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André Mauric F. Ribeiro

Leticia P. Sanglard

Warren M. Snelling

R. Mark Thallman

Larry A. Kuehn

See next page for additional authors

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Authors

André Mauric F. Ribeiro, Leticia P. Sanglard, Warren M. Snelling, R. Mark Thallman, Larry A. Kuehn, and Matthew L. Spangler

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Genetic parameters, heterosis, and breed effects for body condition score and mature cow weight in beef cattle

André Mauric F. Ribeiro,[†,‡] Leticia P. Sanglard,[†] Warren M. Snelling,[‖] R. Mark Thallman,[‖] Larry A. Kuehn,[‖] and Matthew L. Spangler[†,1]

[†]Department of Animal Science, University of Nebraska, Lincoln, NE 68583, USA
[‡]Cargill Animal Nutrition, Campinas, SP 13091-611, Brazil
[‖]USDA, ARS, Roman L Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933, USA

André Mauric F. Ribeiro and Leticia P. Sanglard contributed equally to this manuscript.
[1]Corresponding author: mspangler2@unl.edu

Abstract

Understanding the genetic relationship between mature cow weight (**MWT**) and body condition score (**BCS**) is useful to implement selection programs focused on cow efficiency. The objectives of this study were to estimate genetic parameters, heterosis, and breed effects for MWT and BCS. In total, 25,035 and 24,522 overlapping records were available for MWT and BCS on 6,138 and 6,131 cows, respectively, from the Germplasm Evaluation program, a crossbred beef population at the U.S. Meat Animal Research Center. Pedigree was available for 48,013 individuals. Univariate animal models were used to estimate heritabilities for each trait by parity. Bivariate animal models were used to estimate genetic correlations between parities within a trait and between traits within parities. Bivariate repeatability animal models were used to estimate genetic correlations between traits across parities. Estimates of heritability for different parities ranged from 0.43 ± 0.05 to 0.55 ± 0.07 for MWT and from 0.12 ± 0.03 to 0.25 ± 0.04 for BCS and were lower with the repeatability model at 0.40 ± 0.02 and 0.11 ± 0.01 for MWT and BCS, respectively. Estimates of repeatability were high for MWT (0.67 ± 0.005) and low for BCS (0.22 ± 0.006). Estimates of genetic correlation for MWT and BCS between parities were, in general, high, especially between consecutive parities. Estimates of genetic correlation between MWT and BCS were positive and moderate, ranging from 0.32 ± 0.09 to 0.68 ± 0.14. The direct heterosis estimates were 21.56 ± 3.53 kg ($P \leq 0.001$) for MWT and 0.095 ± 0.034 ($P \leq 0.001$) for BCS. Ordered by decreasing MWT, the breeds ranked Brahman, Charolais, Angus, Simmental, Salers, Hereford, Santa Gertrudis, Chiangus, Brangus, Red Angus, Shorthorn, Maine-Anjou, Gelbvieh, Beefmaster, Limousin, and Braunvieh. Ordered by decreasing BCS, the breeds ranked Brahman, Red Angus, Charolais, Angus, Hereford, Brangus, Beefmaster, Chiangus, Salers, Simmental, Maine-Anjou, Limousin, Santa Gertrudis, Shorthorn, Gelbvieh, and Braunvieh. Estimates of breed differences for MWT were also adjusted for BCS (**AMWT**), and in general, AMWT depicted smaller differences between breeds with some degree of re-ranking ($r = 0.59$). These results suggest that MWT and BCS are at least moderately genetically correlated and that they would respond favorably to selection. Estimates of breed differences and heterotic effects could be used to parameterize multibreed genetic evaluations for indicators of cow maintenance energy requirements.

Lay Summary

The current study estimated the genetic relationship between mature cow weight (**MWT**) and body condition score (**BCS**), heterosis, and breed effects for these traits in a crossbred beef population. In total, 25,035 and 24,522 overlapping records were available for MWT and BCS, respectively. Pedigree was available for 48,013 individuals. Heritability and genetic correlations were estimated within a trait between parities, between traits within parities, and between traits across parities. Estimates of heritability ranged from 0.40 ± 0.02 to 0.55 ± 0.07 for MWT and from 0.11 ± 0.01 to 0.25 ± 0.04 for BCS. Genetic correlations within a trait and between parities were, in general, high. Estimates of genetic correlation between MWT and BCS were positive and moderate, ranging from 0.32 ± 0.09 to 0.68 ± 0.14. Heterosis effects were 21.56 ± 3.53 kg for MWT and 0.095 ± 0.034 for BCS. For both traits, Brahman and Braunvieh were associated with the highest and lowest breed effects, respectively. These results suggest that MWT and BCS would respond favorably to selection and are moderately genetically correlated. Breed differences and heterotic effects could be used to parameterize multibreed genetic evaluations for indicators of cow maintenance energy requirements.

Key words: beef cattle, body condition score, breed effects, genetic parameters, heterosis, mature weight

Abbreviations: AI, artificial insemination; AMWT, adjusted mature cow weight; BCS, body condition score; EBV, estimated breeding values; GPE, germplasm evaluation; h^2, heritability; MWT, mature cow weight; USMARC, U.S. Meat Animal Research Center

Introduction

Mature cow weight (**MWT**) and body condition score (**BCS**) are important components to be considered in breeding objectives as indicators of cow efficiency and to obtain a balance between greater early growth and moderate to lower MWT. MWT is an indicator of maintenance energy requirements that are associated with a substantial fraction of production costs in a cowherd operation (MacNeil and Mott, 2000). On average, heavier cows require more energy and thus greater feed consumption to maintain their body condition while conducting basal activities, such as grazing, walking, ruminating, and breathing (Bir et al., 2018). However, although not

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being directly selected on in genetic programs, MWT has been increasing over the years (Beck et al., 2017). This change is because MWT has a positive genetic correlation with early growth traits (e.g., weaning weight and yearling weight), which have been under direct selection pressure (Hickson and Pitchford, 2021). Moreover, MWT is influenced by BCS, which is associated with muscle mass and fat deposition (Marlowe and Morrow, 1985). Thus, cows with similar MWT may have different maintenance energy requirements. Previous studies have suggested adjusting MWT for BCS by including BCS as a linear covariate in the model (Gregory et al., 1992; Arango et al., 2002a; Nephawe et al., 2004). However, this adjustment may lead to a loss of information given that MWT and BCS are genetically correlated (Arango et al., 2002a; Silveira et al., 2015). Therefore, understanding the genetic relationship between these traits would be useful to implement optimal selection programs for cow efficiency. Crossbreeding has been shown to be an efficient approach to improve productivity in beef cattle. The use of crossbreeding has two major advantages: heterosis or hybrid vigor, which is the superiority of crossbred animals compared with the performance average of the parents, and breed complementarity, which is the advantage derived from breeding cows that excel in cow productivity traits (including small size) and are adapted to their environment to sires that excel in terminal traits, including high growth rate (Weaber, 2021). Nonetheless, heterosis is not uniformly advantageous; heterosis for MWT increases production costs assuming a proportional increase in energy requirements. Using a crossbred beef population comprising the Germplasm Evaluation (**GPE**) project from the U.S. Meat Animal Research Center (**USMARC**), previous reports have presented breed differences and heterosis across generations for birth, weaning, yearling weights, MWT, and calving difficulty (Schiermiester et al., 2015; Ahlberg et al., 2016; Zimmermann et al., 2021). However, there are no recent estimates of breed effects and heterosis for BCS for beef cattle in the literature and, more specifically, for the GPE project. Assessing breed effects for traits of interest allow the comparison of estimated breeding values (**EBV**) across breeds and provide additional information for selecting breeds for a crossbreeding system (Weaber, 2021). Thus, the objectives of this study were to estimate genetic parameters for MWT and BCS and assess heterosis and breed effects for BCS and MWT in a structured crossbred population.

Material and Methods

Animals

All methods and animal care described in this study followed the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 2010) and were approved by the USMARC Animal Care and Use Committee.

Animals used in this study were from the USMARC GPE program, as described by previous studies (Schiermiester et al., 2015; Ahlberg et al., 2016; Zimmermann et al., 2019). Cows were born between 1999 and 2018, with a maximum age of 14 yr. Most cows were sired through artificial insemination (**AI**) by bulls sampled to be highly representative of the following breeds: Angus, Beefmaster, Brahman, Brangus, Braunvieh, Charolais, Chianina, Gelbvieh, Hereford, Limousin, Maine-Anjou, Red Angus, Salers, Santa Gertrudis, Shorthorn, and Simmental. The remaining cows were sired through natural service by bulls raised at USMARC and sired by the above AI sires. The USMARC base cows were populations of Angus, Hereford, Charolais, Simmental, Red Angus × Simmental, MARC II (¼ Simmental, ¼ Hereford, ¼ Angus, and ¼ Gelbvieh), and MARC III (¼ Angus, ¼ Hereford, ¼ Pinzgauer, and ¼ Red Poll) and were considered as separate genetic groups from the AI sires to account for differences in genetic means. Only the AI sire genetic groups were reported as breed effects because the base cows do not represent recent samples of their respective breeds. Genetic group fractions were determined based on pedigree information and fitted as covariates in the mixed models described in the later section for the estimation of genetic group effects.

Breed heterozygosity was calculated as one minus the sum of the products of breed fractions of the sire and dam. For estimation 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 as described by Schiermiester et al. (2015), and composite breeds were characterized according to their nominal breed composition. For estimation of heterosis, composite breeds were assumed to consist of founder breeds as follows: 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 ($^1/_5$ Chianina and $^4/_5$ Angus), and Red Angus × Simmental (½ Red Angus and ½ Simmental).

Data

Complete details of data collection and management are reported by Zimmermann et al. (2019). In brief, cows were exposed to breeding annually, and MWT and BCS records used in the current study were collected at palpation to determine pregnancy status following breeding. Cows from cycle VII (Cushman et al., 2007) used for this project were born in spring calving seasons between 1999 and 2008. Cows from the continuous sampling phase of GPE were born in spring and fall calving seasons between 2007 and 2018. BCS was determined based on a subjective classification scale of nine points (1 being severely emaciated and 9 extremely obese) based on the Guidelines for Uniform Beef Improvement Programs (BIF, USDA, 1996). Data were edited such that nonpregnant cows were removed and parities greater than 8 (~9 yr of age) were removed. In total, 25,035 and 24,522 overlapping records were available for MWT and BCS on 6,138 and 6,131 cows, respectively. The distributions and summary statistics of the data can be seen in Figure 1. Pedigree from the GPE project was available for 48,013 individuals from 7 generations.

Statistical analyses

Heritability (**h²**) was estimated from univariate models for MWT and BCS for each parity separately or by using a repeatability model. Bivariate models were fitted to obtain the genetic correlations between parities within a trait, between traits within parities, and between traits using a repeatability model. Fixed effects included contemporary group (combination of birth year and season; $n = 31$), and heterosis, age in days, and breed composition fitted as covariates. Random effects included residuals and additive direct genetic effects with (co)variance proportional to the numerator relationship matrix. For the repeatability models, the fixed effect of parity (1–8) and random effect of permanent environment were added to the model to account for repeated records.

Analyses were performed in ASReml version 4 (Gilmour et al., 2015).

Adjustment of MWT for BCS

Breed effects for mature weight are reported both unadjusted (MWT) and adjusted for BCS (**AMWT**). This adjustment was performed using the genetic regression of MWT on BCS, that is, the genetic covariance between these traits divided by the genetic variance of BCS. The product of the breed effect estimates for BCS and the genetic regression was subtracted from the breed effect estimate for MWT to yield the breed effect estimate for AMWT. This removed genetic variance due to BCS from MWT such that AMWT is genetically independent of BCS.

Results

Genetic parameters for MWT and BCS

Univariate estimates (Table 1) of h^2 for MWT ranged from 0.43 ± 0.05 (Parity 6) to 0.55 ± 0.07 (Parity 8) and were greater than for BCS, which ranged from 0.13 ± 0.07 (Parity 8) to 0.25 ± 0.04 (Parity 5). Estimates of h^2 based on repeatability models were slightly lower for both traits: 0.40 ± 0.02 and 0.11 ± 0.01 for MWT and BCS, respectively. Estimates of repeatability were high for MWT (0.67 ± 0.005) and low for BCS (0.22 ± 0.006), similar to those obtained from the bivariate repeatability model (0.69 and 0.22, respectively).

Estimates of genetic correlation (Table 2) for MWT between parities were, in general, high (>0.81), particularly between consecutive parities. For BCS, the estimates of genetic correlation were lower than for MWT, ranging from 0.35 ± 0.11 (between parities 1 and 5) to 0.98 ± 0.19 (between parities 4 and 7). Estimates of genetic correlation between MWT and BCS (Table 3) were positive and moderate, ranging from 0.32 ± 0.09 (Parity 3) to 0.68 ± 0.14 (Parity 8). From the repeatability model, the estimate of genetic correlation of MWT with BCS was 0.43 ± 0.04. The estimates of permanent environmental and residual correlations were 0.85 ± 0.03 and 0.50 ± 0.005, respectively. The permanent environmental variances were 2,627.8 ± 165.0 kg^2 and 0.07 ± 0.007 and residual variances were 3,023.1 ± 27.9 kg^2 and 0.53 ± 0.005 for MWT and BCS, respectively.

Heterosis and breed effects

The direct heterosis estimates were 0.095 ± 0.034 ($P \le 0.001$) for BCS and 21.56 ± 3.53 kg ($P \le 0.001$) for MWT. Breed effects based on the bivariate repeatability model for 16 breeds

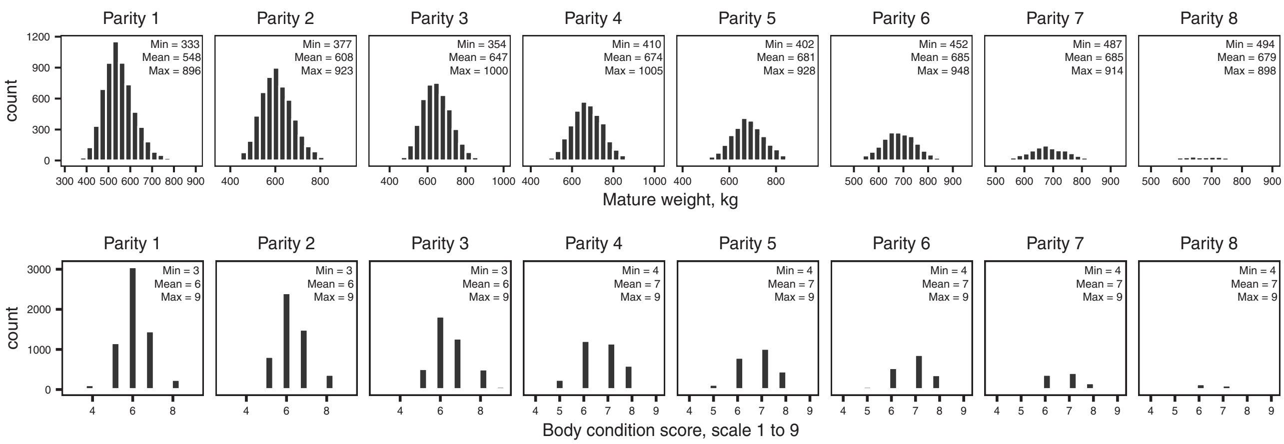

Figure 1. Histograms and statistical summary (minimum, min; mean; and maximum, max) for MWT (kg) and BCS (1–9) by parity.

Table 1. Genetic parameters estimates (standard errors in parentheses) for MWT (kg) and BCS (1–9) by parity and using univariate parity-specific and repeatability models

	Mature cow weight, kg			Body condition score		
	Heritability	Genetic variance	Residual variance	Heritability	Genetic variance	Residual variance
Parity 1	0.47 (0.03)	1,463.12 (97.02)	1,637.43 (74.19)	0.15 (0.02)	0.08 (0.01)	0.43 (0.01)
Parity 2	0.48 (0.03)	1,812.41 (124.99)	1,961.58 (95.59)	0.14 (0.03)	0.08 (0.01)	0.49 (0.02)
Parity 3	0.52 (0.03)	2,102.72 (147.83)	1,938.95 (110.86)	0.12 (0.03)	0.07 (0.01)	0.51 (0.02)
Parity 4	0.44 (0.04)	1,911.58 (185.23)	2,436.03 (155.48)	0.13 (0.04)	0.08 (0.02)	0.52 (0.02)
Parity 5	0.50 (0.04)	2,100.66 (199.57)	2,075.97 (160.21)	0.25 (0.04)	0.14 (0.03)	0.42 (0.02)
Parity 6	0.43 (0.05)	1,779.08 (230.64)	2,366.08 (198.38)	0.31 (0.05)	0.17 (0.03)	0.39 (0.03)
Parity 7	0.50 (0.06)	1,891.63 (255.33)	1,920.22 (214.59)	0.16 (0.05)	0.09 (0.03)	0.49 (0.03)
Parity 8	0.55 (0.07)	2,191.19 (339.07)	1,827.02 (284.55)	0.13 (0.07)	0.07 (0.04)	0.49 (0.04)
Repeatability[1]	0.40 (0.02)	1,230.95 (83.79)	1,472.22 (15.13)	0.11 (0.01)	0.07 (0.01)	0.52 (<0.01)

[1]Estimates of permanent environment variance were 1,191.94 (74.82) and 0.075 (0.0068) for MWT and BCS, respectively. Estimates of repeatability were 0.68 and 0.22 for MWT and BCS, respectively.

Table 2. Genetic correlations[1] (standard errors in parentheses) between parities within traits of MWT (upper diagonal) and BCS (lower diagonal)

	Parity 1	Parity 2	Parity 3	Parity 4	Parity 5	Parity 6	Parity 7	Parity 8
Parity 1		0.99 (0.01)	0.97 (0.01)	0.97 (0.02)	0.82 (0.03)	0.88 (0.03)	0.88 (0.03)	0.81 (0.04)
Parity 2	0.90 (0.08)		0.99 (0.01)	0.99 (0.01)	0.87 (0.02)	0.89 (0.03)	0.92 (0.03)	0.88 (0.04)
Parity 3	0.89 (0.10)	0.82 (0.09)		0.99 (0.01)	0.89 (0.02)	0.95 (0.02)	0.94 (0.02)	0.89 (0.03)
Parity 4	0.68 (0.13)	0.89 (0.13)	0.77 (0.11)		0.99 (0.02)	0.94 (0.03)	0.99 (0.03)	0.92 (0.04)
Parity 5	0.35 (0.11)	0.64 (0.13)	0.66 (0.12)	0.91 (0.11)		0.93 (0.02)	0.89 (0.03)	0.85 (0.04)
Parity 6	0.34 (0.11)	0.40 (0.13)	0.66 (0.13)	0.71 (0.15)	0.60 (0.11)		0.99 (0.02)	0.95 (0.03)
Parity 7	0.50 (0.15)	0.66 (0.17)	0.87 (0.17)	0.98 (0.19)	0.70 (0.16)	0.96 (0.16)		0.99 (0.02)
Parity 8	0.48 (0.19)	0.51 (0.25)	0.70 (0.24)	0.85 (0.25)	0.96 (0.34)	0.89 (0.16)	0.96 (0.28)	

[1]Estimated from bivariate analyses of pairs of parities within trait.

Table 3. Genetic correlations[1] (standard errors in parentheses) between MWT and BCS for each parity and using a repeatability model

	Genetic correlation
Parity 1	0.56 (0.07)
Parity 2	0.45 (0.08)
Parity 3	0.32 (0.09)
Parity 4	0.59 (0.14)
Parity 5	0.41 (0.10)
Parity 6	0.47 (0.11)
Parity 7	0.44 (0.15)
Parity 8	0.68 (0.14)
Repeatability	0.43 (0.04)

[1]Estimated from bivariate analyses of MWT and BCS within parity or with the repeatability model.

Table 4. Breed solutions[1] (standard errors in parentheses) from repeatability models for BCS (1–9), MWT (kg) and AMWT (kg)

Breeds	MWT	AMWT[2]	BCS
Angus	0	0	0
Red Angus	−21.7 (9.3)	−24.4 (8.2)	0.04 (0.08)
Beefmaster	−34.5 (11.7)	−25.8 (10.3)	−0.13 (0.10)
Brahman	9.5 (13.6)	4.2 (12.0)	0.08 (0.12)
Brangus	−20.4 (11.2)	−12.4 (9.9)	−0.12 (0.10)
Braunvieh	−88.3 (13.3)	−51.5 (11.8)	−0.55 (0.11)
Charolais	6.5 (9.2)	6.5 (8.1)	0.004 (0.08)
Chiangus	−15.0 (12.0)	−3.6 (10.6)	−0.17 (0.10)
Gelbvieh	−32.3 (9.3)	3.2 (8.2)	−0.53 (0.08)
Hereford	−13.8 (8.7)	−6.5 (7.6)	−0.11 (0.07)
Limousin	−34.6 (9.2)	−7.9 (8.1)	−0.40 (0.07)
Maine-Anjou	−28.4 (11.8)	−9.0 (10.4)	−0.29 (0.10)
Salers	−9.1 (12.7)	4.3 (11.2)	−0.20 (0.10)
Santa Gertrudis	−15.0 (12.5)	12.4 (11.1)	−0.41 (0.10)
Shorthorn	−22.6 (11.2)	10.9 (9.9)	−0.50 (0.09)
Simmental	−7.7 (8.9)	7.0 (7.8)	−0.22 (0.07)

[1]Using Angus as reference; from bivariate model with mature weight.
[2]Calculated as:
Breed solution for MWT-Breed solution for BCS$*\frac{\text{genetic covariance}_{\text{MWT, BCS}}}{\text{genetic variance}_{\text{BCS}}}$. The genetic regression to adjust MWT was 147.4.

evaluated in the GPE program at the USMARC for BCS are expressed as deviations from Angus (Table 4). Currently, EBV for BCS are not published by U.S. beef breed organizations and few such organizations report EBV for MWT. Therefore, the breed effects reported herein are not corrected for any inherent differences between the bulls sampled and used via AI and their respective breed mean genetic values. Breed effects using a different model for MWT have been recently reported by Zimmermann et al. (2021). The Pearson correlation between their solutions and those reported herein was 0.92. Brahman, Charolais, and Angus were associated with greater MWT and BCS. Brangus, Chiangus, Hereford, Salers, and Simmental had similar intermediate estimates for MWT and BCS. Braunvieh, Gelbvieh, and Limousin had similar lower estimates for MWT and BCS. After adjusting MWT such that AMWT is genetically independent of BCS, Santa Gertrudis and Shorthorn were associated with greater AMWT, followed by Simmental and Charolais. Red Angus, Beefmaster, and Braunvieh had the lowest estimates.

Discussion

One of the main costs in a cowherd operation is feed expenses, mainly used for maintenance requirements of a mature cow (MacNeil and Mott, 2000; Ramsey et al., 2005). Thus, selecting cows with lower energy maintenance will increase herd profitability. Collecting data directly related to energy requirements such as individual feed intake and calorimetry data is expensive, time-consuming, and not practical in extensive production settings. Instead, having an indicator trait such as MWT would be more feasible. Maintenance energy requirements based on MWT are more properly estimated when body condition is considered because individuals with similar MWT, but different muscle mass and fat deposition will most likely have different requirements. Given MWT and BCS are genetically correlated, including BCS as a covariate to adjust MWT will reduce the additive genetic variation associated with MWT and result in a trait with a different interpretation than MWT. Therefore, in this study, we estimated the genetic relationship between MWT and BCS to investigate the possibility of joint genetic evaluation to enable selection for reduced maintenance energy of cows.

Genetic parameters for MWT and BCS

The estimate of h^2 was high (>0.40) for MWT and moderate for BCS (<0.31) in all models analyzed. This indicates that both traits would respond to selection, although greater response would be expected for MWT. These estimates are in agreement with previous reports. Zimmermann et al. (2021), using a subset of the animals in the present analysis, reported a h^2 of 0.56 ± 0.03 for MWT at 6 yr of age predicted from growth curves. Other studies using animals from different ages and cycles of the GPE project have reported similar estimates of h^2 for MWT, ranging from 0.22 to 0.61 (MacNeil et al., 1984; Jenkins et al., 1991). Arango et al. (2002a), using animals from cycles I to IV ranging in age from 2 to 6 yr, reported a h^2 of 0.49 ± 0.04 and 0.16 ± 0.02 for MWT and BCS, respectively. Nephawe et al. (2004), using animals from cycles I to IV older than 4 yr of age, reported a h^2 of 0.52 ± 0.04 and 0.16 ± 0.02 for MWT (not adjusted for BCS) and BCS, respectively. Both studies (Arango et al., 2002a; Nephawe et al., 2004) also reported greater estimates of h^2 for MWT when BCS was fitted as covariate (i.e., adjusted MWT), of 0.57 ± 0.04 and 0.54 ± 0.04, respectively. When fitting BCS as a covariate, the authors observed a decrease in the permanent environment and phenotypic variances. Skeletal growth is nearly completed at 3 yr of age, and further increases in MWT are due primarily to muscle and fat deposition (Guilbert and Gregory, 1952) suggesting that indeed BCS contributes to phenotypic variation in MWT at advanced ages.

Similarly, estimates of repeatability were high for MWT (0.68) and moderate for BCS (0.22), indicating that MWT records from one parity are indicative of performance in subsequent parities. Conversely, for BCS, it may be advantageous to have multiple records. Arango et al. (2002a) and Nephawe et al. (2004) reported similar estimates of repeatability of 0.65–0.72 and 0.30–0.35 for MWT and BCS, respectively, using animals from the GPE project from cycles I to IV.

The high estimates of genetic correlation for MWT between parities indicate that this trait can be considered the same across parities. These results are also in accordance with previous reports of genetic correlations between ages and seasons. Arango et al. (2002a) reported estimates close to unity for genetic correlations between ages for MWT. Also correlating across ages, Rumph et al. (2000) reported genetic correlations greater than 0.86 between MWT at different ages (2–8 yr) in Hereford cows. For BCS, the genetic correlations were slightly lower when the parity differences increased similar to what was observed by Arango et al. (2002a) among ages. Mao et al. (2004), analyzing BCS across different parities, reported a similar pattern of high genetic correlation in consecutive parities with a small decrease between parities further apart. In general, the decrease in genetic correlation in the current study was greatest between earlier parities (1–2) and later parities (5–8). This may be due to more energy being directed to milk production in later parities compared with earlier parities when the animal may be still growing. Overall, there was a slight increase in the average BCS from parities 1 to 3 (average BCS of 6) to parities 4 to 8 (average BCS of 7). Mao et al. (2004) reported greater genetic variance estimates for BCS for parities 3 and greater compared with parities 1 and 2, while average BCS did not change between parities. These results indicate that genetic factors influencing BCS may change due to changes in repartition of energy for growth, maintenance, and production across different parities.

Increasing MWT is associated with increased feed costs attributed to cow energy requirements (Snelling et al., 2019). Previous studies have shown a positive genetic relationship between early growth traits (weaning weight and yearling weight) and MWT, likely contributing to an increase in MWT overtime (Schoeman, 1996). However, cows with similar MWT but different BCS may have different maintenance energy requirements due to differences in fat deposition. Estimates of genetic correlation between MWT and BCS were moderate and positive (0.43) and within the range reported in the literature, from 0.20 to 0.76 (Brinks et al., 1964; Marlowe and Morrow, 1985; Arango et al., 2002a), suggesting that although they are genetically correlated, it is possible to place direct selection pressure on these two traits in opposite directions.

Heterosis and breed effects

The significant positive effects of heterosis for MWT and BCS indicate that the use of crossbred animals contributes to an increase in MWT and BCS. The estimate of heterosis for MWT obtained from the current study (21.56 kg) was greater than that reported by Zimmermann et al. (2021) of 15.3 kg, but similar to previous reports ranging from 22 to 28 kg among Hereford, Angus, Brahman, and Shorthorn cross (Gregory et al., 1966; Stewart and Martin, 1981). Previous studies have reported that heterosis effects on MWT are partially due to heterosis effects on BCS and that adjusting MWT for BCS has resulted in a reduction of the heterosis effect on MWT by 23% (Gregory et al., 1992; Arango et al., 2002a).

Breed-of-sire effects for BCS, MWT, and AMWT of GPE cycles I–IV were reported by Arango et al. (2002a, 2002b, 2004), and Arango and Van Vleck (2002). Current estimates of breed differences are very different from the estimates resulting from sires sampled between 1969 and 1985. One reason for differences is that the current estimates are presented as breed differences while the earlier estimates were reported as breed-of-sire differences, which, by definition, are half of breed differences. Reporting breed-of-sire differences was an artifact of the experimental design used earlier in the GPE project. This difference is important to recognize but does not affect the breed rankings. The more important reason is the vast difference in selection pressure for growth and composition applied to the various breeds over the last several decades, resulted in different correlated responses in mature size and BCS. Additionally, a few breeds have developed estimated progeny differences that allow putting direct downward selection pressure on MWT to attenuate the correlated response, while most breeds have not.

Brahman cows were associated with greater MWT and BCS. This high breed effect is likely influenced by two factors: most of the Brahman cows were spring calving, and palpation in September (fall) was the time of year in which the previous seasonal effects were most favorable for Brahman compared with *Bos taurus* breeds; it is likely that Brahmans evaluated in March (spring) would have ranked lower. Additionally, there were no purebred Brahmans in the population; much of the Brahman breed effect came from F_1 cows expressing 100% breed heterozygosity, but the adjustment to remove heterosis from the breed effect was based on a pooled estimate of heterosis that is probably less than the heterosis between Brahman and *B. taurus*. This may have slightly inflated the Brahman estimate for MWT and BCS.

The largest differences in the breed effects were between Brahman and Braunvieh for both traits, of 97.8 kg and 0.63, respectively, with some breeds having very similar estimates. Given the similarity of breed effects within MWT and BCS, breeds could be generally classified into three major groups: Brahman, Charolais, and Angus with greater MWT and BCS; Brangus, Chiangus, Salers, and Maine-Anjou with intermediate; and Limousin, Gelbvieh, and Braunvieh with lower MWT and BCS. Simmental was associated with greater MWT but lower BCS. This could be due to the historical dual-purpose nature of this breed associated with late maturity which leads to an increased growth of leaner carcasses. Recently, Zimmermann et al. (2021) reported breed effects for predicted MWT at 6 yr of age. Given EBV for MWT are not widely available in the U.S. beef industry, the authors adjusted the breed effects for MWT based on EBV for yearling weight to account for the difference between the AI sires used and the average genetic value of their respective breed. The Pearson correlation between their estimates (both unadjusted and adjusted for differences in sire genetic merit) and estimates for MWT from the current study was high (0.92). Brahman, Charolais, Angus, and Hereford were among the top five breeds associated with greater MWT, and Shorthorn, Gelbvieh, and Braunvieh were among the bottom five breeds in all ranks.

In general, adjusting AMWT reduced the differences among breeds illustrating that breed differences in MWT are in part due to inherent differences in BCS. Arango et al. (2002b) reported minimal re-ranking among groups of breeds between unadjusted MWT and MWT adjusted for BCS by fitting BCS as a linear covariate. In the current study, the Spearman correlation between MWT and AMWT breed solutions was 0.59. Although moderate, breeds certainly re-rank due to the relatively large differences between some breeds for BCS. Estimates of AMWT are neither more nor less useful than estimates of MWT; they simply require different interpretation. Looking at estimates of MWT, AMWT, and BCS together and properly considering the differences in interpretation may produce deeper understanding of breed differences than looking at only two of the traits. Nonetheless, an economically optimized and properly weighted selection index that includes MWT and BCS with other traits should yield identical results to an economically optimized and properly weighted selection index that includes AMWT and BCS with the same other traits. Regardless of the choice of "trait" (MWT or AMWT), it is imperative that breed differences and genetic parameters for MWT and BCS are available to correctly form comprehensive selection indexes.

Conclusion

Estimates of heritability for both MWT and BCS suggest that both traits would respond favorably to selection. The moderate genetic correlation between them suggests that although selection for one could lead to a correlated increase in the other, it would be possible to place direct selection pressure on both traits to move them in divergent directions. Genetic correlations between parities suggest that although MWT could be considered the same trait across age, differences exist between parities for BCS. Similarly, estimates of repeatability were higher for MWT than for BCS and thus the collection of BCS records across ages would enhance the accuracy of genetic predictions for BCS more than for MWT. Heterotic effects were significant for both traits, and this knowledge coupled with breed differences would prove useful for implementing a multibreed genetic evaluation for improved cow maintenance energy requirements.

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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