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December 2002

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Arango, Jesus; Cundiff, Larry V.; and Van Vleck, L. Dale, "Genetic parameters for weight, weight adjusted for body condition score, height, and body condition score in beef cows" (2002). *Faculty Papers and Publications in Animal Science*. 232.

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Genetic parameters for weight, weight adjusted for body condition score, height, and body condition score in beef cows^{1,2}

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ABSTRACT: Weight (CW, n = 61,798), weight adjusted for condition score (WA), hip height (CH, n = 56,494), and condition score (CS, n = 61,434) of cows (2 through 8 yr of age) produced by crosses of 22 sire breeds with Angus and Hereford dams in the first four cycles of the Germplasm Evaluation (GPE) Program at the U.S. Meat Animal Research Center were used to estimate genetic parameters with REML. The model included sire breed, dam breed, age in years, season of measurement (1 to 4) and their interactions, and year of birth and pregnancy-lactation code (PL) as fixed effects for CW and CS. The model for CH excluded PL. Random effects were additive genetic and permanent environmental effects. Univariate analyses of all data, by season and by year of age, bivariate analyses be-

tween pairs of seasons and ages (2 to 6), and between traits were done. Estimates of heritability and repeatability over all ages were 0.49, 0.54, 0.68, and 0.16, and 0.65, 0.67, 0.75, and 0.30 for CW, WA, CH, and CS, respectively. Corresponding estimates for each age and season were similar for all traits and cycles. Estimates of genetic and permanent environmental correlations were close to unity for all pairs of seasons and traits. Genetic correlations were greater than 0.92 for all pairs of ages for CW, WA, and CH, and greater than 0.67 for CS. Genetic correlations were 0.80, 0.86, 0.43, and -0.04 for CW-CH, WA-CH, CW-CS, and CH-CS, respectively. Results suggest that repeatability models can be used to model weights and heights in this population.

Key Words: Genetic Correlation, Genetic Parameters, Growth, Heritability

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J. Anim. Sci. 2002. 80:3112–3122

Introduction

Beef cattle have a low rate of reproduction and high maternal cost per market animal. Therefore, two important components that determine efficiency are milk production and mature body weight of cows (Dickerson, 1970; McMorris and Wilton, 1986). Although most genetic evaluation programs of beef breeds report EPD for maternal ability for weaning weight, only one currently produces EPD for mature size (Wilson, 2000). The importance of body size to efficiency has led to defining variables associated with size, mass, and dimension (such as mature weight, mature height, and other body

measurements) to be included in selection programs and as breeding objectives in crossbreeding plans. Understanding of genetic and environmental factors affecting those variables is needed to implement optimal breeding and selection programs. Reliable estimates of genetic and phenotypic parameters of these size-related variables, as well as the relationships among them, are also needed. The goal of this study was to estimate genetic parameters from (co)variance components for cow weight, weight adjusted for condition score, height, and body condition score using repeatability and multivariate models. Previous U.S. Meat Animal Research Center-Germplasm Evaluation (MARC-GPE) reports have included parameter estimates for cow traits; however, there is not a study that includes data from all cycles and ages of cow for weight, height, and body condition score, and treats them with the same models and estimation methods. For instance, MacNeil et al. (1984) used the average of four measures of weight of 7-yr-old cows from Cycle I, whereas Jenkins et al. (1991) fitted the Brody function to data from Cycles I, II, and III to estimate total and within-breed heritability for asymptotic weight adjusted by body condition score. For Cycle IV, Thallman et al. (1999) reported REML

¹In memory of Dr. Gordon E. Dickerson.

²Published as paper no. 13556, Journal Ser., Nebraska Agric. Res. Div., Univ. of Nebraska, Lincoln 68583-0908.

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Received November 1, 2001.

Accepted July 25, 2002.

Table 1. Number of cows (and sires) by breed of sire for Cycles I to IV of the U.S. Meat Animal Research Center Germplasm Evaluation program

Breed of sire	Cycle I	Cycle II	Cycle III	Cycle IV	Total
	(1970 to 1972) ^a	(1973 to 1974)	(1975 to 1976)	(1986 to 1990)	
Hereford	121 (31)	86 (15)	68 (13)	169 (48)	444
Angus	123 (33)	92 (17)	30 (14)	164 (49)	409
Jersey	106 (32)				106
South Devon	109 (27)				109
Simmental	151 (27)				151
Limousin	148 (20)				148
Charolais	123 (26)			82 (32)	205
Red Poll		87 (16)			87
Braunvieh		127 (11)			127
Maine Anjou		86 (17)			86
Chianina		86 (19)			86
Gelbvieh		77 (11)		76 (16)	153
Brahman			101 (17)		101
Sahiwal			86 (6)		86
Pinzgauer			103 (9)	81 (15)	184
Tarentaise			80 (6)		80
Shorthorn				69 (22)	69
Galloway				70 (27)	70
Longhorn				81 (24)	81
Nellore				81 (22)	81
Piedmontese				83 (18)	83
Salers				86 (25)	86
Total	881 (196)	641 (106)	468 (65)	1,042 (298)	3,032

^aBirth years.

estimates of heritability for weight and hip height at 550 d in females.

Materials and Methods

Records from the first four cycles of the GPE program at the MARC were available for weights, heights and body condition scores of Angus and Hereford purebred (Cycles I, II, and IV) and crossbred (F₁) cows (all cycles). Crossbred cows were produced by mating Angus and Hereford dams to 22 breeds of sire. The breeds and number of cows by breed of sire, and the number of sires in each cycle, are presented in Table 1. Hereford-Angus reciprocal crosses were produced in each cycle of the program. Some Angus and Hereford sires used in Cycle I were repeated as reference sires in following cycles to provide genetic ties across all four cycles.

Cycle I began with the 1969 breeding season, with matings through AI of Hereford, Angus, Jersey, South Devon, Limousin, Simmental, and Charolais bulls to Hereford and Angus cows. Calves were born in March, April, and early May of 1970, 1971, and 1972. Cycle II included two calving seasons (1973 and 1974). Hereford and Angus cows from Cycle I were bred by AI to Hereford, Angus, Braunvieh (including four domestic Brown Swiss selected for "beef type" available from AI services, and seven imported Braunvieh sires from Switzerland), Red Poll, Maine Anjou, Gelbvieh, and Chianina bulls. Brown Swiss and Red Poll cows also were included to form a four-breed diallel crossbreeding experiment with Hereford and Angus. Cycle III was initiated with Angus

and Hereford cows from Cycles I and II during the 1974 breeding season bred by AI to Hereford, Angus, Pinzgauer, Tarentaise, Brahman, and Sahiwal sires to produce only F₁ calves in two calving seasons (1975 and 1976). Cycle IV extended over five calving seasons (1986 to 1990). Angus and Hereford cows were bred with semen from Hereford and Angus reference bulls, current Angus bulls (born 1982 to 1984), current Hereford bulls (born 1982 to 1984), Charolais, Galloway, Gelbvieh, Longhorn, Nellore, Piedmontese, Pinzgauer, Salers, and Shorthorn bulls. Detailed information about the design of the experiment is in MARC reports such as GPE (1980).

Calves were born in the spring (March to early May) each year. Males were castrated within 24 h after birth. Calves were allowed to suckle and graze with their dam, and were creep fed from mid-July or early August until weaning in early October at about 200 d of age. The F₁ females (Phase 2) in each cycle were retained to evaluate growth, age at puberty, reproduction, and maternal performance through mature ages. Heifers were managed to have their first calf at 2 yr of age. Details of postweaning management were presented by Laster et al. (1976, 1979) and Gregory et al. (1979) for Cycles I to III, and Cundiff et al. (1998) for Cycle IV. The first three cycles are summarized by Cundiff et al. (1986), Cycle IV is described by Cundiff et al. (1998) and Thallman et al. (1999), and all four are reported by Cundiff et al. (1993).

Cows were on improved pastures (April to November) of cool or summer mixtures of grass. During winter

Table 2. Number of records for weight, height, and body condition score by age (yr) and season of measurement for cows from Cycles I to IV

Age	Trait		
	Weight	Height	Condition score
2	12,011	9,089	11,691
3	11,848	10,063	11,838
4	11,518	10,923	11,507
5	10,638	10,638	10,622
6	9,435	9,434	9,430
7	5,332	5,331	5,330
8	1,016	1,016	1,016
Season			
1	15,785	14,011	15,763
2	14,783	13,011	14,771
3	15,649	14,737	15,641
4	15,581	14,735	15,259
Total	61,798	56,494	61,434
Mean (kg, cm, score) ^a	494 ± 80	128 ± 6	6.3 ± 1.0

^aUnadjusted means ± unadjusted standard deviation.

months (December to March), cows were maintained on grass and legume hay in Cycles I to III, and on corn silage and alfalfa hay in Cycle IV. The length of the breeding season was about 75 d with pregnancy diagnosed by palpation 60 to 75 d after the end of the breeding season. Cows were culled only if they failed to conceive in two successive years or for serious unsoundness (i.e., lameness, unsound udders, prolapse, cancer eye, emaciation). Cows were not culled on the basis of growth criteria. Yearling heifers were weighed at start and end of the mating season and when palpated for pregnancy in the fall. Thereafter, cows were weighed, measured for hip height, and scored for body condition four times each year. One measurement was taken during each season: 1) mid-May (spring), at the start of the breeding season; 2) the beginning of August (summer), at the end of the breeding season; 3) the end of October (fall), at palpation for pregnancy following weaning; and 4) the beginning of February (winter), prior to calving. Body condition score was on a subjective classification scale of nine points (Spitzer, 1986) from (1) extremely thin (emaciated) to (9) extremely fat (obese).

The number of records for each trait by age of cow and season of measurement are in Table 2. A total of 61,798 measurements of weight were available. As weight and condition score may be affected by physiological status of the cow, especially if the cow is rearing a calf or is pregnant, each record of a cow was assigned to one of four physiological codes corresponding to a combination of lactation status (1 = not lactating, 2 = lactating) and pregnancy status (1 = not pregnant, 2 = pregnant). The present study included only records of 24 mo or older cows with assigned physiological code. Original data included cows that were separated from the experiment to be sold or used in other studies. Some edits were needed to provide consistency of data within and across cycles. For Cycle I, records of cows up to 7 yr of age were used. For Cycle II, cows up to 8 yr of age

were included. For Cycle III, cows with records up to 6 yr of age were considered. For Cycle IV, 6 yr of age was the cut off point because limited data were available for older cows. Three birth years (1986, 1987, and 1988) had data until 6 yr of age, whereas cows born in 1989 and 1990 had records until 5 and 4 yr of age respectively. For Cycle-II crossbred cows from the diallel experiment with Red Poll and Brown Swiss dams were excluded. Heterosis and transmitted effects for weight, height, and condition score from that experiment were reported for 2- to 7-yr-old cows (Dearborn et al., 1987). Gregory and Maurer (1991) reported results for those traits at 30, 42, and 54 mo of age.

Data were analyzed by REML, using the MTDFREML programs (Boldman et al., 1995) including sire breed, dam breed, age, season, and their interactions and with year of birth and pregnancy-lactation code as fixed effects for weight and condition score. For height, pregnancy-lactation code was excluded from the previous model. Analyses of adjusted weight included condition score as a linear covariate. Random effects included additive genetic and permanent environmental effects of the cow. Maternal genetic effects were included in preliminary analyses, but were not important and were dropped from final models. Analyses assumed a repeatability model, with measurements across seasons (within age) or over ages considered to be unique traits with constant variances. Univariate analyses were also done for each season of measurement and age (yr). Bivariate models also were used considering measurements in different seasons and ages as different traits to estimate covariances among measurements within a particular age (across seasons within a year) and over ages. These analyses were also done separately for each cycle and using all data.

The equation for the linear model was:

$$y = X\beta + Z_a a + Z_c c + e$$

Table 3. Estimates and standard errors of variance components and parameters overall data for weight, weight adjusted for condition score, height and condition score of cows from Cycles I to IV^a

	Weight, kg	Adjusted weight, kg	Height, cm	Condition score
σ_p^2	2,297	2,094	16.2	0.84
h^2	0.49 \pm 0.04	0.54 \pm 0.04	0.68 \pm 0.04	0.16 \pm 0.02
c^2	0.16 \pm 0.04	0.13 \pm 0.04	0.07 \pm 0.04	0.14 \pm 0.02
e^2	0.35 \pm 0.01	0.34 \pm 0.01	0.25 \pm 0.01	0.70 \pm 0.01

^a σ_p^2 = phenotypic variance; h^2 = heritability; c^2 = fraction due to cow permanent environmental effect; e^2 = fraction due to temporary environmental effects.

where y is the vector of weights, heights, or condition scores; β is the vector of fixed effects; and a and c are vectors of random cow additive genetic and permanent environmental effects with incidence matrices X , Z_a , and Z_c , respectively, and e is the vector of residual effects. From the variance components, three parameters were defined: 1) heritability, $h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$; 2) fraction of permanent environmental variance, $c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$; and 3) fraction of temporary environmental variance, $e^2 = \sigma_e^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$. In addition repeatability (r) was defined as the sum of h^2 and c^2 .

For bivariate analyses, the model was:

$$y_1 = X_1\beta_1 + Z_{a1}a_1 + Z_{c1}c_1 + e_1$$

$$y_2 = X_2\beta_2 + Z_{a2}a_2 + Z_{c2}c_2 + e_2$$

where 1 and 2 represent different seasons or cow ages. Local convergence was declared when the variance of -2 times the log likelihood in the simplex was less than 10^{-8} . Restarts were done to increase the chance of finding a global maximum rather than a local maximum, with convergence declared when -2 times the log likelihood did not change to the third decimal place. When this rule was not met after 10 restarts for multivariate analyses, convergence was declared if the (co)variance estimates did not change after the second decimal point. Standard errors were computed with the "delta" method based on the average information matrix at convergence (e.g., Dudenhoff et al., 1998).

Results and Discussion

Univariate Analyses

Estimates of variance components for analyses, including all cycles, ages, and seasons, are presented in Table 3 for all the traits. Heritability estimates were high for cow weight (0.49), cow weight adjusted for condition score (0.54), and for cow height (0.68), but relatively low for cow body condition score (0.16). Corresponding estimates for the fractions of permanent environmental variance were 0.16, 0.13, 0.07, and 0.14, respectively. Repeatability estimates were 0.65, 0.66, 0.75, and 0.30, respectively. These results suggest that selection should be effective for mature weight and

height and that repeated records for cow weight and height may have little value. Condition score, however, had low heritability and moderate repeatability. With weight adjusted for body condition score, estimates of variance components did not change much. The phenotypic variance decreased by approximately 9%, the estimate of heritability increased by about the same magnitude, and the fraction of permanent environmental variability decreased approximately twice as much. Repeatability was similar (0.65 and 0.67) for both traits. Most of the difference in estimates of heritability between weight and weight adjusted for condition score seems to be explained by differences in variance of permanent environmental effects. Repeated records of weight may represent different environmental and physiological conditions affecting cow fatness that were not completely adjusted by fixed effects in the model but were better removed when weights were adjusted for condition score. Alternatively, since most of relationships were through sires, differences in heritability between the two models may represent direct genetic differences of sires for fatness and/or milking ability as expressed by differences in condition scores of their daughters. Similar results have been found in other studies (Meyer, 1995; Johnston et al., 1996).

MacNeil et al. (1984), with data from the GPE MARC, found estimates of heritability for weight of 0.54 using the average of four measures of weight of 7-yr-old cows from Cycle I. Jenkins et al. (1991), using the Brody function to fit data from Cycle I, II, and III cows, found estimates of total and within-breed heritability of 0.91 and 0.61, respectively, for asymptotic weight adjusted for body condition score and 0.94 and 0.71 for height. Their results suggested that growth patterns could be effectively changed by one generation of breed substitution. Further change could be accomplished by exploiting the intrapopulation additive genetic variation. For Cycle IV, Thallman et al. (1999) reported heritability estimates of 0.22 and 0.40 for weight and hip height at 550 d in females.

The overall estimate of heritability for cow weight in this study agrees with the extensive review of Koots et al. (1994), who reported a pooled estimate of heritability of 0.50 for mature weight from 25 studies. More recent estimates using ANOVA methods include: 0.52 from the average of seven bivariate analyses, using a modified

Henderson method with a sire-maternal grand sire model (Bullock et al., 1993). Estimates from REML of heritability for cow weight ranged from 0.49 to 0.68 according to a study involving Angus-Hereford reciprocal crosses in New Zealand (Morris et al., 1987). Northcutt and Wilson (1993) reported estimates of 0.48 from univariate analyses and of 0.45, 0.51, and 0.51 from bivariate analyses with birth, weaning, and 365-d weight, respectively, from 5- to 12-yr-old Angus cows. Meyer (1995) reported heritability estimates for cow weight in Australian Herefords and a composite breed (Wokalups) ranging from 0.30 to 0.59 depending on the breed and age.

Heritability estimates for cow weight adjusted for body condition score have ranged from 0.38 to 0.76 using ANOVA based methods (e.g., Morrow and Marlowe, 1966; Choy et al., 1996, 1998b) and from 0.45 to 0.79 with REML (Northcutt and Wilson, 1993; Johnston et al., 1996; Wilson, 2000). Predicted asymptotic mature weight and mature weight represent the same genetic trait as shown by Meyer (1995), who found a genetic correlation of 0.99 between them in Australian Hereford and Wokalups.

Estimates of repeatability for cow weight have been between 0.45 and 0.88 using least squares and the paternal half-sib (PHS) method (e.g., Brinks et al., 1962; Fitzhugh et al., 1967; Williams et al., 1979; Field et al., 1988) and between 0.57 and 0.85 using REML (Morris et al., 1987; Meyer, 1995; Johnston et al., 1996).

Cow height was more heritable ($h^2 = 0.68$) and repeatable ($r = 0.75$) than cow weight (Table 3), which agrees with the few previous reports. Estimates of heritability for cow height using ANOVA methods have ranged from 0.54 to 0.75 in Angus, Hereford, and crossbred cows (Brown and Franks, 1964; Neville et al., 1978; Choy et al., 1996, 1998a,b). Estimates of repeatability have ranged from 0.78 to 0.82 (Choy et al., 1996, 1998a,b). Estimates by REML of heritability from field records (Angus) were 0.83 and 0.85 from bivariate analyses with weight and weight adjusted for condition score (Northcutt and Wilson, 1993; Wilson, 2000). Meyer (1995) reported estimates of heritability (0.19 to 0.50) that were less than those reported here; however, the corresponding repeatability estimates (0.73 to 0.83) were similar to the estimate from this study (0.75).

Cow body condition score had the lowest heritability (0.16) and repeatability estimates (0.30) of the traits in the present study (Table 3). Previous estimates using ANOVA methods have ranged from 0.13 to 0.51 (e.g., Brinks et al., 1964; Marlowe and Morrow, 1985; Choy et al., 1996, 1998a,b) for heritability, whereas repeatability estimates have varied from 0.34 to 0.85 (Benyshek and Marlowe, 1973; Williams et al., 1979; Choy et al., 1996, 1998a,b). Meyer (1995), using REML, reported estimates of heritability ranging from 0.12 to 0.16, and of repeatability from 0.20 to 0.25, depending on breed (Hereford or Wokalups) and ages included in the analyses. Johnston et al. (1996) obtained estimates of heritabilities of 0.21, 0.14, and 0.17 and repeatabilit-

ies of 0.32, 0.52, and 0.41 for Angus, Hereford and Polled Hereford cows ($n = 7,536$) included in the Australian BREEDPLAN.

Estimates of variance components by season of measurement are presented in Table 4. Means and phenotypic variances changed among seasons for the two traits related with cow weight, as well as for condition score, which was expected because seasons represent not only different climate and environmental conditions (especially nutritional level), but also different physiological status of the cows, particularly regarding pregnancy and lactation, which may affect fat deposition. Cows were heavier and had better condition scores in summer and fall, as expected. Height did not change across seasons, as anticipated for a skeletal trait in adult animals. Heritability estimates followed the overall age results (Table 3) and were similar across seasons. Estimates of heritabilities were slightly higher for cow weight than for cow weight adjusted for condition score. Heritability estimates for spring (at calving) and fall (at weaning) weights have been reported to be similar using the PHS method (Brinks et al., 1962, 1964; Fitzhugh et al., 1967). Morris et al. (1987) compared REML estimates of heritability of weight taken four times during the year of Angus-Hereford reciprocal crosses in New Zealand. Heritability estimates (0.49 to 0.60) and their differences among seasons were similar to the estimates found in the present study.

Estimates of variance components by age of cow are presented in Table 5. Estimates of phenotypic variances for weight increased with age, suggesting that age accounted for a systematic increase in size. Coefficients of variation were much lower for height (~3%) than for weight (~9%). Phenotypic variances did not change much, and tended to decrease at later ages for height in agreement with previous research. Brown et al. (1956a,b) indicated that skeletal growth was nearly completed at 3 yr of age and that further increases in weight were due primarily to increases in muscle and fat deposition. Phenotypic variances for condition score were similar over the range of 2 to 8 yr of age. With cow weight adjusted for condition score, phenotypic variance relative to cow weight unadjusted for condition score decreased with increase in age, by 11.5% at 2 yr to 26.5% at 8 yr. Heritability estimates tended to increase from 2 to 5 yr of age, then decreased until 7 yr, and increased again at 8 yr of age for weight, adjusted weight, and height. However, the estimates did not show a significant trend across ages, ranging from 0.47 to 0.58, 0.51 to 0.63, and 0.59 to 0.72, respectively. Heritability estimates for condition score were about 0.20 for all ages, except for an estimate of 0.51 for 8-yr-old cows, which may be due to the limited number of cows.

Gregory et al. (1995) reported heritability estimates by age (2- to 5-yr-old) for nine pure breeds and three generations (F_1 , F_2 , and F_3) of composite cows from the Germplasm Utilization program at MARC and concluded that estimates of heritability for cow weight

Table 4. Estimates of variance components and parameters for weight, weight adjusted for body condition score, height, and condition score by season for measurement for cows from Cycles I to IV^a

	Season			
	Spring (1)	Summer (2)	Fall (3)	Winter (4)
Weight (kg)				
σ_p^2	2,140	2,090	2,654	2,156
h^2	0.57 ± 0.06	0.61 ± 0.05	0.49 ± 0.04	0.55 ± 0.04
c^2	0.17 ± 0.04	0.20 ± 0.05	0.21 ± 0.04	0.11 ± 0.04
e^2	0.26 ± 0.01	0.19 ± 0.01	0.29 ± 0.01	0.34 ± 0.01
Adjusted weight (kg)				
σ_p^2	2,199	2,250	2,846	2,150
h^2	0.54 ± 0.04	0.56 ± 0.05	0.45 ± 0.04	0.51 ± 0.04
c^2	0.12 ± 0.04	0.19 ± 0.04	0.17 ± 0.04	0.05 ± 0.03
e^2	0.35 ± 0.01	0.24 ± 0.01	0.37 ± 0.01	0.44 ± 0.01
Mean ^b	472.1 \pm 78.6	499.2 \pm 77.4	508.3 \pm 75.4	496.8 \pm 85.4
Height (cm)				
σ_p^2	15.8	15.8	15.9	16.5
h^2	0.68 ± 0.04	0.71 ± 0.05	0.72 ± 0.05	0.65 ± 0.04
c^2	0.05 ± 0.04	0.07 ± 0.04	0.06 ± 0.04	0.04 ± 0.04
e^2	0.27 ± 0.01	0.22 ± 0.01	0.22 ± 0.01	0.30 ± 0.01
Mean ^b	127.3 \pm 6.4	127.8 \pm 6.2	127.9 \pm 6.2	127.6 \pm 6.6
Condition score				
σ_p^2	0.81	0.76	0.88	0.85
h^2	0.19 ± 0.02	0.16 ± 0.02	0.17 ± 0.02	0.15 ± 0.02
c^2	0.09 ± 0.02	0.15 ± 0.02	0.11 ± 0.02	0.06 ± 0.02
e^2	0.72 ± 0.01	0.70 ± 0.01	0.72 ± 0.01	0.79 ± 0.01
Mean ^b	6.1 \pm 0.98	6.4 \pm 0.99	6.4 \pm 1.06	6.3 \pm 1.03

^a σ_p^2 =phenotypic variance; h^2 =heritability; c^2 =fraction of total variance due to cow permanent environmental effects; e^2 =fraction of total variance due to temporary environmental effects.

^bUnadjusted mean; mean for weight and weight adjusted for condition score are the same.

were “remarkably similar at all ages,” as was also the case for cow height and cow body condition score, except for 5-yr-old cows that had the lowest heritability estimates of 0.27 and 0.29, respectively. Data from 2,906 Hereford cows resulted in heritability estimates of 0.87, 0.69, 0.66, 0.68, and 0.54 for females aged 2, 3, 4, 5, and 6+ yr, and was 0.60 over all ages (Field et al., 1988). Estimates of heritability by age of cow using REML were presented by Meyer (1995) for Australian Hereford and Wokalups (a synthetic breed) grouped by age (3+, 4+, and 5+ yr). Estimates for weight and weight adjusted for condition score were virtually the same for the 4+ and 5+ groups, but estimates were different for the 3+ group, indicating that 3-yr-old records could not be considered to be mature weights. Estimates for condition score were similar for the age subgroups. Estimates for cow height did not differ between data sets, indicating it to be an earlier maturing trait than weight (Meyer, 1995), as found in the present study.

In general, estimates of heritability and repeatability from the present study agree with previous reports. Cow weight and height had intermediate to large estimates, whereas estimates for body condition score were low to intermediate.

Bivariate Analyses

Results for bivariate analyses are summarized in Tables 6 to 10. Many correlations were close to the bound-

ary (1.00), slowing the search procedure and convergence. Estimates of heritability for weight (Table 6), weight adjusted for body condition score (Table 7), and height (Table 8) were remarkably similar to those from univariate analyses. Genetic correlations between ages were always large for weight (0.92 to 1.00) and height (0.98 to 1.00), tending toward unity between consecutive ages, and decreasing slightly for ages more separated for both traits. Correlations between permanent environmental effects were close to one for successive ages, but decreased with increasing age differences to 0.56 and 0.55 (weights) and 0.72 (height) between extreme ages (2 to 6 yr). Phenotypic correlations followed the same trend as genetic and permanent environmental correlations, ranging from 0.63 to 0.73 for weight, 0.62 to 0.72 for weight adjusted for condition score, and 0.72 to 0.83 for height. Phenotypic correlations were moderate to high (0.56 to 0.86) among seasons of measurement for weights.

Estimates of parameters for cow body condition score (Table 9) were slightly greater than those from univariate analyses. Heritability estimates agreed well with those from univariate analyses for age classes, but were more erratic (0.11 to 0.20) for season classes. Genetic correlations were high, except between extreme ages (0.67). Permanent environmental correlations ranged from 0.31 to 0.88. All genetic and permanent environmental correlations between seasons converged to 1.00.

Table 5. Estimates of variance components and parameters^a for weight, weight adjusted for body condition score, height, and condition score by age for Cycles I to IV

	Age, yr						
	2	3	4	5	6	7	8
Weight, kg							
σ_p^2	1,682	2,376	2,594	2,623	2,737	2,555	2,344
h^2	0.52 ± 0.04	0.51 ± 0.05	0.54 ± 0.05	0.57 ± 0.05	0.54 ± 0.06	0.47 ± 0.08	0.58 ± 0.20
c^2	0.15 ± 0.04	0.19 ± 0.04	0.20 ± 0.05	0.20 ± 0.05	0.22 ± 0.05	0.35 ± 0.08	0.20 ± 0.20
e^2	0.33 ± 0.01	0.30 ± 0.01	0.26 ± 0.01	0.23 ± 0.01	0.24 ± 0.01	0.18 ± 0.01	0.22 ± 0.02
Adjusted weight, kg							
σ_p^2	1,489	1,840	1,966	2,104	2,224	1,972	1,722
h^2	0.55 ± 0.04	0.56 ± 0.05	0.61 ± 0.05	0.63 ± 0.05	0.60 ± 0.06	0.51 ± 0.08	0.53 ± 0.20
c^2	0.12 ± 0.04	0.14 ± 0.04	0.13 ± 0.04	0.13 ± 0.05	0.15 ± 0.05	0.30 ± 0.08	0.22 ± 0.20
e^2	0.33 ± 0.01	0.30 ± 0.01	0.27 ± 0.01	0.24 ± 0.01	0.25 ± 0.01	0.19 ± 0.01	0.25 ± 0.02
Mean ^b	417 ± 60.6	470 ± 68.6	503 ± 68.3	522 ± 67.3	539 ± 65.4	554 ± 65.7	561 ± 65.3
Height, cm							
σ_p^2	15.9	16.5	16.0	15.7	15.0	13.7	12.5
h^2	0.70 ± 0.05	0.69 ± 0.05	0.72 ± 0.05	0.72 ± 0.05	0.68 ± 0.06	0.59 ± 0.08	0.61 ± 0.21
c^2	0.04 ± 0.05	0.08 ± 0.05	0.06 ± 0.05	0.07 ± 0.05	0.15 ± 0.06	0.28 ± 0.08	0.31 ± 0.21
e^2	0.26 ± 0.01	0.23 ± 0.01	0.22 ± 0.01	0.21 ± 0.01	0.17 ± 0.01	0.13 ± 0.01	0.09 ± 0.01
Mean ^b	126.0 ± 6.5	128.2 ± 6.9	127.7 ± 6.8	128.1 ± 6.1	128.1 ± 5.8	127.0 ± 5.5	127.7 ± 5.7
Condition score							
σ_p^2	0.76	0.86	0.80	0.81	0.72	0.77	0.56
h^2	0.22 ± 0.03	0.20 ± 0.03	0.18 ± 0.03	0.21 ± 0.04	0.22 ± 0.04	0.25 ± 0.06	0.51 ± 0.18
c^2	0.16 ± 0.03	0.24 ± 0.03	0.30 ± 0.03	0.25 ± 0.03	0.27 ± 0.04	0.33 ± 0.06	0.10 ± 0.17
e^2	0.61 ± 0.01	0.55 ± 0.01	0.52 ± 0.01	0.54 ± 0.01	0.50 ± 0.01	0.42 ± 0.01	0.39 ± 0.03
Mean ^b	6.0 ± 1.02	6.1 ± 1.03	6.3 ± 1.01	6.3 ± 1.02	6.5 ± 0.97	6.6 ± 1.05	6.6 ± 0.80

^a σ_p^2 = phenotypic variance; h^2 = heritability; c^2 = fraction of total variance due to cow permanent environmental effects; e^2 = fraction of total variance due to temporary environmental effect.

^bUnadjusted mean; mean for weight and weight adjusted for condition score are the same.

Table 6. Estimates of phenotypic standard deviations (σ_p), heritabilities (h^2), and genetic (ρ_a), permanent environmental (ρ_c), temporary environmental (ρ_e), and phenotypic (ρ_p) correlations from bivariate analyses between pairs of ages^a (yr) and seasons^b for weights of cows from Cycles I to IV

Trait									
1st	2nd	σ_{p1}	σ_{p2}	h_1^2	h_2^2	ρ_a	ρ_c	ρ_e	ρ_p
Age									
2	3	40.3	48.2	0.54	0.51	0.98	0.96	−0.05	0.68
	4	40.4	51.1	0.53	0.56	0.97	0.59	0.07	0.65
	5	40.2	51.5	0.52	0.59	0.92	0.61	0.00	0.63
	6	40.3	53.2	0.52	0.56	0.93	0.56	0.13	0.64
3	4	48.2	51.0	0.51	0.55	0.99	0.99	−0.02	0.73
	5	48.3	51.3	0.51	0.58	0.96	0.68	0.18	0.71
	6	48.2	53.2	0.50	0.56	0.95	0.71	0.01	0.67
4	5	51.1	51.5	0.62	0.66	0.99	1.00	−0.20	0.72
	6	50.7	52.9	0.54	0.53	0.98	0.78	0.15	0.73
5	6	50.5	52.2	0.65	0.55	1.0	1.0	−0.17	0.73
Seasons									
1	2	44.7	43.7	0.48	0.55	1.0	1.0	0.53	0.83
	3	44.4	49.2	0.48	0.44	1.0	1.0	0.33	0.72
	4	46.5	48.3	0.51	0.42	1.0	1.0	0.53	0.79
2	3	42.9	48.2	0.55	0.43	1.0	1.0	0.65	0.86
	4	45.0	47.0	0.54	0.41	1.0	1.0	0.21	0.68
3	4	49.5	46.8	0.47	0.41	1.0	1.0	0.04	0.56

^aYear-old.

^b1 = spring, 2 = summer, 3 = fall, and 4 = winter.

Table 7. Estimates of phenotypic standard deviations (σ_p), heritabilities (h^2), and genetic (ρ_a), permanent environmental (ρ_c), temporary environmental (ρ_e), and phenotypic (ρ_p) correlations from bivariate analyses between pairs of ages^a and seasons^b for weight adjusted for condition score for cows from Cycles I to IV

Trait									
1st	2nd	σ_{p1}	σ_{p2}	h_1^2	h_2^2	ρ_a	ρ_c	ρ_e	ρ_p
Age (yr)									
2	3	40.0	47.4	0.54	0.51	0.98	0.96	-0.05	0.67
	4	40.1	49.8	0.53	0.56	0.97	0.58	0.07	0.65
	5	40.0	50.4	0.52	0.59	0.92	0.60	0.00	0.62
	6	40.0	50.5	0.52	0.57	0.94	0.55	0.11	0.64
3	4	47.7	49.7	0.51	0.55	0.99	1.0	-0.02	0.72
	5	47.8	50.2	0.51	0.58	0.96	0.66	0.18	0.70
	6	47.7	50.6	0.51	0.58	0.95	0.71	0.00	0.66
4	5	50.9	51.2	0.62	0.66	0.99	1.0	-0.20	0.72
	6	49.6	50.2	0.55	0.54	0.98	0.75	0.14	0.72
5	6	49.7	49.9	0.60	0.57	1.0	1.0	-0.18	0.72
Seasons									
1	2	44.1	44.0	0.50	0.55	1.0	1.0	0.52	0.83
	3	43.6	49.2	0.49	0.44	1.0	1.0	0.33	0.72
	4	46.3	46.1	0.52	0.46	1.0	1.0	0.48	0.79
2	3	43.1	48.6	0.56	0.44	1.0	1.0	0.65	0.86
	4	44.4	44.6	0.55	0.40	1.0	1.0	0.18	0.68
3	4	50.2	44.8	0.47	0.43	1.0	1.0	0.03	0.57

^aYear-old.

^b1 = spring, 2 = summer, 3 = fall, and 4 = winter.

Phenotypic correlations were intermediate among ages (0.23 to 0.39) and among seasons (0.28 to 0.62).

Previous studies of Cycles I to III of the GPE program agree with the current results (Jenkins et al., 1991).

Table 8. Estimates of phenotypic standard deviations (σ_p), heritabilities (h^2), and genetic (ρ_a), permanent environmental (ρ_c), temporary environmental (ρ_e), and phenotypic (ρ_p) correlations from bivariate analyses between pairs of ages^a and seasons^b for height for cows from Cycles I to IV

Trait									
1st	2nd	σ_{p1}	σ_{p2}	h_1^2	h_2^2	ρ_a	ρ_c	ρ_e	ρ_p
Age (yr)									
2	3	3.99	4.06	0.69	0.69	0.99	1.0	-0.05	0.74
	4	3.98	4.01	0.68	0.72	0.99	0.79	0.00	0.74
	5	3.94	4.01	0.68	0.73	0.98	0.73	-0.04	0.73
	6	3.95	3.91	0.67	0.70	0.99	0.72	0.03	0.75
3	4	4.06	4.01	0.71	0.74	1.0	0.96	0.06	0.78
	5	4.03	3.99	0.69	0.74	0.98	0.98	0.00	0.77
	6	4.04	3.91	0.70	0.72	1.0	0.80	0.00	0.78
4	5	4.19	4.21	0.75	0.77	1.0	1.0	-0.05	0.80
	6	4.00	3.91	0.75	0.75	1.0	1.0	0.00	0.80
5	6	3.96	3.88	0.74	0.74	1.0	1.0	0.01	0.81
Seasons									
1	2	3.97	3.97	0.68	0.73	1.0	1.0	0.19	0.80
	3	3.95	3.94	0.68	0.72	1.0	1.0	0.15	0.79
	4	3.92	4.00	0.67	0.65	1.0	1.0	0.27	0.79
2	3	4.06	4.06	0.73	0.74	1.0	1.0	0.19	0.83
	4	4.02	4.04	0.72	0.66	1.0	1.0	0.20	0.79
3	4	3.65	3.74	0.66	0.60	1.0	1.0	0.09	0.72

^aYear-old.

^b1 = spring, 2 = summer, 3 = fall, and 4 = winter.

Table 9. Estimates of phenotypic standard deviations (σ_p), heritabilities (h^2), and genetic (ρ_a), permanent environmental (ρ_c), temporary environmental (ρ_e), and phenotypic (ρ_p) correlations from bivariate analyses between pairs of ages^a and seasons^b from body condition score for cows from Cycles I to IV

Trait									
1st	2nd	σ_{p1}	σ_{p2}	h_1^2	h_2^2	ρ_a	ρ_c	ρ_e	ρ_p
Age (yr)									
2	3	0.87	0.93	0.22	0.20	0.86	0.88	-0.06	0.32
	4	0.87	0.89	0.22	0.18	0.74	0.41	0.00	0.24
	5	0.87	0.90	0.22	0.21	0.74	0.31	0.01	0.23
	6	0.87	0.85	0.22	0.22	0.67	0.35	0.08	0.27
3	4	0.93	0.89	0.20	0.19	0.90	0.80	0.01	0.39
	5	0.93	0.90	0.20	0.22	0.85	0.42	-0.05	0.26
	6	0.93	0.85	0.19	0.23	0.77	0.38	0.01	0.27
4	5	0.89	0.90	0.18	0.20	0.86	0.85	-0.12	0.34
	6	0.89	0.85	0.18	0.23	0.81	0.49	0.05	0.33
5	6	0.90	0.84	0.20	0.22	0.78	0.86	-0.07	0.36
Seasons									
1	2	0.90	0.87	0.17	0.16	0.98	1.0	0.46	0.61
	3	0.89	0.93	0.19	0.16	1.0	1.0	0.28	0.47
	4	0.89	0.92	0.15	0.12	1.0	1.0	0.33	0.48
2	3	0.84	0.90	0.15	0.11	1.0	1.0	0.51	0.62
	4	0.87	0.91	0.20	0.13	1.0	1.0	0.13	0.35
3	4	0.93	0.92	0.17	0.13	1.0	1.0	0.03	0.28

^aYear-old.

^b1 = spring, 2 = summer, 3 = fall, and 4 = winter.

Smith et al. (1976) reported estimates of genetic correlations between early weights (369 d, 550 d, and 3½ yr) and mature weight (6 to 9 yr) of 0.80, 0.94, and 1.15, and among the early weights from 0.72 to 0.92, for females from a diallel experiment involving Angus, Hereford, and Shorthorn cows. Choy et al. (1998a) reported high Pearson and rank correlations between EPD values for weight (0.98 and 0.96) and height (0.97 and 0.95) and intermediate correlations for condition score (0.69 and 0.68) of Angus cows aged 2+ and 4+ yr. Rumph et al. (2000) reported genetic correlations from 0.86 to 1.00 and 0.79 to 1.00 between weights at different ages (2 to 8 yr) taken in two seasons.

Brinks et al. (1964) reported a large estimate of genetic correlation (0.93) between weights taken in spring and fall for range Hereford cows. Jeffery and Berg (1972) also reported a high genetic correlation (0.87) between cow weights at two times of the year (postcalving and weaning of the calf) in Canadian purebred and crossbred animals.

Results from bivariate analyses between traits over all data are summarized in Table 10. Phenotypic variances agreed closely with values from univariate analyses for all traits with the exception of cow weight, for which the variance was 10% higher with the bivariate analyses. Heritability estimates were the same as for the univariate analyses for all traits. Estimates of genetic correlations were high between size and weight measurements (0.80 and 0.86 between weight and height and between weight adjusted for condition score and height). Estimates of genetic correlations were

moderate (0.43) between weight and condition score and near zero (-0.04) between height and condition score. Permanent environmental correlations were intermediate between height and weight (0.55 and 0.61 for weight and weight adjusted for condition, respectively), high between weight and condition score (0.79), and relatively low between height and condition score (0.26). In general, results reported here indicate no antagonistic relationships between the traits. Selection would be effective for either weight or height, and would produce important correlated responses for both measurements of growth. Selection for condition score would not be as effective, but would exhibit a correlated response with weight. Selection for height would not affect condition score under the nutritional resources of this study.

Previous studies of Cycles I to III of the GPE program have shown estimates similar to the present study. Jenkins et al. (1991) reported high genetic correlations within breed (0.73), between breeds (0.87), and total (0.76) between asymptotic mature weight (estimated from records adjusted for condition score) and mature height (7 yr). Estimates of 0.73, 0.59, and 0.70 and 0.59 and 0.58 were found between 500-d weight and mature height. Data from nine purebred and three generations (F_1 , F_2 , and F_3) of composite populations from the Germplasm Utilization program at MARC yielded estimates of genetic correlations of 0.74, 0.48, and 0.00 between weight and height, weight and condition score, and height and condition score of 2-yr-old cows, and 0.47, 0.56, and -0.14 at 5 yr of age (Gregory et al., 1995).

Table 10. Estimates of phenotypic standard deviations (σ_p), heritabilities (h^2), and genetic (ρ_a), permanent environmental (ρ_c), temporary environmental (ρ_e), and phenotypic (ρ_p) correlations from bivariate analyses using all data from cows from Cycles I to IV

Trait ^a									
1st	2nd	σ_{p1}	σ_{p2}	h_1^2	h_2^2	ρ_a	ρ_c	ρ_e	ρ_p
CW	CH	50.44	4.01	0.50	0.68	0.80	0.55	0.23	0.59
CW	CS	50.49	0.92	0.50	0.16	0.43	0.79	0.50	0.48
WA	CH	44.94	4.01	0.54	0.68	0.86	0.61	0.23	0.64
CH	CS	4.01	0.92	0.68	0.16	-0.04	0.26	0.11	0.05

^aCW = weight (kg); WA = weight adjusted for condition score (kg); CH = height (cm); CS = body condition score.

Least squares estimates of phenotypic correlations between cow weight and height have been reported to be from 0.06 to 0.89 (Brown et al., 1956a,b,c; Nelsen et al., 1985; Thompson et al., 1983; Naazie et al., 1989; Choy et al., 1996, 1998a,b), but most estimates were intermediate to high, averaging 0.59, the same estimate obtained in the present study. Estimates of genetic correlations have been relatively high (0.68 to 0.79), as reported by Choy et al. (1996, 1998a,b). Estimates of correlations by REML between cow weight and height also agree with the present study. Northcutt et al. (1992) and Northcutt and Wilson (1993) reported estimates of 0.58, 0.56, and 0.78 for phenotypic, environmental, and genetic correlations, respectively, for Angus field data. Meyer (1995) obtained estimates for the corresponding correlations of 0.59 and 0.55, 0.88 and 1.00, and 0.76 and 0.67 in Australian Herefords and Wokulups. Correlations between cow weight adjusted for condition score and height were reported to be 0.54 to 0.61 and 0.66 to 0.85 for phenotypic and genetic correlations (Choy et al., 1998b; Northcutt and Wilson, 1993; Wilson, 2000).

Estimates of genetic correlations between weight and conditions have ranged from 0.20 to 0.76, averaging 0.46 (Brinks et al., 1964; Marlowe and Morrow, 1985; Choy et al., 1996, 1998a,b). Meyer (1995), using REML, obtained estimates for phenotypic, environmental, and genetic correlations between weight and condition score of 0.60 and 0.58, 0.85 and 0.74, and 0.78 and 0.64 for Australian Hereford and Wokulups, respectively.

Estimates of the genetic correlation between cow height and cow condition have been 0.02 to 0.30, averaging 0.11 (Choy et al., 1996, 1998a,b) for Angus cows. Estimates of correlations by REML between height and condition score include an estimate of 0.10 for the environmental correlation for Angus (Northcutt et al., 1992). Meyer (1995) reported estimates of 0.19 and 0.04, -0.28 and 1.00, and 0.76 and -0.39 for phenotypic, environmental, and genetic correlations in Australian Hereford and Wokulups, respectively.

Implications

Intermediate to high estimates of heritability indicate that genetic changes in cow weight and cow height

can be accomplished easily by selection. Measures of weight or height at different ages or seasons can be considered to be the same genetic trait. A repeatability model would be adequate to model cow weights and cow heights in this population. Condition score had smaller estimates of heritability and repeatability than weights and height. Condition score may be useful for evaluating cow weight at constant fatness rather than as an independent trait for selection. Results indicate no antagonistic relationships among height, weight, and condition score. Selection would be effective for either weight or height, and would produce important correlated responses for both measurements of growth. Selection for condition score would not be as effective but would be changed by correlated response if selection is for weight. Selection for height would not be expected to affect condition score. Measures of height at early ages might be used in multiple-trait approaches to select indirectly for optimal mature weight. An unanswered question is how to select for optimal condition for each season.

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