Genetic correlations among weight and cumulative productivity of crossbred beef cows¹

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ABSTRACT: Mature weight of beef cows in the United States has been increasing as a correlated response to selection for calf growth. Unfavorable genetic correlations between cow weight and various measures of female fertility, stayability, and lifetime production suggest declining cow productivity might also be expected as a correlated response to growth selection. National cattle evaluations, however, show increasing trends for stayability and sustained fertility. Random regression (RR) models were employed to further examine genetic relationships among cow weight and productivity, and to assess cumulative productivity traits observed throughout cows' productive lives. Records were from 13,707 females born in the Germplasm Evaluation (GPE) project and mated to calve first as 2-yr olds. Weights observed at pregnancy testing ($n = 65,086$) and calf production from each exposure to breeding ($n = 71,583$) were included in uni- and bivariate RR analyses. Production following each breeding season was added to previous production to obtain cumulative production records for each season that the female was exposed to breeding. Zero was added if the cow failed to produce after a breeding season. The number of pregnancies,

calves born and calves weaned, as well as age and weight of weaned calves, were accumulated. Projected age-specific heritability (h^2) estimates for cumulative production were low (<0.1) at age 2 but increased with age (0.12 to 0.26 at age 6; 0.32 to 0.48 at age 10). Estimated h^2 for cow weight were high, fluctuating between 0.6 and 0.7 from ages 2 through 10. Genetic correlations (r_g) were positive among all ages within each trait. Between ages 3 and 9, estimated r_g were negative between cumulative weaning productivity and cow weight. The correlations were usually weak enough (<-0.2) that small correlated declines from following yearling weight trends might be overcome by culling females after their first reproductive failure. More noticeable increases might be realized by selection among sires with EBV based on productivity of several daughters. The RR EBV for cow weight and cumulative weight weaned represent major sources of variation in cow costs and income, and can be incorporated into economic selection indexes to project differences in cow profitability and value at any age. The RR approach utilizes all available records, enabling later productivity to be projected from observations on young cows.

Key words: beef cattle; cow weight; productivity; random regression

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INTRODUCTION

The increasing mature weight of United States beef cows is concerning (Olson et al., 2011). Heavier cows have higher nutrient requirements (National Academies of Science, Engineering and Medicine [NASEM], 2016) and therefore higher feed costs to meet those requirements. Reproductive efficiency

may be compromised if requirements are not met. Genetic correlations between cow weight and one-time measures of female fertility and stayability were unfavorable in a sample of Irish crossbred cattle records (Berry and Evans, 2014) as well as an experimental Hereford herd (Mwansa et al., 2002). Earlier reports (Hawkins et al., 1965; Stewart and Martin, 1981) also indicated unfavorable relationships between cow weight, number of calves weaned, and total weight weaned per cow. The negative correlations between cow weight and stayability or lifetime production in previous studies make the increasing trends for stayability or sustained cow fertility reported by major United States beef breed associations (American Gelbvieh Association, American Hereford Association, American Simmental Association, North American Limousin Foundation, and Red Angus Association of America) somewhat surprising. If increasing mature cow weight is a correlated response to selection emphasizing calf growth, and cow weight is negatively correlated to stayability, a decrease in stayability is also expected without some selection for stayability or fertility.

Annual production records collected through whole-herd reporting programs have enabled improvements to stayability and sustained fertility evaluations. While most evaluations have used binary observations of stayability to an assumed breakeven age (Snelling et al., 1995), recently random regression analysis of consecutive calvings (Jamrozik et al., 2013) has been implemented. Thus, multiple records from each cow can contribute to projecting stayability EPD to different ages (Golden et al., 2018). Other measures of fertility used in beef cow evaluations, such as length of productive life (Coffee et al., 2007), interval between first and second calving (Coffee et al., 2007; Moore et al., 2018), and calves born by a specific age (Moore et al., 2018), utilize a single record per cow. More information might be extracted from annual records into cumulative cow fertility and productivity traits, with a record for each opportunity a cow has to produce a calf. Objectives of this study were to estimate heritabilities of cumulative cow productivity traits and genetic correlations between cow productivity and weight while utilizing all cow records rather than summarizing records into single observations of weight and productivity.

MATERIALS AND METHODS

Animals

Data were obtained from the U.S. Meat Animal Research Center (USMARC) Germplasm

Evaluation (GPE) project in Clay Center, Nebraska. Animals were raised following USMARC standard operating procedures and Federation of Animal Science Societies (FASS, 2010) guidelines. Breeding, calving, and weaning records of GPE females born from 1970 through 2015 were extracted from the USMARC cattle records database. These females represented the eight historic cycles of GPE, as well as the on-going continuous GPE (Ahlberg et al., 2016), initiated with matings for the fall 2007 calving season. Each GPE cycle involved artificially inseminating Angus, Hereford and MARC III composite (Cycles IV to VIII; Gregory et al., 1991) females with semen from industry sires representing five to seven breeds. Cycle VII, a re-evaluation of breeds that had become the most influential in the US beef industry (Angus, Charolais, Gelbvieh, Hereford, Limousin, Red Angus, and Simmental; Wheeler et al., 2005) transitioned into the continuous GPE project that periodically samples average information (AI) sires representing the 7 Cycle VII breeds and 11 less numerous breeds (Beefmaster, Brahman, Brangus, Braunvieh, ChiAngus, Maine Anjou, Salers, Santa Gertrudis, Shorthorn, South Devon, and Tarentaise) that conduct national cattle evaluations for beef production traits.

In the GPE cycles, F_1 females were bred to calve first as 2-yr-old heifers, and kept in the project for six to seven matings to produce spring-born calves in order to evaluate mature cows sired by the different breeds. Except for Cycle VII, heifers were bred to one sire breed not represented in the cycle, and cows to another breed not in the cycle to produce F_1 calves from the F_1 females. In Cycle VII, heifers and 2 yr olds were bred to MARC III bulls, and 3 yr olds and older females bred to F_1 bulls sired by one of the seven breeds with a Hereford or Angus dam to produce two-, three-, and four-breed cross calves. Breeding seasons were ~63 d in length. Culling was intentionally minimal to reduce bias; females were removed if they were severely injured or were open following two consecutive breeding seasons.

Continuous GPE introduced fall calving; so, open females are exposed in the next breeding season (spring to fall, or fall to spring). Under the continuous GPE culling policy, cows are generally removed after they are open twice (not necessarily in consecutive breeding seasons), and for lameness, udder conformation, temperament, and other issues detrimental to animal or handler welfare. Cows may be culled the first time they are open, if they are the oldest among the group of open females and the size of the group exceeds the quota for shifting to the next season. Designed AI matings in

continuous GPE included breeding AI-sired yearling heifers to sires from the same breed as their sire who have calving ease direct or birth weight EPD in the best half of sires sampled from that breed, and breeding designated groups of cows to sires covering the range of EPD for each breed. Each breeding season, about half of the females are assigned to groups designated for AI mating with a single insemination followed by natural service. The remainder is bred using natural service for the full season. Heifers are exposed to Angus and MARC III bulls from the USMARC selection project (Bennett, 2008), and cows to F_1 and purebred bulls generated within GPE. Matings are assigned by breed composition groups (F_1 , 50% to <75%; backcross, 75% to <87.5%; and purebred, $\geq 87.5\%$ of any single breed) and birth year $\times$ season, and females retain the same group designation as long as they remain in the GPE project.

Traits

The number of pregnancies, calves born, calves weaned, age of calves weaned (d), and weight of calves weaned (kg) were accumulated on 13,707 females born in the GPE project from Spring 1970 through Fall 2015, and mated to produce a GPE project calf as a 2-yr old. Production from the first and 57,876 subsequent matings was accumulated until the female disappeared from GPE (died, culled, or transferred to another project) or was censored (2,729 were mated for 2018 calves that were not born or weaned when data were extracted). Binary pregnancy was determined by rectal palpation or ultrasound following each mating, and 65,086 weight (kg) records taken at pregnancy testing were available. After pregnancy testing, 68,696 calving and weaning events were recorded; 2,887 females were pregnant when they were culled; so, whether or not those pregnancies resulted in calves born or weaned was not observed. The number of calves born included twins, and the weaning traits included calves that were not fostered by another female. Calf weights were not adjusted for age, so that cumulative weaning weight would reflect differences in calf weight due to age, favoring cows who conceived earlier and weaned older, heavier calves. Similarly, age-of-dam adjustments of calf weight were not necessary because comparisons of cumulative measures were between same-age cows in the same opportunity group (birth year-season $\times$ breed composition group).

Cumulative production records were created for each breeding season, starting with records from

mating each female to calve as a 2-yr old. For each subsequent breeding season, results were added to totals from the previous seasons to create records of total production through that breeding season. Age for the observation was the age (yr) that the cow would be at calving and was incremented by 0.5 yr if the female shifted between breeding for spring and fall calving. Cow weight for each breeding season was the weight recorded at palpation following that season.

Analysis

Univariate analyses were conducted for each cumulative production trait and cow weights measured at palpation. The random regression models had the general form:

$$y = Xb + Za + Wc + e$$

where y is the vector of observations, b is a vector of fixed effects, a and c are vectors of random regression coefficients for additive genetic (a) and permanent environmental (c) effects, and e is a vector of residuals. X , Z , and W are incidence matrices relating observations to fixed, random additive, and permanent environmental effects. Assumed expectations (E) and (co)variance structure (V) were

$$E \begin{bmatrix} y \\ a \\ c \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \end{bmatrix}; \quad V \begin{bmatrix} a \\ c \\ e \end{bmatrix} = \begin{bmatrix} K_a \otimes A & 0 & 0 \\ 0 & K_c \otimes I & 0 \\ 0 & 0 & R \end{bmatrix}$$

where K_a and K_c are (co)variance matrices between random regression coefficients for additive genetic and permanent environmental effects, A is the numerator relationship matrix, I is an identity matrix, $\otimes$ is the Kronecker product between matrices, and R is a matrix of residuals.

To examine relationships between cumulative weaning traits and cow weight, bivariate analyses extended K_a and K_c to include covariances among the random regression coefficients for weight and productivity. Each bivariate y included observations for a cumulative weaning production trait and pregnancy test weight, b included fixed effects for both traits, a and c contained random additive genetic and permanent environmental effects for both traits.

Fixed effects were age at intended calving (e.g., 2, 3, 4, ... for females bred to calve as 2-, 3-, 4-, ... yr olds, whether or not they actually calved), birth year-season-composition opportunity groups for cumulative production traits, and breeding year-season-location mating groups reassigned

each season for pregnancy test weights. The model for cumulative weaning weight also included a covariate for cumulative calf sex (males weaned – females weaned). Residual variances were modeled with nine age classes (2 to 2.5, 3 to 3.5, ... 9 to 9.5, 10 yr and older).

Variances and covariances were estimated with restricted maximum likelihood (**REML**) algorithms implemented in **WOMBAT** (Meyer, 2007). Random regression with quadratic Legendre polynomials was chosen after exploratory analyses considered varying degrees of Legendre polynomials and B-spline basis functions. Models were evaluated by iteration behavior, likelihood statistics, and correlations among projected sires' EBV. If the AI REML algorithm did not converge, iteration cycled through AI, and 250 or more rounds of both expectation–maximization (**EM**) and simplex algorithms. After convergence, BLUP of the random

regression coefficients for all 115,119 animals in the pedigree were obtained, and diagonal blocks corresponding to prediction error covariances among the coefficients for each animal were extracted from the sparse inverse of the coefficient matrix in order to project EBV accuracies.

RESULTS

Distributions of accumulated counts for number of pregnancies, calves born and calves weaned, were bi- and tri-modal, reflecting females that succeeded at all opportunities, or failed once or twice to conceive, give birth or wean a calf. (Figure 1). At ages <4 yr, distributions of the continuous traits were bi-modal, with the lower mode containing females who failed to wean a calf (Figure 2). Observations at older ages were more normally distributed, as there was overlap in cumulative calf

Figure 1. Distributions of number of pregnancies (a), number of calves born (b), and number of calves weaned (c) by Germplasm Evaluation project cows at each age at calving. Half-year increments are for cows shifted from fall (spring) to spring (fall) calving seasons.

Figure 2. Distributions of cumulative calf age at weaning (a) and weight weaned (b) by Germplasm Evaluation project cows at each age at calving. Half-year increments are for cows shifted from fall (spring) to spring (fall) calving seasons.

age and weight weaned between cows who weaned younger, lighter calves every year and cows who had older, heavier calves when they did wean a calf, but failed to wean a calf at one opportunity.

Overall heritabilities (Schaeffer, 2016) of the quadratic Legendre polynomial coefficients from univariate analyses of the cumulative production traits were between 0.20 and 0.51 (Table 1). Estimates for cumulative calf age and weight coefficients were somewhat higher than heritabilities of corresponding coefficients for counts of pregnancies, calves born and calves weaned, and cow weight estimates were higher than any of the production trait estimates, between 0.55 and 0.71. Production trait heritability estimates for each age (Figure 3a) were between 0.02 and 0.07 at age 2, and increased through most ages, for a range of 0.07 to 0.19 at age 4, 0.17 to 0.36 at age 8, and 0.30 to 0.52 at age 12. Corresponding cow weight heritability estimates were 0.60 at 2, 0.68 at 4, 0.67 at 8, and 0.81 at 12 yr of age.

The trend of heritability increasing with age was exaggerated in analyses with higher order polynomial functions, both Legendre polynomials and B-splines, with heritability estimates for the oldest ages over 0.70. While the models with higher order polynomials were somewhat more likely, REML iteration did not converge as readily as the models using quadratic Legendre polynomials. Projected sire EBVs were highly correlated to the EBV from

Table 1. Estimated ratios of additive genetic (heritabilities) and permanent environmental variance to phenotypic variance of random regression coefficients for cumulative cow productivity and weight

Trait	Intercept	Linear	Quadratic
<i>Heritabilities¹</i>			
Pregnancies	0.20	0.28	0.17
Calves born	0.28	0.43	0.30
Calves weaned	0.23	0.38	0.28
Calf age	0.41	0.51	0.30
Weight weaned	0.40	0.50	0.37
Cow weight	0.71	0.69	0.55
<i>Permanent environment¹</i>			
Pregnancies	0.77	0.65	0.48
Calves born	0.70	0.52	0.43
Calves weaned	0.72	0.58	0.49
Calf age	0.58	0.46	0.48
Weight weaned	0.58	0.47	0.42
Cow weight	0.22	0.01	0.02

¹All SE < 0.02.

quadratic polynomials. Correlations between same-age sire EBV were >0.95 at ages 2 and 3, and >0.99 for older ages; further analyses and bivariate random regression with higher order polynomials were not attempted, considering the additional computational cost to obtain nearly identical predictions.

Genetic correlations among all ages were positive for all cumulative production traits. Correlations were highest between adjacent ages and diminished

Figure 3. Estimated proportions of variance in cumulative production traits projected to each age due to additive genetic (h^2 ; a) and permanent environmental (c^2 ; b) effects.

with increasing difference between ages. Genetic correlations between ages 2 and 3 (0.70 to 0.85) were lower than between 1-yr differences for ages 3 and older (>0.97 ; Table 2). Genetic correlations between age 2 and ages 6, 8, and 10 were between 0.30 and 0.68 (Table 3). Correlations between ages 3 and 4 and the older ages were higher, but most of the correlations with a difference of 4 or more years between ages were <0.80 . For cow weight, corresponding genetic correlations were generally >0.80 ; correlations for 1-yr difference in age were ≥ 0.98 (Table 2), and >0.80 between the earlier ages and ages 6 and 8 (Table 3). Correlations between the early ages and age 10 were around 0.70; the genetic correlation between ages 8 and 10 was 0.87 for cow weight, but >0.95 for the production traits.

Genetic correlations from bivariate analyses of weaning production and cow weight were consistently negative between weights from age 3 to 9 and production at any age (Figure 4a). Weaker negative correlations were estimated between 2-yr-old

weight and calves weaned or calf age, and 2-yr-old weight was positively correlated with weight weaned. Significant ($P < 0.05$) negative genetic correlations were most pronounced between cumulative weaning age projected to any age, and cow weight between ages 3 and 9. Within this cow age range, estimated genetic correlations between weight and calf age averaged -0.38 ± 0.005 , and were between -0.46 and -0.16 . Weaker negative genetic correlations were estimated between cow weight from ages 3 to 8 and weight weaned, with a mean of -0.15 ± 0.005 and range from -0.22 to -0.02 . Significant ($P < 0.05$) positive genetic correlations were estimated between weights of cows 10 yr and older and weaning productivity at all ages. The correlations were strongest between cow weight and weight weaned, and the positive correlations for weight weaned included cow weights taken at age 9.

Permanent environmental effects on cumulative weaning production were negatively correlated

Table 2. Estimated genetic correlations (SE) between 1-yr age differences for cumulative cow productivity and weight

Ages	Pregnancies	Calves born	Calves weaned	Calf age	Weight weaned	Cow weight
2 and 3	0.85 (0.04)	0.81 (0.06)	0.70 (0.10)	0.70 (0.08)	0.80 (0.04)	0.94 ¹
3 and 4	0.97 (0.01)	0.97 (0.01)	0.99 (0.01)	0.98 (0.01)	0.99 ¹	0.99 ¹
4 and 5	0.99 ¹	0.98 (0.01)	0.99 ¹	0.99 ¹	0.99 ¹	1.00 ¹
5 and 6	0.99 ¹	0.97 (0.01)	0.98 ¹	0.99 ¹	0.98 ¹	1.00 ¹
6 and 7	0.99 ¹	0.97 (0.01)	0.98 ¹	0.99 ¹	0.98 ¹	1.00 ¹
7 and 8	0.99 ¹	0.98 ¹	0.98 ¹	0.99 ¹	0.99 ¹	0.99 ¹
8 and 9	0.99 ¹	0.99 ¹	0.99 ¹	0.99 ¹	0.99 ¹	0.98 ¹
9 and 10	0.99 ¹	0.99 ¹	0.99 ¹	0.99 ¹	0.99 ¹	0.96 ¹
10 and 11	0.99 ¹	1.00 ¹	0.99 ¹	1.00 ¹	0.99 ¹	0.94 (0.01)
11 and 12	1.00 ¹	1.00 ¹	1.00 ¹	1.00 ¹	1.00 ¹	0.95 (0.01)

¹SE < 0.01.**Table 3.** Estimated genetic correlations (SE) between 2- and 3-yr old and later cumulative productivity and weight

Ages	Pregnancies	Calves born	Calves weaned	Calf age	Weight weaned	Cow weight
2 and 4	0.70 (0.08)	0.69 (0.09)	0.61 (0.12)	0.57 (0.10)	0.72 (0.06)	0.88 (0.01)
2 and 6	0.60 (0.10)	0.57 (0.10)	0.64 (0.14)	0.54 (0.11)	0.68 (0.07)	0.82 (0.01)
2 and 8	0.56 (0.10)	0.43 (0.11)	0.66 (0.15)	0.52 (0.11)	0.63 (0.07)	0.80 (0.01)
2 and 10	0.52 (0.11)	0.30 (0.12)	0.61 (0.17)	0.49 (0.12)	0.55 (0.08)	0.66 (0.03)
3 and 4	0.97 (0.01)	0.97 (0.01)	0.99 (0.01)	0.98 (0.01)	0.99 (0.00)	0.99 (0.00)
3 and 6	0.87 (0.04)	0.781(0.04)	0.90 (0.03)	0.90 (0.03)	0.91 (0.02)	0.96 (0.00)
3 and 8	0.73 (0.07)	0.52 (0.07)	0.68 (0.07)	0.75 (0.05)	0.74 (0.04)	0.91 (0.01)
3 and 10	0.57 (0.09)	0.27 (0.09)	0.44 (0.09)	0.59 (0.07)	0.54 (0.05)	0.67 (0.02)

to weight at similar ages; near 0 between young-age weights and production to advanced ages, and positive between production at young and weight at the oldest ages ([Figure 4b](#)). The only meaningful residual correlations between weight and production were for the 2-yr-old class; about 0.5 (0.50 for calves weaned, 0.52 for calf age, and 0.56 for weight weaned). Residual correlations for all other age classes were near 0 (± 0.05).

DISCUSSION

The random regression approach applied to cumulative cow productivity in this study is analogous to random regression applied to include all weights recorded on growing animals ([Andersen and Pedersen, 1996](#); [Legarra et al., 2004](#); [Scalez et al., 2014](#)). Just as young animals accumulate weight as they age, breeding females should accumulate offspring throughout their productive lives. For growth, genetic evaluation with random regression can include all the weights that might be observed periodically, and provide a more complete description of growth over time than weights observed near specific ages or gain assuming linear growth between two points in time. [Schenkel et al. \(2002\)](#)

found random regression of weight measured every 28 d during a 140-d bull test captured non-linearity in test gain that could not be explained by evaluations assuming linear growth over the test period, resulting in re-ranking of the top and bottom bulls in the test.

Random regression has also been suggested for analysis of survival traits ([Schaeffer, 2004](#); [Jamrozik et al., 2008](#); [Jamrozik et al., 2013](#)). Simulation showed random regression may be somewhat better than other approaches for predicting the percentage of sires' daughters that survive to a specific age ([Jamrozik et al., 2008](#)). Random regression of stayability to consecutive calvings has shown that stayability to the second calving is a good indicator of stayability to later calvings ([Jamrozik et al., 2013](#); [Silva et al., 2018](#)), enabling earlier evaluation of sire EBV based on daughters' records than is possible with a single observation of stayability to an older age.

Cumulative Production Traits

Depending on definition, the binary observations of stayability may or may not be indicative of cows' production. If a calf every year from age 2 to

Figure 4. Genetic (a) and permanent environmental (b) correlations among cow weight and cumulative number of calves weaned (left), calf age at weaning (center), and weight weaned (right). Positive correlations are blue and negative are red. Color intensity reflects strength of the correlation. Diagonal blocks of each 2×2 plot depict correlations among ages within trait, off-diagonal blocks depict correlations among ages between cow weight and productivity traits.

age n is required for success at age n , successful cows will have produced $n - 1$ calves and have successful stayability observations for ages 2 through n , and calvings 1 through $n - 1$. If annual calving is not required, cows with successful age n stayability may vary in the number of calves produced by age n , and cows staying to the $(n - 1)$ th calving may vary in age. Therefore, the number of calves produced by age n is equally or more indicative of calf production through age n relative to stayability, particularly if annual calving is not required or cows are not culled after their first reproductive failure. When cows are pregnancy tested after the breeding season, the binary observations are an indicator of which cows will calve. The cumulative number of pregnancies detected after each season a cow is exposed is indicative of the number of calves she has (or will) produce, although there will be some discrepancy due to abortion, mis-diagnosed pregnancy and multiple births. The number of pregnancies and calves born are both indicators of calves weaned; weaned calves are a salable product from the breeding–calving–weaning production cycle, so

the number of calves weaned may be the most economically relevant count trait for typical commercial cow–calf production. The value of a weaned calf is largely determined by weight, and weight of a weaned calf is affected by its age at weaning; so, the cumulative age and weight of calves that a cow weaned are relevant to the income she generates.

Among cows weaning contemporary calves, differences in calf age at weaning are equivalent to differences in days-to-calving (calving date–start of breeding or calving season; Meyer et al., 1990; Johnston and Bunter, 1996; Minick Bormann and Wilson, 2010), a trait used as an indicator of female fertility in Australian cattle evaluations (Breedplan, 2015). The signs of age at weaning and days to calving are opposite; small values for days to calving are desirable, reflecting conception early in the breeding season that should result in early calving and older calves at weaning. Days-to-calving observations for cows who do not calve are the observation for the last cow to calve, plus an explicit penalty to ensure values for noncalvers are always larger (less desirable) than the value of any cow who calved. Weaning age observations of 0 for cows

who do not wean a calf imply a penalty equal to the age of the youngest calf weaned by contemporary females. The sum of weaning ages of all calves weaned by a cow is the number of days that cow has nursed a calf and combines binary reproductive success with a measure of a cow's ability to conceive early at each opportunity.

Weight weaned may be a more complete measure of productivity, combining reproductive success, conception date, and calf growth. Previous works have used weaning weight in a measure of annual or accumulated cow productivity, but included an adjustment for calf age that masks differences between cows due to when their calves were conceived (Koger and Knox, 1947; Santana et al., 2013; Schmidt et al., 2018). The calf age adjustment is needed to fairly compare contemporary calves whose weaning weights are different due to differences in age, but cow productivity should favor cows who conceive early and wean older, heavier calves.

Heritability Estimates

The age-specific random regression heritability estimates suggest little genetic variation in cow productivity at age 2. The number of pregnancies at age 2 is equivalent to heifer pregnancy. The heritability estimate of 0.05 ± 0.01 is similar to the 0.04 ± 0.04 estimated by Morris and Cullen (1994) in an analysis that treated binary heifer pregnancy observations as a normal trait. Higher estimates have been obtained with threshold models (Evans et al., 1999; Doyle et al., 2000; Bormann et al., 2006). Transforming the 2-yr-old estimate to the underlying liability scale ($h^2_u = h^2_p(1 - p)/z^2$; Dempster and Lerner, 1950) yields 0.13 ± 0.03 ; similar to the threshold model estimates for pregnancy in Hereford (Evans et al., 1999) and Angus (Bormann et al., 2006) heifers. Applied to binary counts of calves born and weaned at age 2, the same transformation yields heritability estimates of 0.10 ± 0.03 for calves born and 0.04 ± 0.02 for calves weaned at age 2. At age 8, heritability estimates for calves born (0.24 ± 0.02) and calves weaned (0.23 ± 0.02) are within SE of corresponding estimates (0.17 ± 0.05 calves born; 0.21 ± 0.06 calves weaned) for cumulative production of Hereford cows through 6 yr after first calving (Martinez et al., 2004). Estimated heritability of weight weaned by age 8 in this study (0.36 ± 0.01), however, is greater than the 0.18 ± 0.01 estimated with age-adjusted weaning weights produced by the Hereford cows but matches an estimate (0.37 ± 0.02) of sex-adjusted weight weaned by cows from a synthetic line

(Arthur et al., 1994). The 0.034 ± 0.01 heritability estimate for 2-yr-old calf weaning age observation is somewhat less than estimates ranging from 0.06 to 0.11 for days to calving in heifers (Johnston and Bunter, 1996; Donoghue et al., 2004; Minick Bormann and Wilson, 2010). Heritability estimated with repeatability models of multiple days-to-calving observations on individual cows is usually similar to heritability of heifer days to calving (Meyer et al., 1990; Johnston and Bunter, 1996; Forni and Albuquerque, 2005), generally lower than the random regression estimates of cumulative weaning age for ages 5 and older.

Random regression estimates of cow weight heritability fluctuated between 0.60 and 0.70 up to age 11, within the range of reported heritability estimates. Estimates from field data collected by breed associations tend to be somewhat lower, around 0.50 (Bullock et al., 1993; Northcutt and Wilson, 1993) while higher heritabilities were obtained from experimental herds (Brinks et al., 1962; Burrow, 2001; MacNeil, 2005). Age-specific heritability estimates increased dramatically up to the maximum observed age of 12.5 yr. Heritabilities of the cumulative production traits are also high at the oldest ages. Inflated heritability estimates at extreme ages are a common artifact of random regression analyses, particularly if data are sparse at the extremes (Jamrozik et al., 2001; Meyer, 2005; Bohmanova et al., 2008). Schaeffer and Jamrozik (2008), however, suggest that this inflation is not a concern, contending that heritabilities of the regression coefficients (Table 1), not projected age-specific heritabilities, are critical. Still, the general agreement between random regression projections through most of the age range and pertinent estimates found in the literature is reassuring.

Relationships Between Cow Weight and Productivity

The generally negative genetic correlations between cow weight and cumulative productivity agree with negative relationships between weight and stayability (Mwansa et al., 2002; Berry and Evans, 2014) and between weight and lifetime productivity (Hawkins et al., 1965; Stewart and Martin, 1981). Morris et al. (1987) found negative genetic correlations between cow weight and weaning rate, and between cow weight and actual weaning weight, but a positive correlation between cow weight and age-adjusted weaning weight. Other estimates suggest neutral to favorable relationships. The genetic

correlation between cow weight and days to calving was favorable in tropical composite cattle (Burrow, 2001), and days to calving and calving success were not impacted by 15 yr of selection for 550 d weight in Nelore cattle (Mercadante et al., 2003).

Negative genetic correlations between cow weight and cumulative production were strongest for cumulative weaning age and weakest for weight weaned; heavy cows may conceive somewhat later or have longer gestations, but their calves tend to have heavier birth weights and grow faster to compensate for younger age at weaning. A phenotypic regression of 0.92 d gestation per 100 kg increase in cow weight (McMorris and Wilton, 1986) suggests longer gestation may partly explain younger calf age at weaning associated with increased cow weight. A similar phenotypic regression, 1.00 ± 0.08 d gestation per 100 kg was obtained from breeding and calving records of artificially inseminated GPE cows. Genetic correlations between cow weight and gestation length were not found in literature, but the positive genetic correlations between birth weight and gestation length (Bourdon and Brinks, 1982; Mujibi and Crews, 2009) coupled with strong positive genetic correlations between birth weight and mature cow weight (Bullock et al., 1993; Meyer, 1995) suggest cow weight should be positively correlated with gestation length, contributing to a negative relationship between cow weight and calf age at weaning.

The generally negative genetic correlations between cow weight and productivity indicate cumulative productivity should decrease with increasing mature weight, unless there is some selection for cow productivity. Correlated responses, however, may not be noticeable over year-to-year fluctuation in cow productivity due to weather and various factors affecting production. Genetic variance of 6-yr-old weight estimated in this study is about four times greater than genetic variance of yearling weight in GPE (Kuehn and Thallman, 2017). Assuming a genetic correlation of 0.8 between yearling and 6-yr-old cow weights (Bullock et al., 1993; Meyer, 1995), the 0.7 kg/yr EPD trend for yearling weight in industry cattle (Kuehn and Thallman, 2017) translates to a 6-yr-old cow weight genetic trend of about 1.1 kg/yr ($0.8 \times 0.7 \text{ kg/yr} \times (4 \text{ kg}^2/\text{kg}^2)^{0.5}$). Applying genetic covariances between 6-yr-old weight and cumulative production suggests the industry yearling weight trend might reduce cumulative production of 6-yr-old cows by 0.002 calves per year, 0.9 d of cumulative age at weaning per year, and 0.5 kg of weight weaned per year. Culling females who failed to wean a calf as a 2- or 3-yr-old

could compensate for that reduction. Assuming a 5-yr generation interval, products of the selection differentials for projected 6-yr-old EBV of females that weaned a calf as both 2- and 3-yr-olds (0.04 calves weaned, 11.1 d calf age, and 19.0 kg weaned) and average accuracies ($r_{\text{EBV},\text{BV}}$) of 6-yr-old EBV (0.49 calves weaned, 0.61 calf age, 0.60 weight weaned) suggests improvements of 0.002 calves per year, 0.7 d calf age and 1.2 kg per year could largely compensate for losses in cow fertility and productivity correlated to the industry trend of increasing yearling weight.

Selecting males by productivity of related females can increase progress over culling non-productive females. Without EBV, simply choosing sons of cows who weaned a calf every year through age 6 could marginally increase response above culling unproductive 2- and 3-yr olds (Table 4). Choosing the top 10% of sons of females with productivity records by productivity EBV could approximately triple annual progress in 6-yr-old cumulative productivity, from 0.002 to 0.007 calves, 0.7 to 3.1 d calf age, and 1.1 to 3.7 kg weaned. In this case, non-parent sons' EBV are based primarily on their dams' records, and their accuracy is low relative to accuracy of their dams' EBV. Faster progress could be made by more accurate selection among sires with recorded daughters. Using the top 10% of sires with at least 1 (10) daughter(s) could increase annual change to 0.018 (0.033) calves, 7.4 (14.1) d calf age and 9.0 (17.0) kg weaned.

Permanent environmental correlations between cow weight and productivity are usually more negative than the corresponding genetic correlations. Perhaps this is a result of managing groups of diverse cows, some groups with over 500 kg difference between the smallest and largest cows. If grazed forage available and supplemental feed provided for the group average are inadequate to meet demands of the largest cows in the group, their reproductive performance may be compromised. BCS observed concurrently with the pregnancy test weights, however, indicate nutrition was more than adequate for the heavy cows. Cows heavier than the group mean + 1SD had higher BCS than cows within 1SD of the mean, and fat to very fat cows were more frequent in the heavy cows (24%) than near-average cows (8.5%). Much literature (e.g., Richards et al., 1986; Short et al., 1990; Hess et al., 2005) suggests favorable phenotypic relationships between BCS and reproductive performance but seldom includes cows having BCS approaching obesity. Reproductive performance, reflected by calving and calf survival rates, was reported to suffer in cows fed

Table 4. Expected response to selection for cumulative cow production through 6 yr of age

Trait	Selection differential ¹		Accuracy ²		Annual response ³
Selection criteria	Female	male	female	male	
Calves weaned (<i>n</i>)					
CF ⁴	0.044	0	0.49	0	0.002
CF + Son ⁵	0.044	0.046	0.49	0.32	0.004
CF + SonEBV ⁶	0.044	0.154	0.49	0.32	0.007
CF + SireEBV ⁷	0.044	0.293	0.49	0.53	0.018
CF + PSireEBV ⁸	0.044	0.510	0.49	0.61	0.033
Calf age (d)					
CF	11.29	0	0.61	0	0.69
CF + Son ⁶	11.29	12.07	0.61	0.40	1.17
CF + SonEBV	11.29	67.96	0.61	0.36	3.15
CF + SireEBV	11.29	108.99	0.61	0.62	7.41
CF + PSireEBV	11.29	184.79	0.61	0.73	14.19
Weight weaned (kg)					
CF ^b	19.32	0	0.60	0	1.17
CF + Son ⁶	19.32	16.98	0.60	0.39	1.82
CF + SonEBV	19.32	71.79	0.60	0.35	3.70
CF + SireEBV	19.32	130.26	0.60	0.60	9.02
CF + PSireEBV	19.32	229.60	0.60	0.69	16.96

¹Estimated breeding value (EBV) projected to age 6; mean EBV_{selected} – mean EBV_{candidates}.

²Correlation between EBV and true breeding value.

³Assuming 5 yr generation interval.

⁴Cull females who did not wean a calf as a 2- and 3-yr old.

⁵Select sons of 6-yr old and older cows who weaned a calf every year through age 6.

⁶Select top 10% of sons by productivity EBV projected to age 6.

⁷Select top 10% of sires by productivity EBV projected to age 6.

⁸Select top 10% of sires with at least 10 daughters by productivity EBV projected to age 6.

to obesity (Arnett et al., 1971; Jenkins and Ferrell, 1994), and pregnancy rates found to decline from moderate to obese BCS in a study that did include obese cows (Cooke et al., 2009). Further investigation to examine genetic relationships among cow weight, body condition, and productivity appears warranted, perhaps including measures of carcass fat and milk production that may be related to cow condition.

Estimated genetic and permanent environmental correlations suggest neutral to favorable relationships among weights of cows older than 9 yr and productivity of younger cows, in contrast to the generally unfavorable relationships among weight and productivity through younger ages. This may be a random regression artifact related to sparse data and inflated heritability estimates at extreme ages. About 4% of the weight and productivity observations were of cows older than 9, representing 24% of the opportunity groups and 11% of GPE cows bred to calve first as 2-yr olds. While this study used all available records, the GPE project design dictated that most cow groups be removed from the project by age 9, so impact of the older cow records

on estimated (co)variances and genetic predictions should be investigated.

Selection for Cumulative Production

Each cumulative production trait examined in this study is indicative of income generated by a cow and could be included in economic selection indices. The number of pregnancies by a given age requires assumptions about fetal loss between pregnancy testing and calving, and calf survival from birth to weaning but could be combined with direct and maternal weaning weight EBV (if available) and assumed calf prices to predict value of potential calves. Number of calves born eliminates assumptions about fetal loss, and number of calves weaned the assumptions about calf survival. Cumulative calf age at weaning is essentially the number of days that female has nursed a calf. The EBV for days nursing by a given cow age could be combined with direct and maternal weaning weight or preweaning gain EBV, expressed in kilograms per day rather than kilograms at a standard weaning age (e.g., 205 d), to express total weight of calves produced by that cow age. That weight would differ

from an expression of weight weaned that is a function of 205-d weaning weight EBV and opportunities to produce a calf by that age, perhaps also assuming probabilities of producing a calf at every opportunity up to that age. Cumulative weight weaned requires the fewest assumptions about gross income generated by a cow, but inclusion in an index with calf weaning weight (adjusted for age) to address growth potential will require additional multivariate covariance estimation to establish appropriate economic weights.

The value of calves produced by a cow plus the cow's market value needs to be balanced against costs of developing her from a heifer calf into a productive cow, and producing those calves. Including cow weight in an economic index can explicitly account for variation in cost related to feed required for development and maintenance. Further variation in feed costs can be explained by variation in milk production, either by combining weight and maternal weaning weight EBV into a maintenance energy EBV (MacNeil and Mott, 2000; Evans et al., 2002; Williams et al., 2009) and valuing that EBV in the index, or accounting for effects that maternal weaning weight EBV have on cow costs (MacNeil and Newman, 1994; Tang et al., 2011). The cumulative weight weaned EBV from the current analysis, however, does not separate direct and maternal effects. Model refinements might attempt to partition a milk effect from weight weaned, although variation in milk affecting weight weaned may be trivial relative to variation due to reproductive success or failure, and ages of calves that were weaned. A function of cumulative calf age at weaning and maternal weaning weight EBV may be more straightforward to account for variation in cow costs due to level of milk production and the number of days the cow was producing milk.

Cow weight, along with age, is also needed in economic indexes to account for variation in cow market value. Older culls, sold for cow beef, are valued by weight. Young breeding age females might be valued more for expected future production. Age-specific predictions of cow profitability (calf income + cow value – production cost) could be developed from random regression projections of production and weight EBV at each age, where calf income is a function of cumulative production through that age, cow value is a function of weight and projected production through later ages, and production costs are a function of cow weight and age, and possibly ages of calves at weaning. Contributions of age-specific profitability to herd profitability might be derived by including age distribution of the herd. Additionally, projections

of total cow effects (EBV + permanent environmental effects) on weight and productivity might inform cow marketing decisions. Cows projected to be the highest cost, least productive cows through advanced ages might be sold at younger ages than low cost, highly productive cows.

Results of this study indicate that cumulative cow production traits are heritable, and can be improved with selection. Continuous weaning production traits, days nursing (sum of calves' ages at weaning) and weight weaned (sum of calves weaning weights), were estimated to be more heritable than count traits, number of pregnancies detected, number of calves born and number of calves weaned. Parallels exist between the continuous traits and previously defined traits that favor early calving, but age and weight at weaning are more amenable to accumulation and imply larger penalties for failure to wean a calf. Random regression of cumulative productivity can include all records observed annually on cows, and project a rich suite of EBV for production to any age, perhaps providing more information for selection than EBV for one or two values extracted from the complete set of production records available on a cow. Agreeing with literature, negative genetic correlations among cow weight and weaning production traits were observed, although culling unproductive females may overcome declines in productivity that might be correlated to selection for calf growth resulting in increased cow weight. Further investigation into genetic relationships among cow weight and productivity is warranted; these data indicate a possibility that gestation length increasing with cow weight might be partly responsible for negative correlations between cow weight and calf age at weaning. At least in the cows studied, productivity losses might be related more to obesity than inadequate nutrition for heavy cows. Random regression projections of cow weight and productivity reflect traits responsible for variation in individual cow income and expense, and can be incorporated into comprehensive indexes to select for cow and calf profitability.

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