weight and <−1% difference in yearling weights of the heifers. However, responses to selection for a single weight or gain period tend to be partially maintained throughout a cow's lifetime (Archer et al., 1998). Unlike responses in weight, select lines in this experiment were shorter as yearlings (Bennett et al., 2008) and at every subsequent measurement. Taken with Meyer's (1995) suggestion that cannon bone length at birth could be an early indicator of mature size, skeletal measures at younger ages seem to offer a means of manipulating mature size that is somewhat independent of early weights.

Calving success was calculated as either a percentage of heifers starting the experiment or cows bred the previous year. Differences were significant only for second parity when select lines exceeded control lines. Differences in third and fourth parity calving success were not significant but tended to be greater for select lines as a percentage of original heifers only because the once open culling policy reduced the number of control cows after second parity. Calving difficulty in first parity heifers has been reported to be associated with delayed and reduced conception at their second parity (Brinks et al., 1973; Laster et al., 1973) and there was more calving difficulty in control line heifers. However, second parity cows in select lines experiencing no, moderate, or substantial difficulty as heifers had calving success rates of 89%, 87%, and 86 %, respectively. Corresponding success rates in control lines were 83%, 82%, and 83 % respectively. Calving difficulty difference as heifers does not appear to explain the line difference in calving success at second parity. Doornbos et al. (1984) reported that a shorter duration of labor was associated with earlier return to estrus and higher pregnancy rates at palpation. This is a possible explanation of the results seen in this experiment, but the duration of labor was not measured.

Calf Measurements

Calves of select line dams were born 3.3 days earlier ($P < 0.001$) than those with control line

Table 2. Average differences in birth and weaning weights between randomly sampled select and control heifers

Trait	Average	Select—control	1996–1997
Birth weight, kg	37.3	−2.6 ± 0.5**	0.2 ± 0.4
Weaning weight, kg	217.5	0.2 ± 1.5	−6.9 ± 2.6*

Table 3. Individual cow traits

Trait and parameter	Average	Select—Control	SED	*P*
Cow mature weight (parameter *A*), kg	621.4	−20.7	4.95	<0.001
Cow weight parameter *B*[a]	0.852	−0.009	0.013	0.48
Cow weight maturing rate *k*, week^{-1}	0.0112	0.0003	0.0003	0.33
Cow mature height (parameter *A*), cm	136.5	−2.3	0.4	<0.001
Cow height parameter *B*[a]	0.112	−0.018	0.004	<0.001
Cow height maturing rate *k*, week^{-1}	0.0105	−0.0001	0.0005	0.89
Cow condition score[b]	5.98	−0.04	0.04	0.30
Calves per cow bred				
First parity, %	85.9	1.7	2.8	0.55
Second parity, %	85.5	6.1	3.0	0.04
Third parity, %	87.9	0.5	3.1	0.88
Fourth parity, %	81.2	−0.7	4.1	0.86
Calves per original heifer				
First parity, %	85.9	1.6	2.8	0.58
Second parity, %	74.0	7.3	3.5	0.04
Third parity, %	66.9	5.9	3.8	0.12
Fourth parity, %	56.6	4.4	4.2	0.30

[a]Equation extrapolated proportion of *A* remaining at 0 wk of age.

[b]The interaction with herd-life measurement events was not significant (P = 0.28). Repeatability across measurement events was estimated to be 0.34.

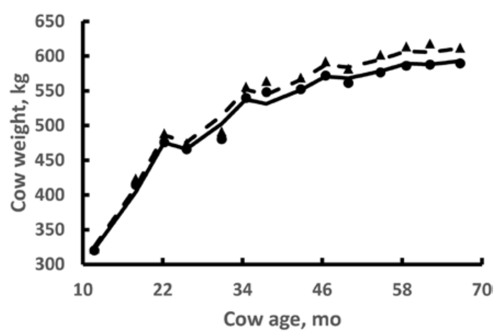

Figure 1. Cow weights at herd-life management events for select (circles) and control lines (triangles). Solutions for select (solid line) and control (dashed line) lines from modified Brody equations are shown.

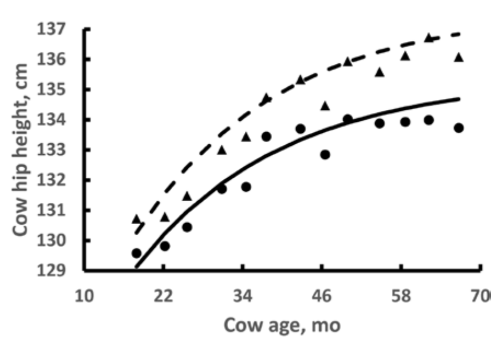

Figure 2. Cow hip heights at herd-life management events for select (circles) and control lines (triangles). Solutions for select (solid line) and control (dashed line) lines from modified Brody equations are shown.

dams. This could reflect greater fertility, shorter postpartum interval, or shorter gestation length of select line fetuses and dams.

Significant average differences showed that calves from heifers and cows in select lines had lighter birth weights and fewer births were assisted (Table 4). However, differences for calf birth weight, survival to weaning, and percentage assisted at birth significantly depended on the parity of their dam. Table 5 shows the parity × line means for these traits and percentages of difficult births (P = 0.06 for interaction). Parity is confounded with sire line in these data with younger cows bred to sires within their line and older cows of both lines bred to the same sires. The difference in birth weights between lines at third and fourth parity is about half of the difference at first parity and illustrates the contribution of both sire and dam to calf birth weights.

Calves from first parity dams in select lines were born with substantially less calving difficulty and increased survival to weaning (Table 5). Older cows have much less calving difficulty and greater survival to weaning and differences between lines are negligible.

Breeding values for heifer calving ease were estimated from a multitrait model including calving difficulty scores on heifers (only) and birth weight, weaning weight, and postweaning gain on all animals (Bennett, 2008). Most information for the calving ease breeding value was supplied by birth weights because there were many more birth weights than heifer calving scores, birth weight had high heritability and genetic correlation with direct calving ease scores (Bennett and Gregory, 2001). Additionally, industry sires were screened

Table 4. Selection line effects and interactions for calf traits

Calf trait	Mean	Select—control	SED	Selection *P*	Selection × population *P*	Selection × sex *P*	Selection × parity *P*
Birth date, d	85.0	−3.3	0.84	<0.001	0.76	0.38	0.57
Birth weight, kg	38.1	−3.3	0.31	<0.001	0.78	0.09	<0.001
Weaned wt., kg	218.1	−2.2	1.5	0.16	0.17	0.16	0.58
Survival[a], %	92.0	1.3	1.5	0.40	0.31	0.61	<0.001
Assisted calving[a], %	10.5	−7.0	1.8	<0.001	0.95	0.96	0.03
Difficult calving[a], %	1.22	−0.26	0.74	0.73	0.46	0.90	0.06

[a]Parities 2, 3, and 4 were analyzed as a single parity for survival and calving traits.

Table 5. Interaction of parity and selection line for calf traits at birth and survival to weaning

Line	Parity	*N*	Birth weight, kg	Survival, %	Assisted calving, %	Difficult calving, %
Select	1	615	33.2	86.8	16.4	2.6
	2	552	35.7			
	3	492	38.5			
	4	388	38.5			
	2, 3, 4	552		93.8	2.8	0.5
Control	1	160	37.6	70.9	39.3	8.7
	2	130	40.1			
	3	118	40.2			
	4	95	41.1			
	2, 3, 4	130		94.6	3.9	0.2

into purebred herds based on birth weight EPD because calving ease EPD was not uniformly available in national genetic evaluations of purebreds at that time. Birth weight is known to affect calf survival in a curvilinear fashion. Heavy calves are more likely to have difficult calvings and light calves also experience some calving and perinatal complications (Eriksson et al., 2004). Dystocia and other complications can lead to being stillborn or subsequent death. As a result, researchers have examined relationships between birth weight and survival (Morris et al., 1986; Johanson and Berger, 2003).

In preceding generations of the populations used in this experiment, Gregory et al. (1991) found that dystocia incidence in heifers increased linearly with birth weight but survival to weaning decreased at both ends of the phenotypic distribution. A sharp decrease (84% to 70%) occurred for calves that were over 1.5 SD below the mean compared to those between 0.5 and 1.5 SD below the mean. The 1.13 SD difference in birth weight between select and control line calves born to heifers would be enough to push many calves in the select line into the low birth weight, lower survival category. However, 197 lighter, 218 middle, and 200 heavier birth weight single-born calves relative to their select line means all had weaning survival rates of 89%. Within control lines, 52 lighter, 58 middle, and 50 heavier calves had survival rates of 81%, 81%, and 70%, respectively. Birth weight of the lighter control calves averaged 33.3 kg and select line middleweight calves averaged 33.0 kg. The phenotypic relationship between low birth weight and reduced survival to weaning did not predict the higher survival of calves when birth weights were reduced by genetic selection for heifer calving ease.

Steer Carcass Measurements

Steers born in 1997 and 1998 were sampled from 112 sires and 197 dams in select lines (204 steers) and 45 sires and 82 dams in control lines (91 steers). Carcass weights adjusted for age were nearly equal and the only significant difference was adjusted fat thickness (Table 6). Steers from select lines had 11% greater fat depth. Similar carcass weights but 3.3% smaller cow mature weights in select lines were observed (Table 3); therefore, select line steers were slaughtered at a greater proportion of cow mature weight. Greater fat depth is consistent with greater compositional maturity. If fed to similar fat depth, select steers would have been harvested at lighter carcass weights than control steers.

System Traits

System inputs. System traits were calculated from totals of unadjusted measurements for each combination of population, line, and the year before dividing by the original number of heifers assigned to it. Differences between lines within line and population were averaged across the two sampling years. The SE of average differences across the seven populations was used to test the overall difference between select and control lines.

Herd life traits showed trends of about 10% more calves weaned ($P = 0.07$) and about 5% longer herd life ($P = 0.10$) for heifers starting the experiment in select lines (Table 7). Dividing calf traits by a number of calves born or weaned (Table 8) resulted in differences for birth date and weight similar to adjusted data. Differences in calving success in second parity (Table 3) and survival of calves born to heifers (Table 5) contribute to these trends.

System-level traits related to inputs and cost of inputs were calculated (Table 8). Weights measured throughout a heifer's herd life following weaning were used to estimate weight gain until the last measurement before death, being culled, or completing the experiment. These weights and the days between weights were used to estimate total metabolic weight maintained until death, culling, or completion. Additional measures related to inputs were fetal growth (total birth weight), lactation days (total weaning age), and suckled calf gain (total weaning weight minus birth weight) were calculated over a heifer's herd life. Herd-life total incidences of calving assistance, difficult calvings, and malpresentations were calculated for heifers beginning the experiment.

Some traits differed between individual animal or system comparisons of the select and control lines. Calving assistance in select lines was less in both comparisons. However, weight gain of cows from weaning until culled or sold and metabolic weight maintained of select and control line cows were similar in the comparison of the system but mature weights of the select lines were less when compared as individual cows. Individually, calf weaning weights were similar but calves in the select lines suckled longer and gained more weight. These differences are caused by trends in longer herd life and greater survival of calves born to first-calf heifers in select lines (Table 7).

System outputs. System-level traits related to outputs and the value of outputs are also shown in Table 9. The last weights of cows that were alive when culled or completing the experiment were summed by age class and standardized to heifers beginning the experiment. Herd-life weaning weight was calculated from the total weight of weaned calves or from the total weight of weaned calves minus weaning weight of the heifer to account for the cost of replacement heifers (net weaned calf weight). Control lines produced a more marketable weight of heifers and cows less than 32-mo of age because more were culled after being open after breeding for second parity (Table 3) and because weights of control cows were starting to increase relative to select lines at that age (Fig. 1). Increased outputs of the calf and older cow weights

Table 6. Carcass traits in steer progeny born in 1998 and 1999

Carcass trait	Select	Control	Difference	SED	*P*
Hot carcass weight, kg	368.9	370.0	−1.1	3.8	0.77
Loin muscle area, cm^2	88.52	88.54	−0.02	0.92	0.98
Adjusted fat thickness, cm	0.898	0.805	0.093	0.044	0.04
Internal KPH [a], %	2.10	2.07	0.04	0.05	0.48
Marbling score[b]	521.5	509.0	12.5	7.9	0.11
Yield grade[c]	2.505	2.414	0.091	0.071	0.20
N	204	91			

[a]Estimated internal kidney, pelvic, and heart fat %.

[b]Marbling scores of 400 = slight^{00}, 500 = small^{00}, 600 = modest^{00}, etc. (USDA, 2020).

[c]Yield grade = 2.50 + (0.9843 × adjusted fat thickness, cm) + (0.2 × kidney, heart, and pelvic fat %) + (0.00838 × hot carcass weight, kg) - (0.0496 × longissimus area, cm^2).

Table 7. Cow herd life and number of calves born and weaned

Trait, per heifer	Average	Select—control	SE	*t* value	*P*
Calves born	2.82	0.188	0.106	1.77	0.13
Calves weaned	2.58	0.250	0.116	2.16	0.07
Herd lifetime, mo	51.7	2.44	1.23	1.98	0.10
Calved every year	0.55	0.043	0.031	1.39	0.21

Table 8. Calf traits from birth to weaning

Trait, per calf	Average	Select—control	SE	*t* value	*P*
Birth date, d	–	−2.98	0.88	−3.39	0.01
Birth weight, kg	38.1	−2.79	0.41	−6.78	0.001
Weaning age, d	185.9	2.95	1.76	1.68	0.14
Weaning weight, kg	212.5	1.40	3.47	0.40	0.70

Table 9. Inputs and outputs differences in select and control line systems standardized to a single sampled heifer at the beginning of the experiment

Trait standardized to a single original heifer	Average	Select—control	SE	*P*
Inputs				
Weight gain of cow, kg	329.8	−2.6	9.1	0.79
Metabolic weight maintained[a], d × $kg^{0.75}$	132,749	5,499	4,459	0.26
Assisted calvings per herd life, score 2 to 8	0.321	−0.184	0.032	0.001
Difficult calvings per herd life, score 5 to 7	0.059	−0.048	0.025	0.11
Malpresentations per herd life, score 8	0.085	−0.016	0.021	0.46
Lactation time, d	490.5	53.99	18.59	0.03
Fetal growth (birth weight), kg	105.7	−1.95	4.15	0.66
Weight gain of suckled calves, kg	453.0	55.1	19.3	0.03
Outputs				
Marketable heifer weight[b], ≤ 32-mo-old, kg	108.7	−34.5	8.1	0.005
Marketable cow weight[b], > 32-mo-old, kg	425.6	32.0	13.4	0.05
Weaned calf weight, kg	557.5	54.6	22.7	0.05
Net weaned calf weight, kg	340.0	54.4	22.7	0.05

[a]Summation of daily metabolic weight of heifers beginning at weaning and ending on the last weigh date before death, culling, or termination of the experiment.

[b]All cows alive at culling or at termination of the experiment are included in marketable cow weight.

from select lines were significant or trending. Calf weaned weights exceeded control lines by 10% and net weaned weight by 17%. Increased marketable weights of younger cows from control lines were nearly offset by increased marketable weights of older cows from select lines. However, the value of younger cow weight is higher than older cow weight.

Systems experimentation. The systems compared are 1) use of heifers selected for calving ease and then bred to calving ease bulls as young cows, and 2) use of heifers with the same growth potential and no history of calving ease selection bred to similar bulls. Both lines within a population were bred to the same bulls as females aged, further isolating system differences to calving ease genetic effects. Both systems were terminated after four parities and females were culled after being open once. The third system of interest is breeding young females in control lines to bulls from select lines, but additional experimental resources were not available.

The systems compared are not the same as commercial production systems but they do capture some dynamics of commercial production which usually keep cows much longer, may have different culling policies, and use cattle that often differ inversely in both calving ease and growth. Direct experimental evaluation of systems has limitations in statistical power and the number of variations compared. In this experiment, replication of experimental selection lines provided an unusual opportunity with some level of statistical power. Calving ease effects on the system could be isolated because breeding values for growth through yearling age in control and selection lines within each population were manipulated to be the same (Bennett, 2008).

Conclusion

The principal question addressed by this research is whether a genetic difference in calving ease, independent of growth to yearling age, had negative effects on cow productivity. Component trait effects show cows that as heifers had calves with fewer and easier assists that then survived better to weaning; in their second parity had better calving success; and were shorter and lighter at maturity. Experimental evaluation of a system estimated that the average heifer with better calving ease would produce 10% more weaned calf weight with no difference in cow weight gain or metabolic weight maintained. Herd-life productivity of heifers selected for calving ease and growth was found to be greater than those selected only for the same level of growth.

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Conflict of interest statement. The authors declare that they have no competing interests.

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