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Breed and heterotic effects for mature weight in beef cattle

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Abstract

Cow mature weight (**MWT**) is heritable and affects the costs and efficiency of a breeding operation. Cow weight is also influenced by the environment, and the relationship between the size and profitability of a cow varies depending on production system. Producers, therefore, need tools to incorporate MWT in their selection of cattle breeds and herd replacements. The objective of this study was to estimate breed and heterotic effects for MWT using weight-age data on crossbred cows. Cow's MWT at 6 yr was predicted from the estimated parameter values—asymptotic weight and maturation constant (***k***)—from the fit of the Brody function to their individual data. Values were obtained for 5,156 crossbred cows from the U.S. Meat Animal Research Center (**USMARC**) Germplasm Evaluation Program using 108,957 weight records collected from approximately weaning up to 6 yr of age. The cows were produced from crosses among 18 beef breeds. A bivariate animal model was fitted to the MWT and *k* obtained for each cow. The fixed effects were birth year-season contemporary group and covariates of direct and maternal breed fractions, direct and maternal heterosis, and age at final weighing. The random effects were direct additive and residual. A maternal additive random effect was also fitted for *k*. In a separate analysis from that used to estimate breed effects and (co)variances, cow MWT was regressed on sire yearling weight (**YWT**) Expected Progeny Differences by its addition as a covariate to the animal model fitted for MWT. That regression coefficient was then used to adjust breed solutions for sire selection in the USMARC herd. Direct heterosis was 15.3 ± 2.6 kg for MWT and 0.000118 ± 0.000029 d^{-1} for *k*. Maternal heterosis was −5.7 ± 3.0 kg for MWT and 0.000130 ± 0.000035 d^{-1} for *k*. Direct additive heritabilities were 0.56 ± 0.03 for MWT and 0.23 ± 0.03 for *k*. The maternal additive heritability for *k* was 0.11 ± 0.02. The direct additive correlation between MWT and *k* was negligible (0.08 ± 0.09). Adjusted for sire sampling, Angus was heaviest at maturity of the breeds compared. Deviations from Angus ranged from −8.9 kg (Charolais) to −136.7 kg (Braunvieh). Ordered by decreasing MWT, the breeds ranked Angus, Charolais, Hereford, Brahman, Salers, Santa Gertrudis, Simmental, Maine Anjou, Limousin, Red Angus, Brangus, Chiangus, Shorthorn, Gelbvieh, Beefmaster, and Braunvieh. These breed effects for MWT can inform breeding programs where cow size is considered a key component of the overall profitability.

Key words: beef cattle, breed effect, Brody function, genetic parameters, heterosis, mature weight

Abbreviations

AI	artificial insemination
BW	body weight
EPD	Expected Progeny Differences
GPE	Germplasm Evaluation
k	maturation constant
MWT	mature weight
YWT	yearling weight

Introduction

Cow mature weight (**MWT**) has increased considerably over the past 30 yr (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016). Between 1975 and 2005, the average weight of cows at slaughter increased from 475 to 621 kg, along with production costs (McMurry, 2008). Selection pressure for faster growth and heavier slaughter weight has contributed to this increase in MWT (Jenkins and Ferrell, 2006). On the average, larger cows require greater daily intake than smaller cows (Walker et al., 2015). Whether larger cows are more, less, or equally efficient as smaller cows is equivocal. In studies conducted in different climactic areas, the conclusions differed (Scasta et al., 2015; Walker et al., 2015; Beck et al., 2016), suggesting that efficiency is influenced by environment. A variety of biological types of cows are available to suit the diverse environments and management conditions found in beef operations in the United States (Arango and Van Vleck, 2002). The challenge is identifying the best choice.

Crossbreeding is a valuable tool for matching cow genotype to environment. Mating unlike breeds with complementary strengths can create a combination of traits that make the progeny optimally suited to their production environment. Additionally, when unlike alleles combine, the resulting progeny may display heterosis, a superiority of the crossbred progeny over the average of the parental breeds (Weaber, 2010).

The USDA, ARS, U.S. Meat Animal Research Center (**USMARC**) in Clay Center, Nebraska, publishes across-breed adjustment factors for 18 breeds on various traits using crossbred animals from its Germplasm Evaluation (**GPE**) program; doing so allows producers to compare Expected Progeny Differences (**EPD**) from animals of different breeds (Kuehn and Thallman, 2017). However, MWT is not currently among traits analyzed.

Breed effects for MWT can provide additional information to aid in breed choice and utilization. They can also be used to calculate across-breed adjustment factors should MWT EPD become more widely available. The objective of this study was to estimate breed and heterotic effects for MWT in 18 beef breeds using data from GPE cattle. The MWT had been obtained by fitting a Brody function to weight-age data on individual cows (Zimmermann et al., 2019). (Co)variances for MWT and the maturation constant from the fit of the Brody function were also estimated.

Materials and Methods

Animals

Animals were raised in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 2010), and their care was approved by the USMARC Animal Care and Use Committee.

Cows were from the USMARC GPE program as described by Zimmermann et al. (2019). Briefly, they were from Cycle VII and continuous sampling phases of GPE, born between 1999 and 2014, and reached a maximum of 14 yr of age. Most cows were sired through artificial insemination (**AI**) by bulls that were highly influential within the following breeds: Angus, Hereford, Red Angus, Shorthorn, South Devon, Beefmaster, Brahman, Brangus, Santa Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine Anjou, Salers, Simmental, and Tarentaise. The remaining cows were sired through natural service by bulls raised at USMARC and sired by the above AI sires. Dams of the cows were USMARC base cows or cows produced in the GPE program (sired almost exclusively by bulls from the breeds described above). The USMARC base cows were populations of Angus, Hereford, Charolais, Simmental, MARC II (¼ each Simmental, Hereford, Angus, and Gelbvieh), and MARC III (¼ each Angus, Hereford, Pinzgauer, and Red Poll) bred at USMARC with occasional introductions of industry germplasm. Most of the cows ranged from 50% to 87.5% influence of the above AI sires, with the remainder being from USMARC base populations. Breed composition of cows sired by purebred bulls ranged from 50% to 100% the breed of their sire. Some cows were sired by F_1 bulls produced at USMARC; those cows were four-way crosses, three-way crosses, or F_2.

Cows with weight records not extending past 3 yr of age or with missing pedigree data were excluded. Additionally, weight records were removed after 6 yr of age, after a gap between subsequent records greater than 2 yr, and after the start of a feed restriction diet. Birth weight records were not included as no weights were available to describe growth between birth and weaning. Most cows had three records per year, reflecting three physiological states. Weight records were generally collected at palpation to determine pregnancy status following breeding, when pregnant cows were brought in for brand clipping (third trimester) before calving, and during lactation before cows were exposed for breeding for the next calving season. In total, 108,857 weight records on 5,156 crossbred GPE cows sired by 787 bulls were ultimately considered (Zimmermann et al., 2019).

Brody growth function

The fit of several growth functions was evaluated with these data, and the Brody function was found to be the most suitable (Zimmermann et al., 2019). It generated more consistent estimates of MWT even when the timeframe weights were recorded was limited (through 3 yr of age). The form of the Brody function fitted was $W_t = A[1 - e^{-k(t-t^*)}]$, where W_t is the body weight (**BW**) at a certain age, in days, A (kg) is the asymptotic weight, $\boldsymbol{k}$ (d^{-1}) is the maturation constant, t is the observed age, and t^* is the time origin of the curve (St. Taylor, 1965). As noted by Kaps et al. (1999), values of k are indicative of both growth rate and the rate of change in growth rate. Growth was modeled from weaning ($t^* = 180$) to older ages.

Weight at 6 yr of age, considered as maturity, was obtained from the parameter values obtained from the fit of the Brody function to weight-age data on individual cows with no other effects in the model. Therefore, those predictions were not independent of the estimates of asymptotic weight and k or any errors associated with those estimates. The estimated values of MWT and k were used as response variables in subsequent analyses.

Breed and heterotic effects

The covariates for direct and maternal heterosis were allocated as the regression on expected breed heterozygosity fraction. This fraction was calculated as 1 minus the sum of the products of breed fractions of the sire and dam. For calculation of heterosis, AI sires and commercial cows of the same breed were considered the same breed. Red Angus was assumed to be the same as Angus based on Schiermiester et al. (2015), and composite breeds were characterized according to their nominal breed composition. Composite breeds consisted of MARC II (¼ Angus, ¼ Hereford, ¼ Simmental, and ¼ Gelbvieh), MARC III (¼ Angus, ¼ Hereford, ¼ Red Poll, and ¼ Pinzgauer), Brangus (⅜ Brahman and ⅝ Angus), Santa Gertrudis (⅜ Brahman and ⅝ Shorthorn), Beefmaster (½ Brahman, ¼ Hereford, and ¼ Shorthorn), Chiangus (½ Chianina and ½ Angus), and Red Angus × Simmental (½ Red Angus, and ½ Simmental) cross cows.

Direct and maternal breed fractions were determined based on pedigree information. Founder animals, sires, or dams with known breed but unknown parentage were assigned to their respective breeds and used to assign breed fractions throughout the pedigree; each animal was assigned half of its sire breed and half of its dam breed. For breed fraction calculation, all breeds, and subpopulations within those breeds (e.g., AI sires versus commercial dams of the same breed), including composites, were considered separate genetic groups. Breed fractions assigned for each individual, and for their dam, were fitted as covariates for the estimation of direct and maternal breed effects.

Analyses

(Co)variance components and model selection

ASReml version 4 (Gilmour et al., 2015) was used to estimate variance components for parameter values obtained from the Brody function (MWT, k) fitting an animal model. Convergence was judged by changes in the residual maximum log-likelihood value and variance parameters using the default criterion.

In the models analyzed, the fixed effects included were birth year-season contemporary group, and covariates covariates of breed fractions (direct and maternal) and heterosis (direct and maternal). The Brody function generated consistent MWT regardless of the timeframe weights were collected on individual cows (Zimmermann et al., 2019). Still, to avoid any potential bias given different lengths of data recording, the cow's age (d) at her final weighing was also fitted. In the initial models evaluated, direct and maternal additive (with and without their covariance), an uncorrelated maternal permanent environment, and residual were included as random effects.

Fitting univariate models for MWT and k, the significance of random effects was tested by adding each effect marginally and performing a log-likelihood ratio test between the incrementally simpler and more complex model. With the test, −2 times the difference in log-likelihoods was compared with a χ^2 value with 1 df and α of 0.05. Additionally, variance component estimates and ratios were compared between models to evaluate whether variance partitioning was reasonable. The process for model selection of random effects is summarized in Table 1.

For MWT, including permanent environment—the uncorrelated maternal environmental effect of dams on their daughters' MWT—in addition to direct additive and residual effects improved model fit based on the log-likelihood ratio test (P = 0.022). However, the estimate of the permanent environmental variance was near zero and was fixed at that boundary. Furthermore, comparing the Akaike information criterion, the information loss was small with the simpler model excluding permanent environment. The Bayesian information criterion also was lowest when only the direct additive and residual variances were included in the model fitted. For k, all goodness-of-fit statistics indicated that a model that included the direct additive, maternal additive, and residual effects best described these data.

Based on this evidence, the random terms selected for the "best-fit" univariate model for MWT included direct additive and residual effects. For k, the maternal additive effect was also included. These selected models were then used in a bivariate analysis. The covariance between the direct additive effect for MWT with both the direct and maternal effect for k was fitted, along with the covariance among residuals for the pair of traits. Only solutions from the fit of the bivariate model are reported.

Breed effects

Solutions for direct and maternal breed fraction were obtained for MWT and k. Simple correlations among breed solutions were obtained and tested against zero with a two-sided t-test using Genstat for Windows 21st Edition software (VSN International, 2020).

Direct breed solutions for MWT were adjusted for sire sampling in a similar manner to Kuehn and Thallman (2017). However, EPD for MWT were not available in many breeds. Breed solutions, therefore, were adjusted for sire sampling at USMARC using the sires' yearling weight (**YWT**) EPD as a proxy. YWT was chosen as a basis for adjustment because it was commonly

Table 1. Log-likelihood values (LogL) and Akaike (AIC) and Bayesian (BIC) information criterion, from the fit of a univariate animal model to MWT (kg) and k (×10,000 d^{-1})

Random	MWT[1]			k		
Effects[2]	ΔLog_L[3]	ΔAIC[4]	ΔBIC[4]	ΔLog_L[3]	ΔAIC[4]	ΔBIC[4]
σ_e^2, σ_d^2	**0**	**0**	**0**	−23.60	+21.60	+15.07
$\sigma_e^2, \sigma_d^2, \sigma_m^2$	+0.52	+1.48	+8.01	**0**	**0**	**0**
$\sigma_e^2, \sigma_d^2, \sigma_m^2, \sigma_{dm}$	n/a[5]			n/a[5]		
$\sigma_e^2, \sigma_d^2, \sigma_c^2$	+5.22	−3.22	+3.31	−9.80	+9.68	+9.68
$\sigma_e^2, \sigma_d^2, \sigma_m^2, \sigma_c^2$	+5.72	−1.71	+11.35	−1.80	+3.70	+10.23

[1]Estimated at 6 yr of age.
[2]σ_e^2, residual variance; σ_d^2, direct additive variance; σ_m^2, maternal additive variance; σ_{dm}, direct-maternal additive covariance; and σ_c^2, uncorrelated permanent environmental variance.
[3]Minus two times the log-likelihood expressed as a deviation from the model chosen as the "best-fit" model (in bold). Positive values refer to an increase in the log-likelihood, indicating a "better" fit (with 1 df, χ^2 threshold values are 3.841 and 6.635 for α of 0.05 and 0.01, respectively).
[4]Expressed as a deviation from the model chosen as the "best-fit" model (in bold). Positive values refer to a loss in information or "poorer" fit.
[5]Log-likelihood failed to converge with all goodness-of-fit statistics indicative of poorer fit.

reported and was closer to maturity than other weight traits. The equation used was:

$$M_i = USMARC\,(i) + 2b\left[EPD(i)_{average} - EPD(i)_{USMARC}\right]$$

Where M_i is the adjusted breed effect for MWT for breed i, *USMARC(i)* is the breed solution for MWT for breed *i* from analysis of USMARC data, b is the regression coefficient relating estimated MWT from the Brody function to sire YWT EPD, $EPD(i)_{average}$ is the breed reported average EPD for animals born in 2017, and $EPD(i)_{USMARC}$ is the weighted mean YWT EPD of bulls sampled at USMARC with progeny in the analysis; the sum of individual sire numerator relationship coefficients to descendants with phenotypes was used as the weighting factor. Since solutions were expressed as breed solutions rather than breed of sire solutions, b was doubled in applying the adjustment. The YWT EPD used to obtain both the breed averages for 2017-born animals and the weighted averages of bulls sampled at USMARC were extracted from genetic evaluations conducted in 2019.

Values of the regression coefficient (b) were obtained by its addition to the univariate animal model already described for MWT. The YWT EPD were assigned based on the relationship between individuals with a phenotypic record and sires with a YWT EPD. Offspring of sires with EPD received their respective sire's full EPD, and subsequent generations of offspring received the EPD diluted by a factor of one-half for each generation of separation. Sires with EPDs were removed from the pedigree in these analyses.

For all analyses, each of the USMARC base genetic groups was included as well as AI breed groups. For Angus, Hereford, Charolais, and Simmental, the USMARC base genetic groups were distinct from the corresponding AI breed genetic groups. Only AI breed group estimates were reported because only they are directly applicable to well-defined industry populations. Estimates were not reported for South Devon and Tarentaise because very few cows of those breeds had reached maturity.

Results

Heterosis

The mean MWT and k were 650.0 (SD 64.0) and 0.0023 d^{-1} (SD 0.0008 d^{-1}), respectively (Zimmermann et al., 2019). The direct heterosis estimate for MWT was 15.3 ± 2.6 kg or, as a percentage of the mean, 2.4%. Maternal heterosis was negative at −5.8 ± 3.0 kg or −0.9%. Both direct and maternal heterosis estimates for k were positive (0.000118 ± 0.000029 d^{-1}or 5.1% and 0.000130 ± 0.000035 d^{-1} or 5.7%, respectively).

Genetic parameters

Estimates of (co)variances, and the ratios among them for direct, maternal, and residual effects, on MWT and k are provided in Table 2. The MWT at 6 yr of age was highly heritable (0.56 ± 0.03), while the direct additive effect of k was moderately heritable (0.23 ± 0.03). The maternal additive effect of k was less heritable (0.11 ± 0.02). The total heritability for k, defined as $\left(\sigma_d^2 + 0.5 \times \sigma_m^2\right)/\sigma_p^2$, where σ_d^2, σ_m^2, and σ_p^2 are the direct additive, maternal additive, and phenotypic variances, respectively, as in Willham (1972), was 0.28 ± 0.03. The correlation between the direct additive effect for MWT and the maternal additive effects for k was moderate and negative (−0.21 ± 0.09). A positive yet small correlation was estimated between direct additive effects for MWT and k (0.08 ± 0.09). However, the residual (−0.40 ± 0.04) and phenotypic (−0.24 ± 0.02) correlations between MWT and k were negative.

Breed solutions

Solutions for the direct breed factions for MWT are provided in Table 3 for 16 breeds evaluated in the GPE program at the USMARC. They were expressed as deviations from Angus. Breed YWT EPD, which were used to calculate adjusted breed effects for MWT, are also given. The estimate of the regression coefficient of cow MWT on sire YWT EPD was 0.868 ± 0.099 kg/kg. Once adjusting for sire sampling, Angus was the heaviest, whereas Braunvieh was the lightest breed (136.7 kg less than Angus).

In Table 4, estimates of direct breed solutions for k are provided. Their values were independent of the corresponding breed solutions for MWT (r = −0.010; P = 0.970). Estimates of maternal breed solutions for MWT and k also are provided in Table 4. There was little relationship between the maternal breed solutions for the pair of traits (r = 0.069; P = 0.798). For MWT, the direct and maternal breed solutions were inversely correlated (r = −0.494; P = 0.052); for k, they were positively although not significantly correlated (r = 0.240; P = 0.371).

Discussion

Heterosis

Direct heterosis for MWT was 15.3 ± 2.6 kg (or 2.4%). Cattle with an expected heterozygosity of 1 (parents from different breeds), therefore, would be expected to gain an extra 15.3 kg of weight

Table 2. Parameter value estimates for direct additive, maternal additive, and residual effects for MWT[1] (kg) and k (×10,000 d^{-1})

Trait[2,3]	MWT_d	k_d	k_m	MWT_r	k_r
MWT_d	1,740.42 (114.58) **0.56** (0.03)	9.69 (10.31)	−17.35 (7.48)		
k_d	0.09 (0.09)	8.17 (1.19) **0.23** (0.03)	n/a[4]		
k_m	−0.21 (0.09)	n/a[4]	4.01 (0.81) **0.11** (0.02)		
MWT_r				1,388.80 (82.72)	−72.42 (7.35)
k_r				−0.40 (0.04)	23.90 (1.02)

[1]Estimate at 6 yr of age.
[2]Variances and heritabilites (in bold) along the diagonal, covariances above the diagonal, and correlations below the diagonal. Corresponding SE are in parentheses.
[3]Subscript d indicates direct additive effect, m indicates maternal additive effect, and r indicates residual effect.
[4]Covariance between direct and maternal additive effects of k was not fitted. Log-likelihood failed to converge with all goodness-of-fit statistics indicative of poorer fit.

Table 3. Direct breed solutions for MWT (kg), average EPD for YWT (kg), and adjusted breed effects for MWT for 16 breeds evaluated in the GPE program at the USMARC[1]

	Direct breed solution for MWT[2]		Industry average YWT EPD[3]	USMARC average YWT EPD		Direct breed effect for MWT[2,4]
	(1)		(2)	(3)		(4)
Breed	Est.	SE	Est.	Est.	Acc.	Est.
Angus	0.0	0.0	43.5	27.3	0.80	0
Red Angus	−21.4	12.0	40.5	37.7	0.86	−44.8
Beefmaster	−38.3	15.5	18.7	20.0	0.82	−68.8
Brahman	−2.5	16.7	13.1	7.8	0.37	−21.4
Brangus	−26.8	15.4	22.5	19.1	0.71	−49.2
Braunvieh	−112.9	16.4	33.9	31.4	0.36	−136.7
Charolais	4.8	11.7	24.5	16.1	0.65	−8.9
Chiangus	−25.7	15.7	31.8	32.1	0.66	−54.5
Gelbvieh	−51.3	12.2	40.8	33.1	0.75	−66.1
Hereford	3.8	11.5	36.7	32.7	0.64	−17.5
Limousin	−32.2	12.1	43.1	33.2	0.83	−43.3
Maine Anjou	−9.4	15.3	25.8	25.4	0.44	−36.9
Salers	−8.4	16.2	37.6	30.8	0.74	−24.8
Santa Gertrudis	−1.8	16.3	4.1	4.3	0.53	−30.3
Shorthorn	−33.7	15.2	34.5	33.5	0.63	−60.2
Simmental	−14.8	11.7	45.8	40.3	0.88	−33.4

[1]Solutions are deviations from Angus. The YWT EPD were extracted from genetic evaluations conducted in 2019.
[2]Estimate of MWT differences at 6 yr of age.
[3]Average of 2017-born animals.
[4]$(4) = (1) + 2 \times b\ [(2) - (3)]$, where $b = 0.868 \pm 0.099$ kg /kg is the regression of MWT phenotype at USMARC on sire's YWT EPD from breed association genetic evaluation from 2019.

Table 4. Direct breed solutions for k (×10,000 d^{-1}), and maternal breed solutions for MWT (kg) and k, for 16 breeds evaluated in the GPE program at the USMARC[1]

			Maternal breed solution			
	Direct breed solutionfor k		MWT[2]		k	
Breed	Est.	SE	Est.	SE	Est.	SE
Angus	0.00	0.00	0.0	0.0	0.00	0.00
Red Angus	−1.62	1.14	11.7	10.0	−1.15	1.30
Beefmaster	−3.90	1.54	24.9	21.6	−4.12	2.51
Brahman	−3.22	1.65	−37.9	19.6	−1.16	2.30
Brangus	−0.64	1.55	−2.4	21.1	−7.54	2.43
Braunvieh	−3.46	1.59	20.6	18.3	5.75	2.21
Charolais	−1.35	1.11	0.5	9.8	−3.42	1.27
Chiangus	−4.21	1.52	28.0	18.2	0.58	2.18
Gelbvieh	0.52	1.16	10.1	10.1	1.12	1.30
Hereford	−4.63	1.10	2.3	9.9	−4.01	1.28
Limousin	−4.14	1.15	1.7	10.0	−0.44	1.30
Maine Anjou	−4.67	1.50	2.4	18.1	−7.97	2.17
Salers	−5.60	1.56	4.6	17.4	1.28	2.12
Santa Gertrudis	−3.70	1.57	0.4	17.3	−0.08	2.07
Shorthorn	−3.07	1.49	9.4	17.2	−0.32	2.06
Simmental	1.33	1.12	9.7	9.8	0.82	1.27

[1]Solutions are deviations from Angus.
[2]Estimate of MWT differences at 6 yr of age.

due to heterosis, relative to the weighted parental average. This amount of direct heterosis was lower than that estimated by Gregory et al. (1966) among Hereford, Angus, and Shorthorn cross heifers (22 to 24 kg). Stewart and Martin (1981) obtained heterosis values for mature weight of 7% (28 ± 8 kg) in reciprocal crosses of Angus and Shorthorn cattle. In crosses among Angus, Brahman, and Hereford cattle, Nelsen et al. (1982) reported higher estimates of percent direct heterosis of 5.0% to 10.7% for asymptotic mature weights estimated from the fit of the Brody function.

Maternal heterosis for MWT was less substantial (−5.8 ± 3.0 kg or −0.9%). Still, a negative value suggests that heterosis in the dam would cause offspring to be lighter at maturity. Few studies report the effects of maternal heterosis past weaning. Olson et al. (1978) found that maternal heterosis reduced postweaning average daily gain, with a general reduction in maternal heterotic effects in weights at more advanced ages. Nelsen et al. (1982) estimated values of maternal heterosis closer to zero in their crosses of three cattle breeds (−3.6% ± 3.0% to 1.3% ± 3.6%).

Both direct and maternal heterosis values for *k* were positive, indicating that heterosis, both in the individual and in the dam, would be expected to increase the rate at which a cow approaches MWT. Gregory et al. (1966) and Smith et al. (1976) postulated that heterosis hastens maturation. The results obtained in the present study support that conjecture. Still, Stewart and Martin (1981) observed no heterosis for maturation rate.

(Co)variance ratios

The estimate of direct heritability for MWT was 0.56 ± 0.03. This agrees with several published literature values, which were generally between 0.40 and 0.60 (DeNise and Brinks, 1985; Bullock et al., 1993; Meyer, 1995; Kaps et al., 1999). Heritability for the live weight of steers at 445 d of age in the same overall population (GPE cycle VII) was also reported to be near 0.50 (0.48 ± 0.15; Wheeler et al., 2005). Brown et al. (1972), however, estimated lower values in Hereford (0.34 ± 0.25) and Angus (0.21 ± 0.21) cattle for asymptotic MWT obtained from fitting the Brody function to weight-age data on cows at least 42 mo of age. Conversely, MacNeil (2005) reported a higher direct heritability (0.76 ± 0.02) in a composite population of Charolais, Red Angus, and Tarentaise cows for weights adjusted to 5 yr of age.

The direct heritability of *k* was 0.23 ± 0.03, which is similar to many literature values. DeNise and Brinks (1985) reported a heritability of 0.20 ± 0.26 in inbred and line-cross cattle, whereas Kaps et al. (2000) more recently reported a heritability of 0.31 in Angus cattle. Distinct from their estimate in Hereford cattle (0.33 ± 0.25), Brown et al. (1972) obtained a higher value for the direct heritability of *k* in Angus cattle (0.75 ± 0.33). Meyer (1995) estimated the rate of maturing in Australian cattle with the Gompertz growth curve. In cows with at least two weight records at 3 yr of age or older, heritability estimates were 0.32 in Hereford cattle and 0.28 in Wokalups cattle, a synthetic breed.

From the current study, the maternal heritability of *k* was 0.11 ± 0.02. To the authors' knowledge, few comparative estimates appear in the literature. Meyer (1995) reported that maternal heritability estimates for *k* were negligible in Hereford and Wokalups cattle, particularly when fitting an animal model including both maternal additive and permanent environmental effects. In the current study, the model without the permanent environmental effect provided a better fit.

Direct additive effects of MWT and *k* were positively yet negligibly correlated (0.09 ± 0.09); their residual correlation, however, was negative (−0.40 ± 0.04). Substantial (greater than −0.5) negative genetic and residual correlations between asymptotic weight and *k*, however, were reported in the literature (Brown et al., 1972, 1976; DeNise and Brinks, 1985; Meyer, 1995), suggesting cows with heavier weights at maturity reach that weight more slowly. Still, Brown et al. (1976) argued that there was sufficient independence among these parameters in different breeds that this negative genetic correlation between mature weight and *k*, which they considered antagonistic, could be partially overcome through strategic crossbreeding systems.

Breed effects

Given the lack of published MWT EPD, breed solutions were adjusted using YWT EPD to account for sire sampling in the USMARC herd. Daughter MWT was regressed on sire YWT EPD as part of this correction.

Based on the adjusted breed solutions, Angus was heaviest at maturity of the 16 breeds compared. Deviations from Angus ranged from −8.9 kg (Charolais) to −136.7 kg (Braunvieh). Ordered by decreasing MWT, the breeds ranked Angus, Charolais, Hereford, Brahman, Salers, Santa Gertrudis, Simmental, Maine Anjou, Limousin, Red Angus, Brangus, Chiangus, Shorthorn, Gelbvieh, Beefmaster, and Braunvieh. Still, the solutions for these direct breed effects for MWT were similar for many of the breeds.

In cycle I of the GPE Program, Arango et al. (2002a) reported breed of sire differences (relative to the average of Angus and Hereford) in cow BW at 6 yr of age of −61.9, 18.8, 17.7, 25.2, and 58.3 kg for F_1 cows sired by Jersey, South Devon, Limousin, Simmental, and Charolais bulls, respectively, that were born from 1970 to 1972. In cycle II of the GPE Program, Arango et al. (2002b) reported breed of sire differences (relative to the average of Angus and Hereford) in cow BW at 6 yr of age of 2.0, 21.7, 55.4, 64.7, and −18.3 kg for F_1 cows sired by Braunvieh, Gelbvieh, Chianina, Maine Anjou, and Red Poll bulls, respectively, that were born in 1973 and 1974. Dams of both the cycle I and cycle II cows were Angus and Hereford cows. The estimates of breed effects in the current study represent a substantial change in rank between the British (Angus and Hereford) and Continental (Charolais, Simmental, Limousin, Gelbvieh, Braunvieh, and Maine Anjou) breeds that were represented in both the present comparison and either cycle I or cycle II; estimated MWT of the British breeds was similar or greater than those of Continental breeds. These changes are not surprising given the emphasis on selection for growth based on breed genetic trends.

Conclusions

The incorporation of breed effects for MWT in decision-making in crossbreeding programs undoubtedly will depend on individual goals of producers. Beef cattle in the United States are managed across vastly different environments; the optimal size for a mature breeding cow in a beef operation will vary based on the operation's unique environment, management style, breeding objective, and resource availability. No universal recommendations can be offered regarding the favorability of using breeds with larger to smaller MWT. Given the similarity in the estimates of some of the breed effects, there might exist a greater opportunity to change MWT through within breed selection as opposed to breed choice depending on the breeds being considered. For most breeds considered in this study, opportunities to moderate MWT though breed complementarity appear limited. Still, whether an operation's goal is to increase, maintain, or decrease MWT, the information presented can improve the efficacy of breed choice.

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Conflict of interest statement

The authors declare that there is no conflict of interest regarding the publication of this article.

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