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2005

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Gargantini, G.; Cundiff, L. V.; Lunstra, D. D.; and Van Vleck, L. D., "Genetic Relationships Between Male and Female Reproductive Traits in Beef Cattle" (2005). *Roman L. Hruska U.S. Meat Animal Research Center*. 168.

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Genetic Relationships Between Male and Female Reproductive Traits in Beef Cattle¹

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Abstract

Reproductive traits were measured for 234 bulls and 1184 heifers from matings of three dam breeds (Angus, Hereford, and MARC III) with six sire breeds (Angus, Hereford, Brahman, Boran, Tuli, and Belgian Blue) from the Germ Plasm Evaluation (GPE) Program at Roman L. Hruska US Meat Animal Research Center. Male traits were yearling scrotal circumference (YSC), height (YH), and yearling BW; age at puberty (AP1; production of 50 million sperm with $\geq 10\%$ progressive motility); age, scrotal circumference, average testis length, and testicular volume when 500 million sperm were produced with $\geq 50\%$ progressive motility (AP3, SC3, L3 and V3, respectively); and 15-mo BW (15W) and height (15H). Traits of females were age at puberty (AP, first estrus) and pregnancy rate (PR) at 18 mo. The objective was to determine whether indirect selection on male traits would be effective for improving female fertility traits. Selection of males on AP1, AP3, SC3, L3, V3, YH, 15W, and 15H may be useful for

improving PR because of genetic correlations and low heritability for PR. Although no male trait was found to be effective for improving AP in females through indirect selection, YSC and SC3 were the most favorable. If heritability were as large as estimated in this study for AP (0.52), direct rather than indirect selection would seem to be more effective for AP in heifers, although the difficulty of measuring AP in heifers also would need to be considered. Male reproductive traits, such as scrotal circumference and also YH and 15H, however, are easier and less expensive to measure than female reproductive traits, and greater selection intensity can be applied to these male traits.

(Key Words: Beef Cattle, Fertility, Growth, Selection.)

Introduction

For segments of the industry that try to calve heifers at 2 yr of age, much of the success of a beef cow-calf enterprise will depend on having heifers calve at 2 yr of age and to re-breed shortly after first calving. Therefore, for such producers, selection for improving heifer genetic potential for fertility will be important (Doyle et al., 2000). Based on possible selection intensity for males and possibly greater heritabilities, selection for reproductive traits of males might be

more effective than selection directly on female reproductive traits. The objective of this study was to investigate whether indirect selection might be more effective than direct selection for improvement of age at puberty and heifer pregnancy rate (PR) of heifers.

Materials and Methods

Data were from Cycle V of the Germ Plasm Evaluation (GPE) at the Roman L. Hruska US Meat Animal Research Center (Clay Center, NE). The base cow-herd for Cycle V involved about 500 Angus, 350 Hereford, and 550 MARC III composite ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Pinzgauer, and $\frac{1}{4}$ Red Poll) cows. These cows were mated to six sire breeds: Angus, Hereford, Brahman, Boran, Tuli, and Belgian Blue for 3 yr (1992, 1993, and 1994). Angus sires were bred to Hereford and MARC III cows, and Hereford sires were bred to Angus and MARC III cows. All other sire breeds were bred to Angus, Hereford, and MARC III cows. All cows were 4 yr of age or older. The total number of bull and heifer calves by sire by dam breed combination is shown in Table 1. Each year, a sample of about 80 male calves and about 400 female calves was evaluated for growth and pubertal development.

¹Published as paper no. 14841, Journal Series, Nebraska Agric. Res. Div., Univ. of Nebraska, Lincoln 68583-0908.

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TABLE 1. Number of male and female cattle in the analyses by breed of sire and breed of dam and number of sires by breed^a.

Sire breed	Sires (no.)	Dam breed					
		Hereford		Angus		MARC III	
		Male	Female	Male	Female	Male	Female
Hereford	31	—	—	18	65	14	87
Angus	41	8	28	—	—	17	103
Brahman	45	9	36	16	64	22	112
Boran	8	9	33	15	73	19	100
Tuli	9	10	34	14	77	29	133
Belgian Blue	25	11	26	15	79	18	132

^aNumber sires per breed.

Calves were born between mid March and mid May each year. Calves were creep-fed whole oats from mid July until weaning in early October. Bull calves were weaned at about 185 d of age. Following weaning each year, samples of about 80 bull calves were randomly assigned to two drylot pens of approximately 40 bulls each with all sire and dam breeds represented in each pen. The calves were fed a diet of corn silage, rolled corn, and protein-mineral-vitamin supplement (2.69 Mcal of ME/kg of DM; 12.88% CP) for 9 mo.

After weaning and a 42-d adjustment period, the sample of heifers was assigned to two pens per sire breed (Hereford- and Angus-sired females were treated as a single sire breed). Heifers were weighed when assigned to their treatment groups and then every 28 d until moved from drylot to pasture. The heifers were subsequently weighed at the beginning and end of the breeding season. Heifers were palpated approximately 65 d following the end of the breeding season to determine PR. Age at puberty was defined as the date of first observed standing estrus. Females were checked visually twice daily for estrus beginning on February 1 through the end of the breeding season.

For the bulls, BW, hip height, and scrotal circumference were measured at 28-d intervals. Puberty was defined

as the age when a bull first produced an ejaculate containing at least 50×10^6 sperm with $\geq 10\%$ progressive motility (Lunstra et al., 1978). All bulls reached puberty when scrotal circumference was between 30 and 32.5 cm. Age at first freezable semen was defined as the age when a bull first produced an ejaculate containing at least 500×10^6 sperm with $\geq 50\%$ progressive motility (Lunstra et al., 1993). Semen collection ceased for a bull when his ejaculate contained at least 500×10^6 sperm with $\geq 50\%$ progressive motility.

Records for a total of 234 F₁ bulls and 1184 F₁ heifers were evaluated. Means, ranges, and phenotypic variances for growth and fertility traits are summarized in Table 2.

Estimates of genetic parameters were obtained using MTDFREML (Boldman et al., 1995). Traits analyzed for males were yearling height (YH), yearling scrotal circumference (YSC), 15-mo BW (15W), 15-mo scrotal circumference (15SC), age at puberty (AP1), and age (AP3), scrotal circumference (SC3), average testis length (L3), and testicular volume (V3) when a bull first produced freezable semen. Traits analyzed for females were age at puberty (AP) and PR at palpation. To minimize density of the estimating equations and to account for possible interactions, the model included interactions between year and month of birth, and be-

tween age of dam and line (breed group) of the animal as fixed effects; random effects included animal direct genetic, dam-maternal (sum of genetic plus permanent environmental), and residual effects.

Expected responses to direct and indirect selection were calculated for pairs of growth and reproductive traits in both males (M) and females (F) as described by Toelle and Robison (1985) using estimates of (co)variance components from the data. The selection intensity factor for males times one-half (one generation away) used for males ($\frac{1}{2}i_M$) was twice the magnitude of the direct selection intensity factor used for females, $i_F = 0.482$ ($\frac{1}{2}i_M = 2 i_F$). These intensity factors correspond approximately to selection of the best 7 and 70% of males and females, respectively. Efficiency of direct and indirect selection was compared using the ratio (Q) of expected response to direct selection on the female trait ($\Delta G_{F,F}$) and to indirect selection on the male trait ($\Delta G_{F,M}$). Expected responses were based on individual performance using the formulas of Falconer and Mackay (1996): $\Delta G_{F,M} = 0.5 i_M h_F h_M r_{GF,GM} \sigma_{PF}$ and $\Delta G_{F,F} = i_F h_F^2 \sigma_{PF}$, where σ_{PF} = phenotypic standard deviation for the female reproductive trait, h_F and h_M = square roots of the heritabilities of the female and male traits, and $r_{GF,GM}$ = genetic correlation between the male and female traits. The ratio of responses to indirect and direct selection was computed as $Q = \Delta G_{F,M} / \Delta G_{F,F}$. If Q was >1 , indirect selection would be expected to be more effective than direct selection.

Results and Discussion

Estimates of heritability and genetic correlations among growth and reproductive traits are presented in Tables 3, 4, 5, and 6. Heritability estimates for growth were moderate to high; estimates for male yearling BW, 15W, SC3, and V3 were near unity probably because of the relatively small sample size. The heritability estimate for YH in males was low (0.20).

TABLE 2. Estimates of phenotypic variances and unadjusted means and ranges for growth and fertility traits^a.

Item	σ_p^2	Mean	Minimum	Maximum
MYW (kg)	1487.44	436.87	316.24	562.50
YH (cm)	12.32	126.84	111.76	137.79
15H (cm)	13.85	128.60	113.67	142.24
15W (kg)	2254.74	540.93	354.26	728.02
AP1 (d)	2001.86	283.00	168.00	471.00
AP3 (d)	2230.00	355.26	257.00	539.00
SC3 (cm)	3.62	31.59	27.00	38.50
L3 (cm)	0.65	10.86	8.70	13.60
V3 (cm ³)	6189.84	433.67	256.30	746.40
YSC (cm)	4.80	31.88	24.50	38.20
15SC (cm)	5.68	34.18	26.00	40.00
AP (d)	884.17	361.10	282.00	451.00
PR (0 to 1)	0.10	0.89	0.00	1.00

^aMYW = male yearling BW; YH = yearling height in males; 15H = 15-mo BW in males; 15W = 15-mo BW in males; AP1 = age at puberty in bulls defined as when a bull produced 50 million sperm with $\geq 10\%$ progressive motility; AP3, SC3, L3, and V3 = age, scrotal circumference, height, average testis length, and testis volume when a bull produced 500 million sperm with $\geq 50\%$ progressive motility; YSC = yearling scrotal circumference; 15SC = 15-mo scrotal circumference; AP = age at puberty for heifers; and PR = pregnancy rate in heifers.

The estimate of genetic correlation of -0.57 between YSC and AP was similar to estimates of -0.71 and -0.76 reported by Brinks et al. (1978) and Morris et al. (1992).

The heritability estimate of 0.10 for heifer PR (Table 5) agreed with the estimates of 0.12 and 0.13 reported, respectively, by Morris et al. (2000) and Evans et al. (1999). The heritability estimate in the present study for heifer AP of 0.52 generally agreed with estimates of 0.47 and 0.41 reported by Splan et al. (1998) and Laster et al. (1979), respectively. A somewhat greater estimate of 0.61 was reported by MacNeil et al. (1984) using earlier data from GPE. The heritability estimate for heifer PR (0.10) indicates that environmental effects on this trait would make response to direct selection slow, but the heritability estimate for heifer AP (0.52) indicates direct selection would be effective if heritability was that great, although estimates for age at first calving, which is easier to measure, averaged much less (0.06) in the review by Koots et al. (1994).

Estimates of heritability for AP1, average testis length, and testicular volume of 0.47, 0.46 and 0.31, respectively, were moderate. The heritability estimate for height at puberty in bulls was even greater (0.89). In addition, AP1 was low but positively (favorably) correlated with heifer AP (0.16) and moderately negatively (favorably) correlated with heifer PR (-0.45). The estimates of genetic correlations with SC1 have little meaning because of the near-zero heritability estimate for SC1 for the measure at a relatively young age (mean = 283 d). Although SE could not be computed with available software, approximate SE for genetic correlations were large, using the formula of Koots et al. (1994), ranging from 2.55 for small estimates of heritabilities (0.10) and genetic correlation (0.10) to 0.38 for high estimates of heritability (0.50) and a moderate estimate of genetic correlation (0.50).

The expected correlated responses for AP and PR in heifers from direct

The heritability estimate in Table 5 for YSC (0.05) was considerably less than estimates of 0.68 (dairy bulls), 0.52, and 0.49 reported, respectively, by Coulter and Foote (1979), Lunstra and Echtenkamp (1982), and Bourdon and Brinks (1986), but was similar to an estimate of 0.09 reported by Morris et al. (1992). The heritability estimate (0.37) for 15SC was moderate, but less than the estimate of 0.78 reported by Coulter et al. (1976) for

scrotal circumference measured between 12 and 17 mo of age on Holstein bulls. A slightly smaller estimate of 0.32 was reported by Morris et al. (1992) for 15SC. Based on these heritability estimates, 15SC (0.37) should respond more quickly to selection than YSC (0.05). The estimate of genetic correlation of YSC with AP was -0.57 and with PR was 0.35, but YSC and 15SC were estimated to be highly correlated genetically (1.00).

TABLE 3. Heritability estimates (diagonal) and estimates of genetic correlations (off diagonal) among growth traits^{a,b}.

Trait	MYW	YH	15W	15H	AP	PR
MYW	1.00	1.00	1.00	0.21	0.00	0.49
YH		0.20	0.58	1.00	0.66	-0.48
15W			1.00	0.26	-0.04	0.51
15H				0.54	0.35	0.44

^aMYW = male yearling BW, YH = yearling height in males, 15W = 15-mo BW in males, 15H = 15-mo height in males, AP = age at puberty in females, and PR = pregnancy rate in heifers.

^bStandard errors of heritability estimates were 0.33 to 0.40 for MYW, YH, 15W, and 15H.

TABLE 4. Heritability estimates (diagonal) and estimates of genetic correlations (off diagonal) among fertility traits^{a,b}.

Trait	AP3	SC3	L3	V3	W3	H3	AP	PR
AP3	0.33	0.60	0.72	0.63	0.47	0.73	0.05	-0.35
SC3		1.00	0.76	0.97	1.00	0.64	-0.23	-0.97
L3			0.52	0.78	1.00	0.72	-0.14	-0.24
V3				1.00	0.94	0.73	-0.20	-0.67
W3					0.34	0.57	-0.08	0.17
H3						0.45	-0.33	-0.14

^aAP3, SC3, L3, V3, W3, and H3 = age, scrotal circumference, average testis length, testicular volume, BW, and height, respectively, when a bull produced 500 million sperm with $\geq 50\%$ progressive motility; AP = age at puberty in heifers; and PR = pregnancy rate in heifers.

^bStandard errors of heritability estimates ranged from 0.32 to 0.42.

in studies summarized by Koots et al. (1994), has a much smaller estimate of heritability (0.06).

Because of the small heritability estimate for PR, selection on many male traits would be expected to be more effective than direct selection because of generally high heritability estimates and favorable estimates of the genetic correlations.

Implications

Based on estimates of genetic parameters from this set of data, selection of males based on some reproductive and growth traits would be more effective than direct selection to increase PR in heifers. Response to selection using male traits, however, would not be expected to be as effective as direct selection for improving heifer age at puberty in contrast to other studies that have shown that scrotal circumference would be effective for decreasing age at first calving, which has much lower heritability than age at puberty. Estimates of genetic correlations between heifer age at puberty and measures of scrotal circumference in bulls were favorable but small. The estimates of genetic correlations also were favorable between age at puberty in males and females. In addition, response to selection based on heifer age at puberty would not be expected to improve

selection and from indirect selection on some male growth traits (YH, 15H, 15W) and male reproductive traits (AP1, AP3, SC3, L3, V3, YSC, 15SC) are presented in Table 7 based on estimates of parameters from the limited data of this study. The ratio of expected responses from indirect and direct selection shows which would be expected to be more effective based on the estimates of heritability and genetic correlations from this study. Direct selection for heifer

AP would be more effective than indirect selection of males for reproductive or growth traits because of the relatively high heritability estimate for heifer AP. The most favorable male traits for improving female fertility would be scrotal circumference at first freezable semen and YH and 15H based on the estimates of the parameters from this study. Although the sample of data was not large, the reason for the advantage of direct selection is the heritability of 0.52 for age at puberty, which was similar to previous estimates. Previous estimates of the advantage for indirect selection based on scrotal circumference were instead for age at first calving, which,

TABLE 5. Heritability estimates (diagonal) and estimates of genetic correlations (off diagonal) among fertility traits^{a,b}.

Item	YSC	15SC	AP	PR
YSC	0.05	1.00	-0.57	0.35
15SC		0.37	-0.06	0.00
AP			0.52	-0.28
PR				0.10

^aYSC = yearling scrotal circumference, 15SC = 15-mo scrotal circumference, AP = age at puberty in heifers, and PR = pregnancy rate in heifers.

^bStandard errors of heritability estimates were 0.29, 0.35, 0.12, and 0.07, respectively, for YSC, 15SC, AP, and PR.

TABLE 6. Heritability estimates (diagonal) and estimates of genetic correlations (off diagonal) among fertility and growth traits^{a,b}.

Item	AP1	SC1	L1	V1	W1	H1	AP	PR
AP1	0.47	1.00	0.91	1.00	0.68	1.00	0.16	-0.45
SC1		0.00	0.78	0.97	1.00	1.00	1.00	-0.75
L1			0.46	0.95	1.00	0.69	-0.15	0.03
V1				0.31	1.00	1.00	0.05	-0.08
W1					0.49	0.82	0.01	-0.11
H1						0.89	0.26	-0.06

^aAP1, SC1, L1, V1, W1, and H1 = age, scrotal circumference, average testis length, testicular volume, BW, and height at puberty in bulls defined as when a bull produced 50 million sperm with $\geq 10\%$ progressive motility; AP = age at puberty in heifers; PR = pregnancy rate in heifers.

^bStandard errors of heritability estimates ranged from 0.23 to 0.36.

TABLE 7. Expected correlated responses for age at puberty (AP, days) and pregnancy rate (PR, fraction) in heifers from direct selection and from indirect selection on some male traits (Δ) with ratio of indirect to direct expected responses (Q) for age at puberty and for pregnancy rate.

Item ^a	AP		PR	
	Δ	Q	Δ	Q
AP	-7.452	(1.00)	-0.010	(0.63)
PR	-0.914	(0.12)	0.015	(1.00)
AP1	2.264	(0.30)	-0.029	(1.93)
AP3	0.593	(0.08)	-0.019	(1.27)
SC3	-4.753	(0.64)	-0.093	(6.20)
L3	-2.065	(0.28)	-0.016	(1.07)
V3	-4.133	(0.55)	-0.064	(4.27)
YSC	-2.634	(0.35)	0.007	(0.47)
15SC	-0.764	(0.10)	0.001	(0.07)
YH	6.100	(0.82)	-0.030	(2.00)
15H	5.315	(0.71)	0.031	(2.07)
15W	-0.827	(0.11)	0.048	(3.20)

^aAP = age at puberty in heifers; PR = pregnancy rate in heifers; AP1 = age at puberty in bulls defined as when a bull produced 50 million sperm with $\geq 10\%$ progressive motility; AP3, SC3, L3, and V3 = age, scrotal circumference, average testis length, and testicular volume when a bull produced 500 million sperm with $\geq 50\%$ progressive motility; YSC = yearling scrotal circumference; 15SC = 15-mo scrotal circumference; YH = yearling height in males; 15H = 15-mo height in males, and 15W = 15-mo BW in males. Correlated responses were calculated assuming selection of approximately 7% of males and 70% of females for a 2:1 ratio for the selection intensity factors.

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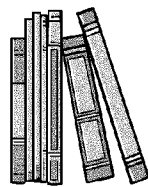
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heifer PR. Other studies, with more data, have suggested more favorable genetic responses for some female fertility traits such as age at first calving from indirect selection based on scrotal circumference of males. Male traits, such as scrotal circumference, are also easier and less expensive to measure than female reproductive traits and can be associated with greater selection intensity.



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