Genetic parameters and relationships between hip height and weight in Brahman cattle^{1,2}

C. A. Vargas*, M. A. Elzo*,3, C. C. Chase, Jr.†, and T. A. Olson*

*University of Florida, Gainesville 32611-0910 and †ARS, USDA, Subtropical Agricultural Research Station, Brooksville, FL 34601-4672

ABSTRACT: Genetic parameters for weaning hip height (WHH), weaning weight (WWT), postweaning hip height growth (PHG), and hip height at 18 mo of age (HH18) and their relationships were estimated for Brahman cattle born from 1984 to 1994 at the Subtropical Agricultural Research Station, Brooksville, FL. Records per trait were 889 WHH, 892 WWT, and 684 HH18. (Co)variances were estimated using REML with a derivative-free algorithm and fitting three two-trait animal models (i.e., WHH-WWT, WHH-PHG, and WWT-HH18). Heritability estimates of WHH direct effects were 0.73 and 0.65 for models WHH-WWT and WHH-PHG and were 0.29 and 0.33 for WWT direct for models WHH-WWT and WWT-HH18, respectively. Estimates of heritability for PHG and HH18 direct were 0.13 and 0.87, respectively. Heritability estimates for maternal effects were 0.10 and 0.09 for WHH for models WHH-WWT and WHH-PHG and 0.18 and 0.18 for WWT for models WHH-WWT and WWT-HH18, respectively. Heritability estimates for PHG and HH18 maternal were 0.00 and 0.03. Estimates of the genetic correlation between direct effects for the different traits were moderate and positive; they were also positive between WHH and WWT maternal and WWT and HH18 mater-

nal but negative (-0.19) between WHH and PHG maternal, which may indicate the existence of compensatory growth. Negative genetic correlations existed between direct and maternal effects for WHH, WWT, PHG, and HH18. The correlation between direct and WWT maternal effects was low and negative, moderate and negative between WHH direct and PHG maternal, and high and negative (-0.80) between WWT direct and HH18 maternal. There is a strong genetic relationship between hip height and weight at weaning that also affects hip height at 18 mo of age. Both product-moment and rank correlations between estimated breeding values (EBV) for direct values indicate that almost all of the same animals would be selected for PHG EBV if the selection criterion used was WHH EBV, and that it is possible to accomplish a preliminary selection for HH18 EBV using WHH EBV. Correlations between breeding values for WHH, WWT, and HH18 indicate that it will be possible to identify animals that will reduce, maintain, or increase hip height while weaning weight is increased. Thus, if the breeding objective is to manipulate growth to 18 mo of age, implementation of multipletrait breeding programs considering hip height and weight at weaning will help to predict hip height at 18 mo of age.

Key Words: Body Weight, Brahman, Genetic Parameters, Height, Variance Components, Zebu

©2000 American Society of Animal Science. All rights reserved.

Introduction

Breeders have used body size characteristics to implement strategies for the genetic improvement of beef cattle (Jenkins et al., 1991). Size recommendations

Received December 28, 1999.

Accepted July 18, 2000.

have usually been based on weight and(or) weight gains (Jenkins et al., 1991; Hoffman, 1997). Hip height has been used to change size. Hip height is negatively related with productivity of beef females (Vargas et al., 1999). A favorable relationship of height with scrotal circumference and unfavorable with age at puberty of heifers have been reported (Vargas et al., 1998). However, neither weight nor hip height alone can account for all genetic differences in size (BIF, 1996). A multipletrait evaluation including both height and weight may be a better option for selection for size. The evaluation of height at various ages and its relationships with weaning weight should improve the evaluation for size and may also aid in the selection for reproductive traits.

J. Anim. Sci. 2000. 78:3045-3052

Early selection decisions for replacement breeding animals is of substantial economic value. For early pre-

¹Names are necessary to report factually on available data; however, the USDA or the University neither guarantees nor warrants the standard of the product, and the use of the name by USDA or the University implies no approval of the product to the exclusion of others that may also be suitable.

²We thank A. C. Warnick, R. E. Larsen, K. J. Senseman, D. Davenport, and the scientific and farm support staff at Brooksville for technical assistance. Published as Florida Agric. Exp. Sta. Journal Series no. R-07232.

³Correspondence: Animal Science Dept., P.O. Box 110910 (phone: 352/392-7564; fax: 352/392-7652; E-mail; elzo@animal.ufl.edu).

diction to be effective, reliable estimates of genetic parameters for associated traits measured at young and older ages and their relationships are needed. Furthermore, the nature of the relationship between estimated breeding values for one trait measured early (e.g., weaning) and another trait measured at a later age (e.g., 18 mo of age) would facilitate the decision making process.

Objectives of this study were 1) to estimate the direct and maternal genetic effects for hip height and weight at weaning, postweaning hip height growth, and hip height at 18 mo of age; 2) to estimate genetic correlations between hip height and weight at weaning, between weaning hip height and postweaning hip height growth, and between weaning weight and hip height at 18 mo of age; and 3) to examine the potential use of estimated breeding values for height or weight at weaning to predict performance for hip height at 18 mo of age in Brahman cattle.

Materials and Methods

Data were collected from Brahman cattle born between 1984 and 1994 at the Subtropical Agricultural Research Station (STARS) located near Brooksville, FL. The Brahman herd at STARS used in this study was composed of purebred and upgraded cattle. The grade cattle descended from Brahman-sired cows, with at least two-thirds Brahman breeding, upgraded for two or three additional generations. Complete pedigree records relating all animals to the base herd were available. The number of sires used per year ranged from two to five. To maintain connectedness of the data across years, up to three sires were used in two consecutive years. Assortative mating based on observed hip height was practiced, and mating groups were formed such that dams and sires were of comparable frame score. The total number of sires and dams that had offspring with records was 28 and 261, respectively. The number of records per trait was 889 weaning hip heights, 892 weaning weights, and 684 hip heights at 18 mo of age. Hip heights were measured according to the Beef Improvement Federation guidelines (BIF, 1996). Postweaning hip height growth was calculated by multiplying postweaning average daily hip height growth by 345. Postweaning average daily growth was calculated based on 205-d and 550-d hip height adjusted in accordance with the BIF (1996) recommendations. Details of the management of calves, bulls, and heifers are described by Vargas et al. (1998, 1999).

The matrix of additive genetic relationship was complete for all animals evaluated in this study. Thus, changes in (co)variances that might have occurred as a result of the assortative mating would not affect the relationship matrix (Sorensen and Kennedy, 1984; Fernando and Gianola, 1990; Henderson, 1990). Data were analyzed using an animal model (Henderson and Quaas, 1976; Quaas and Pollak, 1980). Additive direct and maternal effects were taken into account by includ-

Table 1. Number of observations (n), means, standard deviations (SD) minimums, and maximums for hip height (WHH; cm) and weight (WWT; kg) at weaning, postweaning hip height growth (PHG; cm), and hip height at 18 mo of age (HH18; cm) in Brahman cattle

Traits	n	Mean	SD	Min.	Max.
WHH	889	113.19	6.46	89.00	136.00
WWT	892	216.48	36.59	135.20	327.00
PHG	684	19.90	8.37	4.00	46.60
HH18	684	132.39	8.24	109.50	159.50

ing appropriate random effects into the model's analysis. However, the small size of the data set did not allow convergence when three or more traits were included in the multiple-trait model. Therefore, only bivariate analyses were conducted. Weaning hip height, weaning weight, hip height at 18 mo of age, and postweaning hip height growth were the traits considered. Number of observations, phenotypic means, standard deviations, minimums, and maximums for the traits studied are presented in Table 1. No adjustment of any trait was made before analyses. Fixed effects considered in the model were year, sex of calf, and age of dam for all models, and age of calf at weaning as a linear and quadratic covariate for the weaning traits, and age at measurement as a linear and quadratic covariate for hip height at 18 mo of age. Random effects were direct of the animal, maternal of the dam, and residual. Animal and dam effects were connected through the additive relationship matrix and the matrix of genetic covariances between traits. The full relationship matrix between animals was included by incorporating all pedigree information. The two-trait animal model followed that of Quaas and Pollak (1980).

Thus, the (co)variance parameters to be estimated in each bivariate analysis were two additive genetic variance components ($\sigma_{A_{11}}$ and $\sigma_{A_{22}}$), the additive genetic covariance component between them $(\sigma_{A_{12}})$, two maternal genetic variance components ($\sigma_{\mathbf{M}_{11}}$ and $\sigma_{\mathrm{M}_{\mathrm{99}}}$), the genetic covariance component between them $(\sigma_{\mathbf{M}_{12}})$, four genetic covariance components between direct and maternal effects ($\sigma_{A_1M_1}, \sigma_{A_2M_2}, \sigma_{A_1M_2}$ and $\sigma_{\mathrm{A_2M_1}}$), and three residual error (co)variances ($\sigma_{\mathrm{e_{11}}}$, $\sigma_{\mathbf{e}_{22}}$, and $\sigma_{\mathbf{e}_{12}}$). Three two-trait analyses were conducted. Analyses considered pairing the traits weaning hip height-weaning weight, weaning hip height-postweaning hip height growth, and weaning weight-hip height at 18 mo of age. These pairings were chosen because it was assumed, first, that weaning weightpostweaning hip height growth was adequately explained by weaning weight-hip height at 18 mo of age, and, second, that because weaning hip height and postweaning hip height growth were each constituent parts of hip height at 18 mo of age, the expected collinearity effect might affect convergence in the solutions when

pairing the traits weaning hip height-hip height at 18 mo of age and postweaning hip height growth-hip height at 18 mo of age. Genetic parameters were estimated for weaning hip height, weaning weight, hip height at 18 mo of age, and postweaning hip height growth. Heritability estimates for each trait and the genetic and environmental correlations between direct and maternal effects within each two-trait analysis were also computed.

Analyses were carried out using multiple-trait derivative-free restricted maximum likelihood (MTDFREML) programs (Boldman et al., 1995). The strategy for the estimation of the (co)variances was as follows: 1) starting values for the direct additive genetic variance, maternal additive genetic variance, and covariance between direct and maternal effects were estimated in single-trait analyses; 2) two-trait analyses were initiated holding the (co)variance estimates from single-trait analyses constant until the variance of the value of the simplex function was less than 10^{-3} ; 3) analyses were continued using the apparently converged estimates from step 2 as starting values and reestimating simultaneously all parameters in the model using the same low level of convergence as in step 2; 4) analyses were repeated as in step 3 until $-2 \log$ likelihood did not change in the first two decimal positions; 5) all parameters in the model were simultaneously re-estimated using as initial values the estimates values obtained in step 4 until the variance of the value of the simplex function was less than 10^{-9} ; and 6) to ensure convergence to a global maximum, repeated analyses similar to step 5 were conducted until the smallest -2 log likelihood was found. Changes in -2log likelihood beyond the third decimal position were considered unimportant.

Estimates of breeding values were obtained for each trait within each bivariate model and used to determine the ranking of animals within the herd. Pearson product-moment correlations between estimates of breeding values and Spearman correlations between ranks of animals were calculated for each trait using estimates from each bivariate model.

Results and Discussion

Productive and reproductive characteristics in Brahman cattle seem to be related to hip height (Vargas et al., 1998, 1999). Knowledge of the genetic relationship between hip height and weight at weaning, together with the understanding of the strength of the genetic relationship of each of these two traits with hip height at 18 mo of age, will aid in the decision of whether to include hip height as a selection criterion when developing breeding selection objectives for Brahman cattle.

Hip Height and Weight at Weaning

Estimates of (co)variance components and genetic parameters for weaning hip height and weaning weight are shown in Table 2. The heritability estimate for weaning hip height direct (0.73) found in this Brahman herd was somewhat larger than the estimate of $0.43 \pm$ 0.08 reported by Bourdon and Brinks (1986) for 205d hip height in Hereford cattle. The estimate of the maternal heritability for weaning hip height was 0.10. No comparable values for this estimate were found in the literature. The high weaning hip height direct heritability and a low weaning hip height maternal heritability obtained suggest that Brahman cattle can be selected for hip height at weaning and that genetic progress can be made by relying on direct effects alone. However, the correlation between direct and maternal effects (\mathbf{r}_{AM}) for weaning hip height was high and negative (-0.57), suggesting that some of the same genes possess opposite effects on direct and maternal components of weaning hip height. This negative \mathbf{r}_{AM} estimate seems to indicate a tendency for animals with superior hip height growth genes to have inferior maternal genes and, vice versa (Garrick et al., 1989; Mohiuddin, 1993). Mohiuddin (1993) suggested that this negative correlation may be an indication that genes that partition nutrients for skeletal growth of the young calf are partly incompatible with genes that partition nutrients for lactation. As a consequence, if the breeding objectives in a selection program in Brahman cattle include hip height at weaning, it should also be considered that it may lead to a reduction in maternal ability. Under this circumstance, a possible strategy would be to place emphasis on hip height maternal genetic value in females and direct genetic value for hip height in males (Van Vleck et al., 1977; Mohiuddin, 1993).

Heritability estimates of weaning weight direct and weaning weight maternal effects were 0.29 and 0.18, respectively. These estimates agreed closely with those (0.29 and 0.21) reported by Elzo and Wakeman (1998) but were slightly greater than those (0.23 and 0.16)

Table 2. (Co)variance components and genetic parameters in a bivariate analysis for hip height (WHH) and weight (WWT) at weaning in Brahman cattle^a

		Trait ^b				
Trait	WHHD	WWTD	WHHM	WWTM		
WHHD	$0.73 \\ 17.21$	0.73	-0.57	-0.09		
WWTD	40.39	$0.29 \\ 178.32$	-0.04	-0.03		
WHHM	-3.59	-0.88	$\begin{array}{c} 0.10\\ 2.33\end{array}$	0.63		
WWTM	-4.05	-4.88	10.25	$0.18 \\ 111.84$		

^aDiagonal: heritabilities (line 1) and additive genetic variances (line 2); above diagonal: additive genetic correlations; below diagonal: additive genetic covariances.

^bWHHD = weaning hip height direct; WWTD = weaning weight direct; WHHM = weaning hip height maternal; WWTM = weaning weight maternal.

obtained by Kriese et al. (1991b) and than the average values (0.22 and 0.19) for Brahman and Brahman crosses given by Meyer (1992). Robinson and Rourke (1992) evaluated 200-d weaning weight in two straightbred Brahman herds and reported larger direct effects (0.35 and 0.52) and lower maternal effects (0.04 and 0.07), respectively. These direct and maternal heritability values suggest that genetic progress can be made for increased weaning weight in Brahman cattle.

Weaning weight direct-maternal genetic correlations are reported as negative for most beef breeds (Pollak et al., 1994). The \mathbf{r}_{AM} estimate for weaning weight was almost zero (-0.03) in our study (Table 2). The average \mathbf{r}_{AM} estimate for weaning weight reported by Mohiuddin (1993) for various breeds was -0.15, with a range from -0.91 to 0.26. Quaas et al. (1985) reported a \mathbf{r}_{AM} estimate of -0.04 in Simmental cattle, and MacKinnon et al. (1991) reported a \mathbf{r}_{AM} estimate of 0.00 in Zebu crosses. However, Kriese et al. (1991b) reported a small and positive \mathbf{r}_{AM} estimate (0.15) for Brahman cattle and concluded that both weaning weight direct and weaning weight maternal values should be monitored when selecting Brahman cattle to ensure a balance between direct and maternal values.

Replacement heifer growth guidelines for dairy cattle include wither height with BW as a method to evaluate skeletal growth (Hoffman, 1997). A high and positive genetic correlation (0.73) between weaning hip height direct and weaning weight direct suggests that in Brahman cattle many of the same genes affect the two traits. A genetic correlation of 0.53 ± 0.20 between weight and height measured at 205 d of age was found by Bourdon and Brinks (1986) in Hereford cattle. Thus, selecting for weaning hip height would seemingly lead to selection for weaning weight. This result is of practical importance under some management situations in which weaning hip height could be used as an indicator or secondary trait for weaning weight. The genetic correlation between weaning hip height maternal and weaning weight maternal was moderate and positive (0.63), indicating that maternal effects influence these two traits in a similar manner. The positive and high correlations between weaning hip height and weaning weight for direct and maternal effects suggest that animals that excel in weaning hip height should also excel in weaning weight. Furthermore, genetic correlations between weaning hip height direct and weaning weight maternal, and between weaning hip height maternal and weaning weight direct were negative but near zero (-0.04 and -0.09), suggesting that there is little association between direct-maternal cross-effects for preweaning height and weight.

Hip Height at Weaning and Postweaning Hip Height Growth

Estimates of (co)variance components and genetic parameters for weaning hip height and postweaning hip

Table 3. (Co)variance components and genetic parameters in a bivariate analysis for weaning hip height (WHH) and postweaning hip height growth from weaning up to 18 mo of age (PHG) in Brahman cattle^a

		$\operatorname{Trait^b}$				
Trait	WHHD	PHGD	WHHM	PHGM		
WHHD	$\begin{array}{c} 0.65\\ 16.22\end{array}$	0.27	-0.59	-0.37		
PHGD	2.89	$\begin{array}{c} 0.13 \\ 6.81 \end{array}$	-0.35	-0.71		
WHHM	-3.49	-1.35	$\begin{array}{c} 0.09 \\ 2.18 \end{array}$	-0.19		
PHGM	-0.51	-0.65	-0.10	0.00 0.12		

^aDiagonal: heritabilities (line 1) and additive genetic variances (line 2); above diagonal: additive genetic correlations; below diagonal: additive genetic covariances.

^bWHHD = weaning hip height direct; PHGD = postweaning hip height growth from weaning to 18 mo of age direct; WHHM = weaning hip height maternal; PHGM = postweaning hip height growth from weaning to 18 mo of age maternal.

height growth are presented in Table 3. The heritability estimates for weaning hip height direct (0.65) and weaning hip height maternal (0.09) were comparable to those obtained when weaning hip height was paired with weaning weight. The \mathbf{r}_{AM} estimate between weaning hip height direct and weaning hip height maternal was moderate and negative (-0.59), indicating that there is a loss in maternal performance when emphasis is placed on selection to enhance weaning hip height.

The heritability estimate for postweaning hip height growth direct was rather low (0.13) and that for maternal heritability was 0.00. Because postweaning hip height growth should be closely related to weaning hip height and hip height at 18 mo of age, it was expected that postweaning hip height growth direct would have a heritability comparable to that of those traits. However, postweaning hip height growth was subject to almost a full year of environmental effects likely to increase environmental variance, which resulted in a lower heritability for postweaning hip height growth direct than for the other two growth traits. Eighty-eight percent of the phenotypic variance for postweaning hip height growth is explained by environmental variance (Table 4). This large environmental effect may be the result of postweaning compensatory growth, an effect that seems to be evident when evaluating the relationship between weaning hip height and postweaning hip height growth discussed below. Because the heritability value of postweaning hip height growth maternal was so low, it is evident that the remnant preweaning maternal effects were unimportant for postweaning hip height growth in this herd. The \mathbf{r}_{AM} estimate for postweaning hip height growth was high and negative (-0.71), but, given the near zero value of the variance of postweaning hip height growth remnant preweaning maternal effects, it should be considered unimportant.

The positive and yet fairly low genetic correlation (0.27) between weaning hip height direct and postweaning hip height growth direct (Table 3) indicates that genes regulating rate of early skeletal development had similar influence on postweaning hip height growth (i.e., genes that increase weaning hip height are likely to increase postweaning hip height growth). Thus, selection for hip height can be done effectively using weaning hip height direct in combination with postweaning hip height growth direct, as additional information about the estimated breeding values of individuals is incorporated in the decision. Genetic correlations between weaning hip height direct and postweaning hip height growth maternal and weaning hip height maternal and postweaning hip height growth direct were -0.37 and -0.35, respectively. These results suggest that selecting for greater weaning hip height may decrease performance for direct or maternal effects of postweaning hip height growth. Unexpectedly, a negative and moderate genetic correlation between weaning hip height maternal and postweaning hip height growth maternal (-0.19) was found (Table 3). This last genetic correlation coupled with a negative and high environmental correlation between weaning hip height and postweaning hip height growth (Table 4) may be an indication of the existence of compensatory growth. Thus, calves under a poor preweaning maternal environment for weaning hip height tended to have larger postweaning hip height growth than calves under better preweaning maternal conditions. However, interpretation of these correlations should be made with caution because of the magnitude of the covariance estimates involved (Table 3). Additional work should be carried out to examine this environmental correlation.

Table 4. Environmental and phenotypic (co)variances and correlations in bivariate analyses for growth traits in Brahman cattle^a

	Bivariate model (Trait 1 – Trait 2)				
$Parameter^{bc}$	WHH – WWT	WHH – PHG	WWT – HH18		
$\sigma_{\mathrm{e}_{_{11}}}$	7.79	10.05	318.85		
$\sigma_{\mathrm{e}_{22}}^{11}$	328.25	45.48	8.03		
$\sigma_{\mathbf{e}_{12}}^{\mathbf{e}_{22}}$	17.31	-18.39	3.03		
$\sigma_{P_{11}}^{12}$	23.74	24.97	618.90		
$\sigma_{\mathrm{P}_{22}}^{-11}$	613.53	51.77	31.55		
$\sigma_{\mathrm{P}_{12}}$	65.48	-16.52	55.56		
$r_{e_{12}}^{12}$	0.34	-0.86	0.06		
$r_{P_{12}}^{12}$	0.54	-0.46	0.40		

 $^{a}WHH =$ weaning hip height, PHG = postweaning hip height growth, HH18 = hip height at 18 mo of age, WWT = weaning weight. b Subscripts 1 and 2 refer, respectively, to the first and second trait in the bivariate model.

 ${}^{c}\sigma_{\mathbf{e}_{11}}$ and $\sigma_{\mathbf{e}_{22}}$, environmental variances; $\sigma_{\mathbf{e}_{12}}$, environmental covariance; $\sigma_{\mathbf{P}_{11}}$ and $\sigma_{\mathbf{P}_{22}}$, phenotypic variances; $\sigma_{\mathbf{P}_{12}}$, phenotypic covariance; $\mathbf{r}_{\mathbf{e}_{12}}$, environmental correlation; $\mathbf{r}_{\mathbf{P}_{12}}$, phenotypic correlation; units are cm² for WHH, PHG, and HH18, and kg² for WWT.

Table 5. (Co)variance components and genetic parameters in a bivariate analysis for weaning weight (WWT) and hip height at 18 mo of age (HH18) in Brahman cattle^a

Trait	Trait ^b				
	WWTD	HH18D	WWTM	HH18M	
WWTD	0.33 201.33	0.75	-0.09	-0.80	
HH18D	55.91	$0.87 \\ 27.43$	0.01	-0.98	
WWTM	-13.51	0.32	$0.18 \\ 112.23$	0.18	
HH18M	-10.56	-4.77	1.73	0.03 0.86	

^aDiagonal: heritabilities (line 1) and additive genetic variances (line 2); above diagonal: additive genetic correlations; below diagonal: additive genetic covariances.

^bWWTD = weaning weight direct; HH18D = hip height at 18 mo of age direct; WWTM = weaning weight maternal; HH18M = hip height at 18 mo of age maternal.

Hip Height at 18 Months of Age and Weaning Weight

Variance and covariance components and genetic parameters for hip height at 18 mo of age and weaning weight are given in Table 5. The heritability estimate for hip height at 18 mo of age direct was 0.87. Most literature reports of heritabilities for hip height are from moderate to high in magnitude. Neville et al. (1978), working with Angus, Polled Hereford, and Santa Gertrudis, reported a relatively high pooled heritability estimate of 0.75 for hip height measured at 15 mo of age in replacement heifers. In Brangus, a heritability of 0.62 for mature hip height was reported (Choy et al., 1996). In Hereford cattle, Bourdon and Brinks (1986) found a heritability estimate of 0.55 \pm 0.08 for 365-d hip height. Vargas et al. (1998) in a threetrait animal model obtained a heritability estimate for hip height at 18 mo of age direct of 0.65. In the present study, the heritability value for hip height at 18 mo of age maternal was near zero (0.03), indicating little evidence of maternal effect on postweaning hip height. There was a high and negative genetic correlation between hip height at 18 mo of age maternal and hip height at 18 mo of age direct (-0.98); however, it should be considered unimportant because the heritability value of hip height at 18 mo of age maternal was almost zero.

Heritabilities for the direct and maternal effects of weaning weight were 0.33 and 0.18, respectively, and the genetic correlation between weaning weight direct and weaning weight maternal was -0.09 (Table 5). Reasonably comparable values (0.29, 0.18, and -0.03, respectively) were reported and discussed above when weaning weight was paired in a bivariate model with weaning hip height.

The positive and high (0.75) genetic correlation between the direct effects of hip height at 18 mo of age and weaning weight (Table 5) indicates that selection in Brahman cattle for one trait should result in a direct and positive response in the other trait (i.e., heavier weaning weights will generally be associated with taller animals at 18 mo of age). Similarly, a high and positive genetic correlation (0.61 ± 0.17) in Hereford cattle was found by Bourdon and Brinks (1986) between 205-d weight and 365-d hip height. In Brangus cattle, Kriese et al. (1991a) reported a paternal half-sib genetic correlation of 0.33 ± 0.00 between direct effects for weaning weight and yearling height. The high and positive genetic correlations found between direct effects for hip height at 18 mo of age and weaning weight indicate that reasonably accurate selection decisions for hip height at 18 mo of age could be made based on weaning weight. The genetic correlation between hip height at 18 mo of age maternal and weaning weight maternal was positive and relatively low (0.18). A positive and almost zero genetic correlation (0.01) between direct hip height at 18 mo of age and maternal weaning weight indicates that there is little association between these directmaternal cross-effects. A negative and high correlation between maternal hip height at 18 mo of age and direct weaning weight (-0.80), which may indicate an antagonism between direct genetic effect for weaning weight and maternal effect for hip height at 18 mo of age, should be considered unimportant because the maternal heritability for hip height at 18 mo of age was near zero. Kriese et al. (1991a) reported genetic correlation estimates between yearling hip height direct and weaning weight maternal in Brangus and Hereford bulls of -0.23 and -0.34, respectively.

Most of the heritability estimates for the growth traits analyzed in this study were larger than those reported in the literature. One possible explanation for this result may be due to the method of estimation (Dong and Van Vleck, 1989; Koots et al., 1994). In an animal model in which the relationship matrix traces back to the base population, estimates of heritability are expected to be estimates of variance prior to selection or nonrandom mating, if any, and, therefore, to be greater than other methods (Koots et al., 1994). Similarly, differences in estimate values obtained for one trait when paired with different traits under bivariate models may indicate that under multiple-trait analyses the accompanying trait could determine the value of the parameter estimate obtained.

The moderate to fairly large positive estimates obtained for the correlations between genetic direct effects for the growth traits indicate that performance in one of the paired traits can be used in the prediction of genetic change in the other. Correlations between genetic maternal effects were more variable. Hip height and weight at weaning were affected similarly by maternal effects, as indicated by a high and positive genetic correlation between these effects. The moderate and negative correlation between maternal effects for weaning hip height and postweaning hip height growth may point to the existence of a compensatory postweaning hip height growth effect. The estimate of the maternal genetic correlation between hip height at 18 mo of age and weaning weight was relatively low and positive, suggesting some carry-over of maternal effects through a part-whole relationship; however, given the nearly zero heritability value for the postweaning trait, this result is probably unimportant. Estimates of the correlation between direct and maternal effects for each pair of traits were consistently negative, indicating an antagonistic genetic relationship between growth and maternal ability. Thus, these results emphasize the importance of considering maternal effects for growth traits in general and for hip height traits in particular when developing selection strategies for Brahman cattle.

Breeding Values and Animal Rankings

Shown in Table 6 are the means, standard deviations, minimums, and maximums by model fitted for direct and maternal breeding values for weaning hip height, weaning weight, postweaning hip height growth, and hip height at 18 mo of age of sires, dams, and nonparents. Pearson product-moment correlation between estimates of breeding values and the Spearman rank correlation between ranks of animals for the direct genetic effects for weaning hip height and postweaning hip height growth using the estimates calculated from the weaning hip height-postweaning hip height growth

Table 6. Means, standard deviations, minimums, and maximums for direct and maternal estimated breeding

values (EBV) for hip height (WHH; cm) and weight (WWT; kg) at weaning, postweaning hip height growth (PHG; cm), and hip height at 18 mo of age (HH18; cm) in Brahman cattle (n = 1,442)

Trait/model	Mean	SD	Min.	Max.	
	— Direct EBV —				
Weaning hip height	0.4500	(0000	10 5000		
with WWT with PHG	-0.4588 -0.3206	4.0229 3.9353	-12.7690 -13.2847	10.6255 11.5716	
	-0.3206	3.9303	-13.2847	11.0710	
Weaning weight with WHH	-0.7300	11.8399	-36.5018	36.5202	
with HH18	-0.5276	12.2453	-38.6664	36.4562	
Hip height at 18 mo with WWT	-0.2148	5.4813	-17.6727	18.7243	
Hip height growth					
with WHH	-0.9048	14.0145	-46.5469	43.4798	
	Maternal EBV				
Weaning hip height					
with WWT	0.0601	0.7519	-2.8799	3.2452	
with PHG	-0.0231	0.4767	-1.7943	1.4416	
Weaning weight					
with WHH	-0.6342	5.4028	-20.1553	19.7174	
with HH18	-0.6765	5.2522	-21.6124	18.3423	
Hip height at 18 mo with WWT	0.0247	0.9241	-3.3574	2.9085	
Hip height growth with WHH	0.0320	0.4311	-1.3025	1.4760	

model were 0.99 and 0.99, respectively. The productmoment and rank correlations between estimates of breeding values for weaning hip height (from the model weaning hip height-weaning weight) and estimates of breeding values for hip height at 18 mo of age (from the model weaning weight-hip height at 18 mo of age) were 0.85 and 0.85, respectively. The product-moment correlation and rank correlation between direct estimates of breeding values for weaning weight and hip height at 18 mo of age (weaning weight-hip height at 18 mo of age model) were 0.95 and 0.96, respectively. The magnitude of these correlations indicates that 1) almost all of the same animals would be selected for postweaning hip height growth breeding values if the selection criterion used was breeding values for weaning hip height and 2) it might be possible to accomplish a preliminary selection for estimates of breeding values for hip height at 18 mo of age using estimates of breeding values for weaning hip height. Furthermore, results indicate that it is possible to include both hip height and weight in a multiple-trait selection scheme that would allow finding animals required to excel in one trait and not in the other (e.g., selecting animals with a moderate height and heavy weight).

A practical application of these results can be illustrated by comparing the ranking of bulls and heifers born in 1994 based on their estimated breeding values for weaning hip height and weaning weight with the ranking based on their estimated breeding values for hip height at 18 mo of age. Assume that 20% of bulls and 40% of heifers are to be preselected for breeding purposes at weaning. Results for bulls indicated that 1) of the 20% of the bulls (10 bulls) preselected based on estimated breeding values for weaning hip height, six of them (60%) ranked in the top 20% of the estimated breeding values for hip height at 18 mo of age and 2) of the 20% preselected based on estimated breeding values for weaning weight, five of them (50%) were among the top 20% of the estimated breeding values for hip height at 18 mo of age. Results for heifers showed that 1) of the 40% of heifers (22 heifers) preselected based on estimated breeding values for weaning hip height, 19 of them (86%) ranked in the top 40% of the estimated breeding values for hip height at 18 mo of age and 2) of the 40% preselected based on estimated breeding values for weaning weight, 20 of them (91%) were among the top 40% of the estimated breeding values for hip height at 18 mo of age. If weaning hip height is considered in a multiple-trait evaluation with weaning weight, then either weaning hip height or weaning weight can be used to select animals for hip height at 18 mo of age with similar results. Furthermore, correlations between height and weight at weaning and at 18 mo of age indicate that it will be possible to identify animals in the herd that will reduce, maintain, or increase hip height while weaning weight is increased.

Even though larger data sets will be needed to assess the actual magnitude of growth genetic relationships in the Brahman breed, results in the present study indicate that there is a strong genetic relationship between hip height and weight at weaning that has an impact on hip height measured at 18 mo of age. Furthermore, hip height can be used as an indicator trait to improve the accuracy of selection for more economically important genetically correlated traits. Thus, if the breeding objective is to manipulate growth to 18 mo of age (e.g., maintain or maximize), implementation of multiple-trait breeding programs considering hip height and weight at weaning will help to predict hip height at time of selection (e.g., 18 mo age).

Implications

Hip height at weaning in Brahman cattle is an accurate estimator of hip height growth up to 18 mo of age. Hip height at 18 mo of age is also highly and positively genetically correlated with weaning weight. Results of the relationship between direct and maternal effects for hip height and weight at weaning indicate that a balance between direct and maternal values should be considered when selecting Brahman cattle. Selection for hip height at 18 mo of age based on hip height at weaning should be effective due to the high correlation between their breeding values. Frame score as a categorical trait (1 to 9) is currently used in the beef industry to describe skeletal size in beef cattle; future research should be conducted to identify appropriate frame scores that optimize productivity under specific environment, management, mating system, and market conditions.

Literature Cited

- BIF. 1996. Guidelines for Uniform Beef Improvement Programs. 7th ed. Beef Improvement Federation, Kansas State Univ., Manhattan, KS.
- Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell, and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances [DRAFT]. ARS, USDA, Washington, DC.
- Bourdon, R. M., and J. S. Brinks. 1986. Scrotal circumference in yearling Hereford bulls: Adjustment factors, heritabilities and genetic, environmental and phenotypic relationships with growth traits. J. Anim. Sci. 62:958–967.
- Choy, Y. H., J. S. Brinks, and R. M. Bourdon. 1996. Genetic evaluation of mature weight, hip height and body condition score in an Angus herd. J. Anim. Sci. 74(Suppl. 1):107 (Abstr.).
- Dong, M. C., and L. D. Van Vleck. 1989. Estimates of genetic and environmental (co)variances for first lactation milk yield, survival, and calving interval. J. Dairy Sci. 72:678–684.
- Elzo, M. A., and D. L. Wakeman. 1998. Covariance components and prediction for additive and nonadditive preweaning growth genetic effects in an Angus-Brahman multibreed herd. J. Anim. Sci. 76:1290–1302.
- Fernando, R. L., and D. Gianola. 1990. Statistical inferences in populations undergoing selection or non-random mating. In: D. Gianola and K. Hammond (ed.) Advances in Statistical Methods for Genetic Improvement of Livestock. pp 437–453. Springer-Verlag, Heidelberg, Germany.
- Garrick, D. J., E. J. Pollak, R. L. Quaas, and L. D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. J. Anim. Sci. 67:2515–2528.

- Henderson, C. R. 1990. Accounting for selection and mating biases in genetic evaluations. In: D. Gianola and K. Hammond (ed.) Advances in Statistical Methods for Genetic Improvement of Livestock. pp 413–436. Springer-Verlag, Heidelberg, Germany.
- Henderson, C. R., and R. L. Quaas. 1976. Multiple trait evaluation using relatives' records. J. Anim. Sci. 43:1188–1197.
- Hoffman, P. C. 1997. Optimum body size of Holstein replacement heifers. J. Anim. Sci. 75:836–845.
- Jenkins, T. G., M. Kaps, L. V. Cundiff, and C. L. Ferrell. 1991. Evaluation of between- and within- breed variation in measures of weight-age relationships. J. Anim. Sci. 69:3118–3128.
- Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309–338.
- Kriese, L. A., J. K. Bertrand, and L. L. Benyshek. 1991a. Age adjustment factors, heritabilities and genetic correlations for scrotal circumference and related growth traits in Hereford and Brangus bulls. J. Anim. Sci. 69:478–489.
- Kriese, L. A., J. K. Bertrand, and L. L. Benyshek. 1991b. Genetic and environmental growth trait parameter estimates for Brahman and Brahman-derivative cattle. J. Anim. Sci. 69:2362–2370.
- MacKinnon, M. J., K. Meyer, and D. J. S. Hetzel. 1991. Genetic variation and covariation for growth, parasite resistance and heat tolerance in tropical cattle. Livest. Prod. Sci. 27:105–122.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31:179–203.
- Mohiuddin, G. 1993. Estimates of genetic and phenotypic parameters of some performance traits in beef cattle. Anim. Breed. Abstr. 61:495–522.

- Neville, W. E., Jr., J. B. Smith, B. G. Mullinix, Jr., and W. C. McCormick. 1978. Relationships between pelvic dimensions, between pelvic dimensions and hip height and estimates of heritabilities. J. Anim. Sci. 47:1089–1094.
- Pollak, E. J., C. S. Wang, B. E. Cunningham, L. Klei, and C. P. Van Tassel. 1994. Considerations on the validity of parameters used in national cattle evaluations. In: Proc. 4th Genet. Prediction Workshop, Kansas City, MO.
- Quaas, R. L., M. A. Elzo, and E. J. Pollak. 1985. Analysis of Simmental data: estimation of direct and maternal genetic (co)variances. J. Anim. Sci. 61(Suppl. 1):221 (Abstr.).
- Quaas, R. L., and E. J. Pollak. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. J. Anim. Sci. 51:1277-1287.
- Robinson, D. L., and P. K. O. Rourke. 1992. Genetic parameters for liveweights of beef cattle in the tropics. Aust. J. Agric. Res. 43:1297–1305.
- Sorensen, D. A., and B. W. Kennedy. 1984. Estimation of response to selection using least-squares and mixed methodology. J. Anim. Sci. 58:1097–1106.
- Van Vleck, L. D., D. St. Louis, and J. I. Miller. 1977. Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal effects. J. Anim. Sci. 44:360–367.
- Vargas, C. A., M. A. Elzo, C. C. Chase, Jr., P. J. Chenoweth, and T. A. Olson. 1998. Estimation of genetic parameters for scrotal circumference, age at puberty in heifers, and hip height in Brahman cattle. J. Anim. Sci. 76:2536–2541.
- Vargas, C. A., T. A. Olson, C. C. Chase, Jr., A. C. Hammond, and M. A. Elzo. 1999. Influence of frame size and body condition score on performance of Brahman cattle. J. Anim. Sci. 77:3140–3149.