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Germplasm Evaluation in Beef Cattle—Cycle IV: Postweaning Growth and Puberty of Heifers^{1,2,3}

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ABSTRACT: Postweaning growth, puberty, and pregnancy traits were evaluated for 783 F₁ heifers sired by Angus, Hereford, Charolais, Shorthorn, Galloway, Longhorn, Nellore, Piedmontese, and Salers bulls and out of Angus and Hereford dams in Cycle IV of the Germplasm Evaluation (GPE) Program at the U.S. Meat Animal Research Center. The Hereford and Angus sires included a sample of bulls born from 1982 to 1985 (1980s HA) as well as reference sires born from 1963 to 1970 (REF HA) used in previous cycles of the GPE program. Breed group of sire had a significant ($P < .01$) effect on age and weight at puberty, on 200-, 400-, and 550-d weights, on ADG from 200 to 400 and from 400 to 550 d, and 550-d hip height, but it did not influence ($P < .05$) pregnancy rate. Mean age and weight at puberty were predicted from the cumulative distribution because of censoring of data in each tail of the distribution. Sire breed group rankings (and predicted means in days) for age at puberty were as follows: Piedmontese (332), Shorthorn (338), Charolais (348), REF HA (348), Galloway (351), 1980s HA (352), Salers (355), Longhorn (357), and Nellore (405). Sire breed group rankings (and predicted means in kilo-

grams) for weight at puberty were Longhorn (283), Piedmontese (298), Galloway (305), REF HA (309), Shorthorn (329), 1980s HA (330), Salers (338), Nellore (341), and Charolais (345). Sire breed group rankings (and least squares means in kilograms) for 200-d weight were Charolais (229), Salers (225), Nellore (221), Shorthorn (220), Piedmontese (215), 1980s HA (215), Galloway (209), REF HA (206), and Longhorn (197), with differences > 8.3 kg significant. Rankings for 400-d weight (kilograms) were Charolais (390), Shorthorn (384), Salers (380), 1980s HA (374), Nellore (364), REF HA (356), Piedmontese (353), Galloway (348), and Longhorn (321), with differences > 11.5 kg significant. Rankings for 550-d weight (kilograms) were Charolais (445), Salers (430), Shorthorn (429), 80's HA (422), Nellore (420), Piedmontese (401), REF HA (398), Galloway (389), and Longhorn (371), with differences > 11.7 kg significant. Rankings for 550-d hip height (centimeters) were Nellore (132.2), Charolais (131.9), Salers (129.9), Shorthorn (129.5), Piedmontese (126.7), 1980s HA (126.1), Longhorn (125.3), Galloway (121.7), and REF HA (121.5), with differences > 1.35 cm significant. Breed of sire had significant effects on growth and puberty traits of heifers.

Key Words: Beef Cattle, Breeds, Germplasm, Puberty, Pregnancy, Growth

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Introduction

Comprehensive characterization of germplasm resources available to beef cattle producers requires the evaluation of all economically important traits in beef production. Postweaning growth rate, age at puberty, and pregnancy rate affect both the cost of developing replacements for the breeding herd and the subsequent productivity of those replacements. The objective of this

research was to estimate differences in these traits for Cycle IV of the Germplasm Evaluation (GPE) Program of the U.S. Meat Animal Research Center (MARC). Progeny from Hereford, Angus, Charolais, Shorthorn, Galloway, Longhorn, Nellore, Piedmontese, and Salers

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sires that were mated to Hereford and Angus dams were evaluated for postweaning growth, age and weight at puberty, and pregnancy rate. Results for these traits in other cycles of the GPE Program were reported by Laster et al. (1976, 1979), Gregory et al. (1979), and Freetly and Cundiff (1997). The birth and weaning traits for Cycle IV were reported by Cundiff et al. (1998). The carcass, palatability, and composition traits for Cycle IV were reported by Wheeler et al. (1996, 1997).

Materials and Methods

Postweaning records were collected on 783 females produced by AI matings and born at MARC from 1986 to 1990. The Angus dams were all from the MARC Angus herd, which has been selected primarily for growth. Most of the Hereford dams originated from four distinct lines in a long-term selection experiment (Koch et al., 1995). The lines were selected for 200-d weaning weight (**WWL**), 400-d yearling weight (**YWL**), an index of yearling weight and muscling score (**IXL**), or were unselected controls (**COL**). The remaining Hereford dams were from the MARC Hereford herd that was founded from the WWL, YWL, and IXL lines and has been selected for direct and maternal growth.

In Cycle IV of the GPE Program, a set of reference Hereford and Angus sires (born between 1963 and 1970) that had been used in each of the previous cycles of the GPE Program were used again. In cases of limited semen availability, some original reference sires were replaced by their sons. Collectively, these reference sires and their sons are referred to as "reference Hereford" and "reference Angus." In addition, a new sample of Hereford and Angus sires (born between 1982 and 1985) were included in the evaluation to estimate genetic trend within these breeds and to provide direct ties to a more current sample of the beef cattle population. The newer bulls also provide more direct ties to the national cattle evaluations of the Hereford and Angus breeds. These sires are treated as separate breed groups in the analysis and are referred to as "1980s Hereford" and "1980s Angus." The Charolais sires in this cycle (born between 1981 and 1987) represent a new sample of sires and are distinct from the Charolais sires that were evaluated in Cycle I.

The sires in each breed were selected to be as unrelated as possible and to be representative of unproven sires entering service in purebred herds of the respective breeds. The average EPD of the Hereford, Angus, Charolais, Shorthorn, and Salers sires that were sampled are shown in Table 1. Corresponding data were not available for the Galloway, Longhorn, Nellore, and Piedmontese breeds. Cundiff et al. (1998) presented detailed information regarding the sampling of sires, origins and ages of dams, and other aspects of the experimental design. The distribution of females evaluated by breed group of sire and breed group of dam are shown in Table 2. The number of sires used each year and the number of previously used sires are shown in Table 3.

Table 1. Mean EPD of the sampled sires compared with breed average EPD^a

Breed group of sire	Weaning weight		Yearling weight	
	Sampled sires	1996 breed avg ^b	Sampled sires	1996 breed avg ^b
Ref. Angus	1.8	27.9	4.1	50.9
Ref. Hereford	-1.7	29.5	-3.7	50.5
1980s Angus	24.8	27.9	45.4	50.9
1980s Hereford	31.4	29.5	52.6	50.5
Charolais	11.8	12.0	24.3	21.1
Shorthorn	9.1	12.3	15.2	19.2
Salers	6.9	10.1	12.4	16.5

^aEPD from the Spring 1998 national cattle evaluations of the respective breeds.

^bAverage EPD of all cattle born in 1996 in the respective national cattle evaluations.

The calves were born from late March to the middle of May each year. They were weaned in late September or early October at an average age of 174 d except for 1988, when they were weaned in late August at an average age of 133 d because of drought. Adjusted 200-d weights were computed by multiplying preweaning ADG by 200 and adding birth weight. Adjusted 400-d weights were computed by multiplying ADG (from weaning until the heifers were moved from the feedlot to pasture in April) by 200 and adding adjusted 200-d weight. Adjusted 550-d weights were computed by multiplying ADG during the grazing season by 150 and adding adjusted 400-d weight.

At weaning, the heifers were placed in a drylot on a diet with approximately 2.63 Mcal ME/kg DM and 13.2% CP consisting of 43% corn silage, 31% corn, 19% alfalfa hay, and 8% supplement for 47 d. This was followed by a diet with approximately 2.27 Mcal ME/kg DM and 12.0% CP consisting of 59% corn silage, 37% alfalfa haylage, and 4% supplement for 164 d. The heifers were moved to improved, cool-season pasture in late April, and then moved to improved, warm-season pasture in June, where they remained until pregnancy diagnosis in early October.

The heifers were bred to Red Poll bulls by natural service in multiple-sire pastures. The average beginning date of the breeding season was May 25, and the average ending date was July 28. Pregnancy status was determined by rectal palpation in early October, at which time the 550-d weight and hip height were recorded.

Onset of puberty was defined as the date of the first observed estrus or estimated conception date, whichever occurred first. Conception date was estimated as 285 d before calving date. Before the breeding season, first observed estrus was required to be confirmed by a subsequent estrus within 45 d after the first estrus. Estrus was checked twice daily from an average age of 294 d until the beginning of the breeding season (average age of 403 d) except for the 1987 heifers, which were checked until the middle of the breeding season

Table 2. Number of heifers by breed group of sire and breed group of dam subclass

Breed group of sire	Breed of dam subclasses ^a						Total heifers
	Angus	Hereford					
		COL	WWL	YWL	IXL	MARC	
Ref. Angus	41	21	13	4	4	1	84
Ref. Hereford	45	13	9	7	4	1	79
1980s Angus	16	10	4	3	6	1	40
1980s Hereford	31	8	7	2	3	2	53
Charolais	20	5	6	3	2	0	36
Shorthorn	41	14	4	5	6	3	73
Galloway	39	16	9	6	5	1	76
Longhorn	45	10	11	8	6	1	81
Nellore	47	12	5	7	6	5	82
Piedmontese	48	19	3	13	4	2	89
Salers	55	12	7	8	6	2	90
Total	428	140	78	66	52	19	783

^aCOL = Control line, WWL = weaning weight line, YWL = yearling weight line, IXL = index of yearling weight and muscling score line, and MARC = Hereford population selected primarily for yearling weight.

(average age of 444 d). Before the breeding season, teaser bulls were used as an estrus detection aid. Weight at puberty was interpolated from the preceding and subsequent weights.

The data were analyzed with least squares, mixed-model methods (Harvey, 1985). The fixed effects in the models for all traits included sire breed group (treating reference Hereford and Angus as distinct from 1980s Hereford and Angus), dam breed, line nested within dam breed (Hereford only), age of dam (classes were 3, 4, 5 to 9, 10, 11, and ≥ 12 yr), and birth year. Birth date was included as a covariate in the analysis of hip height only. Sire nested within breed was fit as a random effect. The initial model included all two-factor interactions. The final model for each trait included only the significant ($P < .05$) two-factor interactions, except that the sire breed \times dam breed interaction was always retained because it was required to make the least squares means for Hereford \times Angus crosses estimable. Hypotheses involving sire breed group and its interaction effects were tested using sire within breed as the error

term, and hypotheses involving other fixed effects were tested using the residual mean square as the error term. Heritability, genetic variance, and phenotypic variance were estimated in the final model for each trait following procedures outlined for mixed models by Harvey (1985).

The linear contrast procedure of Harvey (1985) was used to compute the least significant difference (**LSD.05**; $P < .05$) for the contrast between each pair of sire breed groups using the sire within breed mean square as the error term. More comparisons were made than are provided for by independent degrees of freedom. Thus, the error rate over the entire set of comparisons may be different than indicated by the probability level noted ($P < .05$). Instead of presenting all 36 of the pairwise contrasts, only the mean LSD.05 is presented for each trait. Sire breed group differences greater than the mean LSD.05 were considered significant. This procedure for mean separation results in Charolais being declared significantly different from other breed groups slightly more frequently than is justified because of a

Table 3. Number of sires used each year

Breed group of sire	Number of sires ^a					Total ^b
	1986	1987	1988	1989	1990	
Ref. Angus	12	11 (10)	4 (4)	10 (4)	6 (5)	20
Ref. Hereford	10	9 (9)	7 (7)	9 (9)	5 (5)	10
1980s Angus	7	4 (2)	7 (1)	6 (1)	5 (3)	22
1980s Hereford	12	8 (1)	6 (2)	6 (2)	5 (5)	27
Charolais	6	5 (2)	5 (2)	9 (1)	6 (4)	22
Shorthorn	9	11 (5)	4 (0)	7 (6)	12 (10)	22
Galloway	11	8 (2)	7 (3)	8 (4)	11 (9)	27
Longhorn	11	9 (3)	8 (5)	7 (5)	7 (6)	23
Nellore	13	10 (8)	8 (2)	9 (8)	5 (5)	22
Piedmontese	7	7 (5)	9 (4)	5 (2)	5 (2)	20
Salers	14	9 (5)	10 (6)	9 (6)	5 (5)	25

^aNumbers of sires that were repeated from a previous year are shown in parentheses.

^bTotal number of different sires used.

less than average number of observations. Conversely, the reference Hereford-Angus would not be declared different as often as the data would justify because of a larger than average number of observations.

Although the straightbred and reciprocal crossbred progeny were produced from the Hereford and Angus sires, only the pooled means of the reciprocal crosses are reported here. The results of the diallel between reference and 1980s Hereford and Angus are presented separately.

The standard for comparison with previous cycles of the GPE Program is the sire breed group, reference Hereford-Angus, which is computed as the average of the progeny of reference Hereford sires with Angus dams and the progeny of reference Angus sires with Hereford dams. Similarly, 1980s Hereford-Angus refers to the average of the progeny of 1980s Hereford sires with Angus dams and the progeny of 1980s Angus sires with Hereford dams.

Differences between sire breed groups estimate half of the difference in direct breed effects plus any differences that may exist in specific heterosis between the sire breeds and Hereford or Angus. The specific heterosis between Nellore and the *Bos taurus* dams is expected to be greater than the specific heterosis among *Bos taurus* breeds, considering the increased heterosis observed in other *Bos indicus* × *Bos taurus* crosses (Cartwright et al., 1964; Koger, 1980).

Least squares means for age and weight at puberty were computed from a subset of the data that included only those heifers that expressed puberty. These least squares means were biased downward by the censoring of heifers that did not express puberty within the allotted time, especially in the later maturing breeds. Furthermore, based on the distributions of age at puberty reported by Laster et al. (1976, 1979) and Gregory et al. (1979), a substantial proportion of the heifers of the earlier maturing breeds should have reached puberty prior to the initiation of estrus detection, resulting in an upward bias in the mean age at puberty of these breeds and an excess of puberty observations during the first 21 d of estrus detection. The downward bias in age at puberty of later maturing breeds and upward bias in earlier maturing breeds results in underestimation of the differences between breeds. The same biases also apply to weight at puberty.

In Cycle IV, to control costs, estrus detection began when the heifers averaged 54 d older and ended when they averaged 67 d younger than in the previous three cycles of the GPE Program (Laster et al., 1976, 1979; Gregory et al., 1979). To adjust for the biases described above, the cumulative distribution for age at puberty for each breed group was estimated. A least squares analysis of a variable defined as 1 for heifers that had already reached puberty and 0 for heifers that had not yet reached puberty was performed for each of the following ages: 330, 345, 360, 375, and 390 d. At each age, the data set was edited to include only heifers that had a full opportunity to express estrus by the specified age.

The ages examined ranged from 330 to 390 d because the number of available uncensored records was much smaller at 315 or 405 d and the analyses provided results inconsistent with those at 330 or 390 d, respectively.

For example, a heifer born on May 20 was 373 d old when estrus detection ended the following May 28. She could have had her first estrus when she was 374 d old but would not have been observed at 375 d and was edited from the data set for puberty by 375 d. Similarly, heifers younger than 359 or 389 d at the end of estrus were edited from the data sets for puberty by 360 or 390 d, respectively.

Conversely, a heifer born March 28 was 311 d old when estrus detection began the following February 2. She could have had an unobserved estrus when she was 310 d old and then been observed in estrus when she was 331 d old, but she would have been coded as prepubertal at 330 d. Therefore, heifers older than 310 d at the beginning of estrus detection were edited from the data set for puberty by 330 d. However, the heifer born March 28 had been observed for estrus more than 21 d by the time she was 345 d old; therefore, she was included in the data sets for 345, 360, 375, and 390 d.

Thus, the least squares means for the percentage of heifers expected to have reached puberty by 330, 345, 360, 375, or 390 d are unbiased with respect to data censoring, because only records unaffected by censoring remained in each analysis. These least squares means were used to predict the mean and standard deviation of age at puberty for each breed. In previous reports, when estrus detection was initiated at younger ages (250 d, Laster et al., 1976; 240 d, Laster et al., 1979; 230 d, Gregory et al., 1979), age at puberty was found to be approximately normally distributed. Therefore, the inverse cumulative normal function was used to transform the cumulative puberty fractions above into deviates of a standard normal distribution, which were expected to be linearly related to age. The regression of age on the deviates was used to estimate the distribution of age at puberty for each breed. The intercept (predicted age at which the deviate is zero) is the predicted median and mean of age at puberty. This is reported as the “predicted age at puberty” because it is corrected for the censoring of puberty date. The slope (change in age when the deviate changes by one standard deviation) is the predicted standard deviation of age at puberty.

“Predicted weight at puberty” was computed by adjusting the least squares mean for weight at puberty with the appropriate least squares mean for postweaning ADG multiplied by the difference between predicted age at puberty and the least squares mean for age at puberty.

Analysis of variance is generally considered to be robust with respect to distributional assumptions (Box et al., 1978). Because of the lack of a direct test of hypotheses regarding the predicted age and weight at puberty, the least squares analyses of the censored age

Table 4. Mean squares for growth and reproductive traits of females

Source	df ^a	Age at puberty, d	Weight at puberty, kg	200 d weight, kg	ADG 200 to 400 d, kg	400 d weight, kg	ADG 400 to 550 d, kg	550 d weight, kg	550 d hip height ^b , cm	Pregnant at 550 d, %
Sire breed (B)	10	12,725**	23,121**	6,456**	.2410**	27,486**	.1121**	33,800**	1,156.9**	.1582
B × D	10	1,205	948	286	.0170	1,256	.0157	1,652	8.5	.0760
Sire/B ^c	229	1,189	1,054**	546	.0098**	1,063*	.0153*	1,088	14.4**	.0987*
Dam breed (D)	1	8,357**	17,133**	33,466**	.0109	40,977**	1.3130**	1,303	1.4	.8680**
Line/D	4	718	4,240**	4,498**	.0206*	8,015**	.0334*	9,623**	56.4**	.0604
Age of dam (A)	5	1,525	1,803*	2,010**	.0105	3,339**	.0608**	1,738	15.0	.0218
Year of birth (Y)	4	15,920**	9,694**	11,534**	.2479**	39,310**	1.0135**	68,849**	36.7**	.0649
D × Y	—	—	—	1,751**	—	—	—	—	—	—
A × Y	—	—	—	—	—	—	.0225*	—	—	—
Birth date	—	—	—	—	—	—	—	—	23.2	—
Residual	519	1,072	784	466	.0074	860	.0125	923	10.8	.0800

^aDegrees of freedom (df) listed are for ADG from 200 to 400 d, 400-d weight, 550-d weight, and pregnancy rate. For age and weight at puberty, df were the same except that there were 503 residual df. For 200-d weight, df were the same except that there were 4 df for D × Y and 515 residual df. For ADG from 400 to 550 d, df were the same except that there were 14 df for A × Y and 505 residual df. For 550-d hip height, df were the same except that there was 1 df for birth date and 518 residual df.

^bBirth date was included as a linear covariate to adjust to an age-constant basis.

^cSire/B was used as the denominator term to test effects of B and B × D. All other sources of variation were tested against the residual mean square.

*P < .05.

**P < .01.

and weight at puberty were used to determine the significant factors influencing these traits.

Results and Discussion

Puberty

The analysis of variance is presented in Table 4. The effects of sire breed group, dam breed, and year of birth were significant ($P < .01$) for age at puberty. As was the case for 400-d weight, weight at puberty was influenced ($P < .05$) by all main effects considered, but none of the interactions. The overall least squares means for age and weight at puberty were 357 d and 320 kg, respectively.

Although the sire breed × dam breed interaction was not significant for any trait, it was retained in the model for all traits for the purpose of estimating means for the Hereford × Angus cross heifers and because four of the 22 cells in this interaction were straightbred matings and the remaining 18 cells were F₁ matings.

The least squares means for cumulative percentage reaching puberty by 330, 345, 360, 375, and 390 d and the predicted means for age and weight at puberty are reported in Table 5. The means for the range from 330 to 390 d included the 50% point (median) for each sire breed group and dam breed group except for the progeny of Nellore sires. Therefore, the predicted age at puberty should provide an estimate of median age at puberty that is relatively robust with respect to the assumption of normality, despite the censoring of puberty data on both ends of the time period.

Breed of Sire Effects. A higher proportion ($P < .05$) of the progeny of Piedmontese and Shorthorn sires than of the progeny of Charolais and Longhorn sires reached

puberty by 360 d. Progeny of Hereford-Angus, Gallo-way, and Salers sires were intermediate to the progeny of Piedmontese or Shorthorn and Charolais or Longhorn sires for percentage reaching puberty by 360 d. Significantly fewer Nellore-sired heifers than all other breed groups reached puberty by 360 d.

Although only 52% of the Nellore-sired heifers were observed in estrus by the end of the estrus detection period, 94% of them were pregnant by the end of the breeding season. One possible explanation is that many of the Nellore-sired heifers reached puberty during the breeding season and conceived on their first or second estrus. However, this would require that the 48% of the Nellore-sired heifers that were prepubertal at the beginning of the breeding season achieved at least an 88% pregnancy rate during the 64-d breeding season, which seems rather implausible.

It is likely that the lower proportion of Nellore-sired heifers observed in estrus was at least partly due to greater difficulty in detecting estrus in them, as compared with the *Bos taurus* heifers. Plasse et al. (1970) reported that 26% of ovulations in grade Brahman heifers in confinement were silent and that estrus lasted a mean of only 6.7 h. Vaca et al. (1985) suggested that confinement exacerbated the problem of silent estrus in Zebu females. Galina et al. (1982) reported that Brahman × Charolais heifers received only 1.6 mounts per hour during estrus compared with 2.8 mounts per hour for Charolais heifers, suggesting less overt estrus behavior in *Bos indicus* × *Bos taurus* crosses, even during estrus.

It seems likely that behavioral differences between the Nellore-sired and *Bos taurus*-sired heifers caused a greater proportion of the Nellore-sired heifers to be first detected in puberty on their second, third, or later

Table 5. Least squares means for age and weight at puberty corrected for censoring

Item	LS mean for % reaching puberty by specified age in days					Inverse cumulative normal (z) by specified age in days					Predicted age at puberty, d		Predicted weight at puberty, kg	LS Mean % detected in estrus	
	330	345	360	375	390	330	345	360	375	390	Mean ^a	SD ^b	Mean ^c		
Sire breed group															
Ref Her.-Angus	29 ± 6	53 ± 6	64 ± 6	75 ± 5	80 ± 5	-.56	.08	.35	.69	.86	348	41	309	88 ± 5	
1980s Her.-Angus	23 ± 8	42 ± 8	59 ± 8	82 ± 8	85 ± 8	-.73	-.20	.23	.92	1.06	352	31	330	93 ± 6	
Charolais	33 ± 8	52 ± 8	53 ± 8	78 ± 7	94 ± 7	-.45	.04	.08	.78	1.53	348	30	345	94 ± 6	
Shorthorn	43 ± 7	54 ± 7	69 ± 6	81 ± 6	86 ± 6	-.17	.10	.50	.89	1.09	338	45	329	93 ± 5	
Galloway	31 ± 6	43 ± 7	56 ± 6	75 ± 6	84 ± 6	-.49	-.18	.14	.68	.98	351	39	305	88 ± 5	
Longhorn	32 ± 6	33 ± 6	50 ± 6	67 ± 5	79 ± 6	-.47	-.45	-.01	.45	.81	357	41	283	78 ± 5	
Nellore	10 ± 6	14 ± 7	14 ± 6	29 ± 6	40 ± 6	-1.26	-1.10	-1.07	-.55	-.25	405	53	341	52 ± 5	
Piedmontese	48 ± 6	64 ± 7	73 ± 6	83 ± 5	92 ± 6	-.05	.37	.61	.95	1.38	332	43	298	92 ± 5	
Salers	19 ± 6	36 ± 7	58 ± 6	78 ± 5	89 ± 6	-.87	-.37	.21	.77	1.23	355	28	338	97 ± 4	
LSD.05 ^d	16	18	16	15	15									11.8	
Dam breed group															
Angus	37 ± 4	47 ± 4	61 ± 4	78 ± 3	87 ± 4	-.34	-.08	.28	.76	1.13	346	39	324	89 ± 3	
Hereford ^e	25 ± 4	39 ± 5	50 ± 4	66 ± 4	73 ± 4	-.67	-.27	.01	.42	.61	359	45	311	83 ± 4	
COL	25 ± 5	34 ± 6	57 ± 5	71 ± 5	83 ± 6	-.67	-.42	.19	.56	.95	356	35	296	89 ± 5	
WWL	30 ± 7	44 ± 7	60 ± 7	74 ± 7	72 ± 7	-.52	-.16	.24	.65	.57	353	46	305	82 ± 6	
YWL	19 ± 7	40 ± 7	41 ± 7	64 ± 7	72 ± 7	-.87	-.25	-.22	.36	.58	363	41	309	76 ± 6	
IXL	24 ± 8	34 ± 8	41 ± 8	51 ± 8	63 ± 8	-.71	-.42	-.22	.03	.32	372	60	315	74 ± 7	
MARC	27 ± 12	45 ± 12	51 ± 12	72 ± 12	76 ± 12	-.61	-.13	.03	.57	.70	355	44	333	95 ± 9	
No. of records	668	783	780	748	646									783	

^aIntercept of the regression of age on z (the standard normal deviate corresponding to the percentage of heifers having reached puberty).

^bSlope of the regression of age on z (the standard normal deviate corresponding to the percentage of heifers having reached puberty).

^c(wt at puberty LS mean) + (200 to 400 d ADG) × [(predicted age at puberty mean) - (age at puberty LS mean)].

^dBreed group differences larger than the least significant difference (LSD.05) are considered significant ($P < .05$).

^eCOL = Control line, WWL = weaning weight line, YWL = yearling weight line, IXL = index of yearling weight and muscling score line, and MARC = Hereford population selected primarily for yearling weight.

Table 6. Least squares means and standard errors for growth traits and pregnancy rate of females for breed group of sire and breed group of dam

Item	200 d weight, kg	ADG 200 to 400 d, kg	400-d weight, kg	ADG 400 to 550 d, kg	550-d weight, kg	550-d hip height, cm	Pregnant at 550 d, %
Sire breed group							
Ref. Hereford-Angus	206 ± 3	.748 ± .012	356 ± 4	.252 ± .017	398 ± 4	121.5 ± .5	96.4 ± 3.9
1980s Hereford-Angus	215 ± 4	.792 ± .017	374 ± 6	.297 ± .022	422 ± 6	126.1 ± .6	86.0 ± 5.4
Charolais	229 ± 4	.804 ± .017	390 ± 6	.340 ± .023	445 ± 6	131.9 ± .6	84.7 ± 5.4
Shorthorn	220 ± 3	.822 ± .014	384 ± 5	.274 ± .020	429 ± 5	129.5 ± .5	94.2 ± 4.4
Galloway	209 ± 3	.695 ± .013	348 ± 4	.248 ± .019	389 ± 4	121.7 ± .5	86.2 ± 4.2
Longhorn	197 ± 3	.625 ± .013	321 ± 4	.309 ± .019	371 ± 4	125.3 ± .5	96.9 ± 4.0
Nellore	221 ± 3	.711 ± .013	364 ± 4	.353 ± .019	420 ± 4	132.2 ± .5	93.9 ± 4.2
Piedmontese	215 ± 3	.693 ± .014	353 ± 4	.290 ± .020	401 ± 4	126.7 ± .5	100.6 ± 4.3
Salers	225 ± 3	.780 ± .013	380 ± 4	.307 ± .019	430 ± 4	129.9 ± .5	94.5 ± 4.1
LSD.05 ^a	8.3	.035	11.5	.044	11.7	1.35	11.1
Dam breed group							
Angus	225 ± 2	.743 ± .008	373 ± 3	.222 ± .014	411 ± 3	126.6 ± .3	87.1 ± 2.6
Hereford ^c	204 ± 2	.732 ± .010	351 ± 3	.351 ± .015	407 ± 3	126.4 ± .4	97.4 ± 3.0
COL	191 ± 3	.700 ± .011	333 ± 4	.330 ± .018	385 ± 4	124.9 ± .4	92.5 ± 3.7
WWL	201 ± 4	.731 ± .014	348 ± 5	.351 ± .021	404 ± 5	126.5 ± .6	96.0 ± 4.7
YWL	196 ± 4	.739 ± .015	345 ± 5	.346 ± .021	400 ± 5	125.9 ± .6	94.9 ± 4.7
IXL	200 ± 4	.738 ± .017	347 ± 6	.404 ± .024	412 ± 6	126.4 ± .6	100.0 ± 5.5
MARC	230 ± 6	.750 ± .024	381 ± 8	.327 ± .032	432 ± 8	128.6 ± .9	103.6 ± 7.8
Genetic parameters^b							
h^2	.21 ± .15	.37 ± .15	.28 ± .15	.28 ± .15	.22 ± .15	.40 ± .15	.28 ± .15
σ_p	22.2	.0905	30.4	.1159	31.24	3.46	29.3
σ_g	10.2	.0549	16.2	.0608	14.59	2.18	15.6
$2R/\sigma_g$	6.36	7.19	8.51	3.45	10.16	9.81	

^aBreed group differences larger than the least significant difference (LSD.05) are considered significant ($P < .05$).

^bGenetic parameters: h^2 denotes heritability, σ_p denotes phenotypic standard deviation, σ_g denotes square root of estimated additive genetic variance, R denotes range of difference between the highest and lowest breed group means.

^cCOL = Control line, WWL = weaning weight line, YWL = yearling weight line, IXL = index of yearling weight and muscling score line, and MARC = Hereford population selected primarily for yearling weight.

cycle. The resulting increase in bias between observed puberty and physiological puberty in Nellore-sired heifers should be taken into account when interpreting the reported means. The Brahman-sired and Sahiwal-sired heifers in Cycle III of the GPE Program also had high pregnancy rates despite a greater age at puberty (Gregory et al., 1979). Behavioral differences should also be considered when interpreting the age at puberty of these heifers. Nonetheless, *Bos indicus* females exhibit a number of physiological differences relative to *Bos taurus* females (Randel, 1984) and are expected to reach puberty later (Plasse et al., 1968).

Breed of Dam Effects. The progeny of Angus dams reached puberty earlier ($P < .01$) and heavier ($P < .01$) than progeny of Hereford dams.

Hereford Selection Line Effects. Weight at puberty was influenced ($P < .01$) by line within Hereford dams. The weights followed a pattern very similar to that for 200-, 400-, and 550-d weights (Table 6). The MARC Hereford line was consistently heaviest, COL was consistently lightest, and IXL, WWL, and YWL were intermediate and relatively similar. Line within Hereford dams did not significantly influence age at puberty, but the IXL and YWL lines tended to reach puberty later.

Wolfe et al. (1990) evaluated age and weight at puberty in the selection lines resulting in the Hereford

dams in this study. The lines selected for growth tended to reach puberty at a younger age. Direct effects on age at puberty were -24, -11, and -35 d and maternal effects on age at puberty were 11, -7, and 5 d for the WWL, YWL, and IXL relative to COL, respectively. Direct effects on weight at puberty were -15, 1, and 6 kg and maternal effects on weight at puberty were 18, -2, and 2 kg for the WWL, YWL, and IXL relative to COL, respectively. The effects on weight at puberty are consistent with the present study. The effects on age at puberty are generally reversed in direction relative to the present study, but were not significant in either study.

Growth Traits

The effects of sire breed group, line within Hereford dams, and year of birth were significant ($P < .05$) for all growth traits. The overall least squares means for 200-, 400-, and 550-d weights were 214, 362, and 409 kg, respectively. The overall least squares means for average daily gains from 200 to 400 and 400 to 550 d were .738 and .287 kg/d, respectively, and the mean 550-d hip height was 126.5 cm.

Breed of Sire Effects. The least squares means and standard errors for sire breed groups are presented in

Table 6. The progeny of Charolais sires were heaviest at 200, 400, and 550-d of age. The progeny of Salers and Shorthorn sires tended to rank next, followed by the progeny of Nellore and 1980s Hereford-Angus sires. The Piedmontese, reference Hereford-Angus, and Galloway progeny tended to rank next. The Longhorn-sired heifers were significantly lighter than all other sire breed groups at 200, 400, and 550 d.

The sire breed rankings for ADG from 200 to 400 d were quite different from those for ADG from 400 to 550 d. Progeny of Shorthorn, Hereford, Angus, and Galloway sires ranked higher for ADG from 200 to 400 d (feedlot environment, during winter) than for ADG from 400 to 550 d. Conversely, progeny of Nellore, Longhorn, and Piedmontese sires ranked higher for ADG from 400 to 550 d (pasture environment, during summer) than for ADG from 200 to 400 d. Similar results have been reported previously for growth patterns of F₁ cross females by tropically adapted sire breeds vs those by sire breeds that evolved in temperate climates (Gregory et al., 1979; Freetly and Cundiff, 1997).

Paschal et al. (1995) reported that Nellore-sired heifers had 11.8 cm of greater yearling hip height than Angus-sired heifers, which is consistent with the results in the present study, and that Nellore-sired heifers had 26.6 kg greater yearling weight than Angus-sired heifers, which is somewhat different from the results in the present study. In Paschal et al. (1995), the fall-born Nellore-sired and Angus-sired heifers gained .34 and .18 kg/d, respectively, during a summer postweaning period on pasture in Texas, whereas, in the present study, the spring-born progeny of Nellore, reference Hereford-Angus, and 1980s Hereford-Angus sires gained .71, .75, and .79 kg/d, respectively, during a winter postweaning period in a feedlot in Nebraska. Therefore, the genotype × environment interaction described by Olson et al. (1991) seems to apply to comparisons of Nellore, as well as Brahman and Sahiwal, with British breeds.

Progeny of Nellore and Charolais sires were significantly taller at 550 d than progeny of Salers and Shorthorn sires, which were in turn taller than progeny of Piedmontese, Longhorn, and 1980s Hereford-Angus sires. Progeny of Galloway and reference Hereford-Angus sires were significantly shorter than all other breeds.

Breed of Dam Effects. Progeny of Angus dams were heavier ($P < .01$) than progeny of Hereford dams at 200 and 400 d of age. Progeny of Hereford dams gained significantly faster than did progeny of Angus dams from 400 to 550 d. By 550 d, the differences in weight and height were nonsignificant, although the progeny of Angus dams tended to be slightly heavier and taller.

Pregnancy Rate

Pregnancy rate was affected significantly only by sire within breed and breed of dam. The overall least squares mean for pregnancy rate was 92.2%.

Breed of Sire Effects. Sire breed group was not a significant effect in the model for pregnancy rate. Despite a much lower percentage of heifers detected in estrus and a significantly greater age at puberty, the Nellore-sired F₁ cross heifers had a pregnancy rate that was slightly above the overall mean. This is consistent with the report of Riley et al. (1998) that lifetime percentage calf crop at birth was 93.9% in Nellore × Hereford cows compared with 85.2% in Angus × Hereford cows.

Breed of Dam Effects. Although they reached puberty later, F₁ cross progeny of Hereford dams had a higher ($P < .01$) pregnancy rate than those of Angus dams. This difference is larger in magnitude but consistent with those observed in previous cycles of the GPE Program (Laster et al., 1976, 1979; Gregory et al., 1979). These findings are consistent with reports showing greater heterosis in crosses of Herefords with other breeds than in crosses of Angus with the same breeds for reproductive traits (Cundiff et al., 1974; Dearborn et al., 1987).

General

The Piedmontese-sired heifers had the highest percentage reaching puberty by 360 d and had the highest pregnancy rate of all breeds evaluated in this cycle of the GPE Program. The Piedmontese sires used in this study have all been confirmed to be homozygous for a mutation in the myostatin gene (Casas et al., 1999). Homozygosity of this mutation results in the condition commonly known as “double muscling” (McPherron and Lee, 1997; Smith et al., 1997). Double muscling is generally associated with reduced fertility (including delayed puberty) as well as greater leanness (Arthur, 1995). For most traits, the heterozygotes are intermediate to the alternate homozygotes but are more similar to the normal genotype (Arthur, 1995). Because of the low expected frequency of double muscling in the dam populations and the lack of obviously homozygous individuals, the Piedmontese F₁ cross heifers in this study are assumed to be heterozygous for the mutation in myostatin. Therefore, the Piedmontese effect includes both the effect of heterozygosity at myostatin and the sum of the effects at all other loci. Thus, it is not clear whether there is overdominance for fertility at the myostatin locus or whether the Piedmontese background has high inherent fertility, perhaps as compensation for the high frequency of double muscling in the Piedmontese breed.

The Hereford and Angus bulls that were born from 1982 to 1985 sired progeny that were significantly heavier at 200, 400, and 550 d; gained significantly faster from 200 to 400 d and from 400 to 550 d; and were significantly taller at 550 d than progeny of the reference Hereford and Angus bulls that were born from 1963 to 1970.

Estimates of heritabilities and additive genetic and phenotypic standard deviations are presented in Table 6. The estimates for growth traits are consistent with

previous reports, but the heritability for pregnancy rate was greater than most estimates in the literature (Koots et al., 1994; Splan et al., 1998).

The range, R , of differences between sire breed groups estimates half of the additive genetic difference between the respective breeds plus any difference in specific heterosis that may exist between the respective breeds and Hereford or Angus. The magnitude of between-breed differences relative to within-breed variation is expressed as $2R/\sigma_g$, the standardized range of breed means in Table 6. This assessment of variation was not applied to pregnancy rate because the distribution of binomial traits is not expected to be symmetrical. The range of breed means was at least six genetic standard deviations for most growth traits, indicating that differences between breeds are large relative to differences within breeds.

Implications

Significant differences in postweaning growth, age, and weight at puberty exist among heifers sired by Hereford, Angus, Charolais, Shorthorn, Galloway, Longhorn, Nellore, Piedmontese, and Salers bulls. Estimation of these differences is an important component of characterizing the diversity of germplasm available to beef producers for the full spectrum of economically important traits so that the breeds can be optimally combined in breeding systems.

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