

Genetic parameters for fertility and production traits in Red Angus cattle

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ABSTRACT: Heifer pregnancy (HPG) and Stayability (STAY) are female reproductive traits that have EPD reported by the Red Angus Association of America. Challenges arise when making genetic predictions for these traits. Specifically, HPG and STAY phenotypes can only be collected on females retained in the breeding herd and have low heritability estimates. Additionally, STAY is measured late in an animal's life. The objective of this research was to investigate the genetic relationships between HPG or STAY and 13 other traits, which included measurements of growth, carcass, ultrasound, and scrotal circumference. For STAY relationships between mature weight (MW), body condition score (BCS), teat score (TS), and udder suspension score (US) were also evaluated. Data from 142,146 and 164,235 animals were used in the analyses for HPG and STAY, respectively. Genetic relationships were investigated using a series of 2 trait animal models and a REML procedure. In all analyses, the appropriate contemporary groups were included as a fixed effect, and direct genetic as a random effect. Additional fixed effects included as follows: sex for weight, carcass and ultrasound traits, age of dam for weight traits, and age of measurement for ultrasound, carcass, BCS, udder traits,

and MW. Maternal genetic effects for preweaning gain (Pre-WG), weaning weight (WW), and yearling weight (YW) were also modeled. Permanent environmental effects of the dam were modeled for the traits Pre-WG and WW. Permanent environment of the individual for the traits MW, BCS, TS, and US was also included. Heritability estimates were 0.12 ± 0.01 and 0.10 ± 0.01 for HPG and STAY, respectively. Heritability estimates for direct genetic effects of production traits were moderate to high in magnitude, maternal heritability estimates were low, and permanent environmental effects accounted for 0.00 to 0.18 of the total variation. The strongest genetic correlations were those among Pre-WG_D (0.24 ± 0.08), WW_D (0.18 ± 0.08), YW_D (0.20 ± 0.07), ultrasound rib eye area direct (0.16 ± 0.08), and ultrasound backfat direct (0.14 ± 0.08) and HPG. The highest genetic correlations were between STAY and WW_M (0.54 ± 0.05), YW_M (0.36 ± 0.07), backfat (0.53 ± 0.20), marbling score (0.40 ± 0.20), UREA (0.19 ± 0.07), ultrasound backfat (0.37 ± 0.07), TS (0.30 ± 0.11), and US (0.23 ± 0.11). Relationships between HPG or STAY and other traits were minimal. These results suggest that genetic relationships exist between HPG or STAY and other more densely recorded traits.

Key words: beef cattle, genetic correlation, heifer pregnancy, stayability

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J. Anim. Sci. 2018.96:4100–4111
doi: 10.1093/jas/sky294

INTRODUCTION

Beef cattle producers have numerous EPD available to make selection decisions. Of these

selection criteria, female reproductive traits have the ability to greatly improve profitability of a cow calf enterprise (Melton, 1995). The Red Angus Association of America (RAAA) currently publishes 2 EPD for female reproductive traits. The first of these predictions is heifer pregnancy (HPG), a prediction of a female's ability to become pregnant during their first breeding season

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Received May 9, 2018.

Accepted July 24, 2018.

(Crews and Enns, 2008). Additionally, the RAAA provides a prediction for stayability (STAY), which is defined as the ability of a female to produce 5 consecutive calves. Data are collected only on females that produce offspring; therefore, animals, particularly sires, do not realize increases in prediction accuracy until later in life for both traits. In addition, heritability estimates for female reproductive traits are generally low in magnitude (Cammack et al., 2009); therefore, many female progeny need to be retained per sire, in order for them to realize accuracy increases for these predictions.

The objective of this study was to examine the genetic relationships between HPG or STAY and production traits that are measured on both males and females. Being able to characterize these relationships permits the inclusion of more densely recorded phenotypes as correlated traits for each analysis. Traits considered for evaluation included growth, carcass and ultrasound, scrotal circumference (SC), and mature cow measurements (udder scores, mature weight [MW], and body condition score [BCS]). These traits offer the ability to include more information on offspring than what would be traditionally achieved through the current evaluation for reproductive traits.

MATERIALS AND METHODS

Data Collection and Editing

Data used in this study were obtained from a preexisting historical database; therefore, animal care and use committee approval was not obtained.

Observations for HPG and STAY are binary and coded 0 and 1 representing unsuccessful and successful observations, respectively. Observations for HPG were formed by the RAAA and were based on gestation intervals from producer-submitted breeding season information (McAllister et al., 2011). This information includes the date of insemination and the date that an individual female was exposed to a bull. Binary STAY phenotypes were formed using both calf and pedigree information. For a female to receive a successful observation, she must have produced calves in 5 consecutive years, with all progeny born within the same season (± 3 mo of previous years calving month). Reproductive phenotypes used in this study were from individuals with either a HPG or STAY phenotype that were included for EPD calculation for the Spring 2015 RAAA HPG and STAY national cattle evaluation. To increase the tractability of the problem, female

observations for STAY were included if they were a member of a contemporary group (CG) of 60 animals or more ($n = 43,328$), whereas all animals with HPG phenotypes ($n = 29,322$) were used due to the limited number of records. Inclusion of individual phenotypes for traits other than HPG or STAY was accomplished using the RAAA-defined birth work group, which resulted in a total of 142,146 and 164,235 individual animals considered for additional analyses for both HPG and STAY, respectively. Birth work group was chosen to identify individual animals because it included all animals that originated from the same ranch or herd and had their birth information submitted to the association of a female with a HPG or STAY phenotype. These groups of animals were then used to gather phenotypes for all analyses. Production traits in the analyses included birth weight (BWT), 205-d preweaning gain (direct and maternal, **Pre-WG_D**, **Pre-WG_M**), 205-d weaning weight (direct and maternal, **WW_D**, **WW_M**), 160-d post weaning gain (**Post-WG**), 365-d yearling weight (direct and maternal, **YW_D**, **YW_M**), SC, rib eye area (**REA**), backfat (**BF**), marbling score (**MARB**), hot carcass weight (HCW), ultrasound rib eye area (**UREA**), ultrasound backfat (**UBF**), and ultrasound percent intramuscular fat (**UIMF**). Traits evaluated with only STAY included teat score (**TS**), udder suspension score (**US**), MW, and BCS.

In an effort to parallel what is performed in the EPD production runs, observations were adjusted to an age constant end point of 205 d for the weaning traits (Pre-WG, WW), 160 d for Post-WG, and 365 d for the yearling (YW, SC) phenotypes. Observations for MW were adjusted to a constant BCS of 5 based on factors reported by Tennant et al. (2002). To maintain biological relevance of records, truncation points were used to set limits for both age and phenotype. Phenotypic records for all traits were removed from additional consideration if either the animal's age or phenotype was greater than 5 SD from the mean.

CGs for each trait were formed in a similar manner to those used in the national cattle evaluation and are presented in Table 1. A component of all CGs was a breed code (BC) designation which assigned animals to 1 of the 4 categories based on their percent Red Angus. Group 1 contained those individuals that were greater than 87.5% Red Angus and group 2 contained animals that were greater than 50% Red Angus and less than of 87.4% Red Angus. Group 3 contained animals that were greater than 87.5% Red Angus and contain Brahman influence and group 4 were animals that were between

50% and 87.4% Red Angus and contained Brahman influence. For female udder traits, CG was defined as her calf's birth CG when the measurement was taken. MW and BCS CG were defined as the calf's weaning CG when the cow weight was taken. If an animal was a member of a CG that exhibited no phenotypic variation, the data were removed from the analysis. The total number of unique CG for traits evaluated with HPG and STAY analyses is reported in Table 2.

Statistical Analysis

Fixed and random effects included in the model for each trait are summarized in Table 3. Analyses

were conducted as a series of 2 trait animal models using the ASREML 3.0 software package (Gilmour et al., 2009). In each instance, the trait HPG or STAY was included as the first trait in the mixed model, and each production trait was included as the second trait. Due to the binary nature of HPG and STAY, observations were converted to an underlying normal distribution using a probit link function which restricts residual variance to 1 (Gianola and Foulley, 1983; Harville and Mee, 1984); alternatively, all other traits were analyzed as continuous outcomes.

The general matrix form of the equations used in the analysis was as follows:

Table 1. Formal definition of all contemporary groups used for heifer pregnancy, stayability, and production trait evaluation in Red Angus cattle

Contemporary group	Definition
Heifer pregnancy	Weaning work group ¹ , weaning management code ² , breed code ³ , birth work group ¹ , weaning date, yearling work group ¹ , yearling management code ² , heifer pregnancy management code ²
Stayability	Breeder of the individual, breeder of each calf, year of birth of individual
Birth (BCG)	Birth work group ¹ , birth management group ² , breed code ³ , season ¹ and year of birth
Weaning (WCG)	Weaning work group ¹ , weaning management code ² , breed code ³ , birth work group ¹ , weaning date
Yearling (YCG)	WCG, yearling work group ¹ , yearling management code ²
Ultrasound	YCG, ultrasound management code ¹ , ultrasound date
Carcass	Owner, harvest date

¹Parameters defined by the Red Angus Association of America.

²Producer-submitted information.

³Defined as greater than 87.5% Red Angus, 50%–87.4% Red Angus, greater than 87.5% Red Angus with Brahman influence, and 50%–87.4% Red Angus with Brahman influence.

Table 2. Number and average size of contemporary group (CG) for analysis of production traits with the reproductive traits heifer pregnancy and stayability in Red Angus cattle

Trait	Heifer pregnancy models		Stayability models	
	Number of unique CG	Average CG size	Number of unique CG	Average CG size
Heifer pregnancy	2,274	14		
Stayability			462	94
Birth weight	5,494	26	3,569	44
Pre-weaning gain	4,349	31	4,779	30
Weaning weight	4,351	31	4,776	30
Post weaning gain	5,415	19	4,678	19
Yearling weight	5,424	19	4,474	20
Scrotal circumference	1,210	16	832	18
Rib eye area	83	28	46	36
Backfat	84	29	47	36
Marbling	77	29	39	37
Hot carcass weight	84	29	47	37
Ultrasound rib eye area	2,573	15	2,105	13
Ultrasound backfat	2,574	15	2,099	13
Ultrasound intramuscular fat	2,589	15	2,104	13
Teat score			148	7
Suspension score			160	7
Mature weight			1,597	19
BCS			1,264	22

Table 3. Description of models used for heifer pregnancy, stayability, and production traits in Red Angus cattle

Trait ¹	Fixed effects				Random effects		
	Contemporary group	Sex	Age	AOD ²	Direct additive genetic effect	Maternal additive genetic effect	Permanent environment effect
HPG	HPG	No	Yes	No	Yes	No	No
STAY	STAY	No	No	No	Yes	No	No
BWT	Birth	Yes ³	No	Yes	Yes	No	No
Pre-WG	Weaning	Yes ⁴	No	Yes	Yes	Yes	Yes
WW	Weaning	Yes ⁴	No	Yes	Yes	Yes	Yes
Post-WG	Yearling	Yes ⁴	No	Yes	Yes	No	No
YW	Yearling	Yes ⁴	No	Yes	Yes	Yes	Yes
SC	Yearling	No	No	No	Yes	No	No
REA	Carcass	Yes ⁴	Yes	No	Yes	No	No
BF	Carcass	Yes ⁴	Yes	No	Yes	No	No
MARB	Carcass	Yes ⁴	Yes	No	Yes	No	No
HCW	Carcass	Yes ⁴	Yes	No	Yes	No	No
UREA	Ultrasound	Yes ⁴	Yes	No	Yes	No	No
UBF	Ultrasound	Yes ⁴	Yes	No	Yes	No	No
UIMF	Ultrasound	Yes ⁴	Yes	No	Yes	No	No
TS	Calf Birth	No	Yes	No	Yes	No	Yes
US	Calf Birth	No	Yes	No	Yes	No	Yes
MW	Calf Weaning	No	Yes	No	Yes	No	Yes
BCS	Calf Birth	No	Yes	No	Yes	No	Yes

¹HPG= heifer pregnancy, STAY = stayability; BWT= birth weight; Pre-WG = Pre-Weaning Gain; WW = weaning weight; Post-WG = post weaning gain; YW = yearling weight; SC_D= scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

²Defined as 2, 3, 4, 5 to 9, 10, and 11+ years of age.

³Defined as bull and heifer.

⁴Defined as bull, heifer, and steer.

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where y_i is a vector of observations for the traits, X_i and Z_i are incidence matrices relating observations in y to levels of fixed effects in β , and random solutions in u , respectively, and e_i are a vector of residual effect solutions. Variances and means for the random effects included in the models were assumed to be as follows:

$$\begin{aligned} \text{Var} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} &= \begin{bmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{21} & \sigma_2^2 \end{bmatrix} \otimes A \text{ and } \text{Var} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \\ &= \begin{bmatrix} \sigma_{e_1}^2 & \sigma_{e_{12}} \\ \sigma_{e_{21}} & \sigma_{e_2}^2 \end{bmatrix} \otimes I \text{ and } E \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \end{aligned}$$

where A is the numerator relationship matrix, and I is an identity matrix of whose order is equal to the number of animals with each respective phenotype. For the traits SC, REA, BF, MARB, and HCW, the residual correlation was constrained to

be 0, because animals could not express both traits. Furthermore, due to a limited number of animals expressing both traits, the residual correlation between STAY and TS, US, and BCS was also constrained to be 0. All other trait combinations in the analyses the residual correlations were nonzero.

Total pedigree size for each of the 2 trait analyses is summarized in Table 4. Pedigree size varied across analyses because the pedigree was formed by including 3 generations of records for animals with a phenotype.

RESULTS AND DISCUSSION

Summary statistics of the data used in both HPG and STAY analyses are reported in Table 5. Overall, the average success rate for the HPG phenotype was 0.77, which is equivalent to 77% of the heifers becoming pregnant during their first breeding season. Phenotypic averages for HPG were consistent with the published results of McAllister et al. (2011) of 0.80 in Red Angus cattle, Peters et al. (2013) of 0.78 in Brangus cattle, and

Table 4. Description of pedigree size for all 2-trait analyses with heifer pregnancy or stayability in Red Angus cattle

Trait	Heifer pregnancy models			Stayability models		
	Total pedigree size	Number of unique sires	Number of unique dams	Total pedigree size	Number of unique sires	Number of unique dams
Birth weight	248,082	17,104	111,258	251,696	14,741	104,226
Prewaning gain	236,506	16,697	107,216	235,885	14,472	99,878
Weaning Weight	236,507	15,378	107,216	235,877	14,472	99,874
Postweaning gain	190,981	15,428	91,569	186,017	13,442	86,313
Yearling weight	192,849	12,354	92,324	186,017	13,433	86,313
Scrotal circumference	117,314	11,655	63,626	120,611	11,764	65,710
Rib eye area	90,960	11,655	53,716	102,714	11,456	59,350
Backfat	90,933	11,653	53,723	120,760	11,457	59,361
Marbling	90,791	11,656	53,689	102,439	11,455	59,243
Hot carcass weight	91,000	12,536	53,726	102,764	11,457	59,362
Ultrasound rib eye area	128,833	12,536	67,806	126,816	11,861	67,436
Ultrasound backfat	128,881	12,536	67,826	126,855	11,861	67,451
Ultrasound intramuscular fat	128,834	12,536	67,809	126,744	11,861	67,420
Teat score				101,721	11,487	59,172
Suspension score				101,721	11,487	59,172
Mature weight				103,934	11,528	60,186
Body condition score				103,934	11,528	60,186

Evans et al. (1999) of 0.78 in Hereford cattle. The success rate for STAY in this analysis was 0.28, which was consistent with estimates reported from multiple breeds in previous reports (Martinez et al., 2005; Van Melis et al., 2010).

Table 6 summarizes parameter variance, heritability, and the proportion of phenotypic variance explained by permanent environment effects for all studied traits in the HPG analyses. Similarly, Table 7 presents variance parameters for all traits that were evaluated with STAY. For both HPG and STAY, variance parameters are reported as the average of all the estimates obtained from each of the 2-trait analyses. Overall, heritability for HPG was 0.12 ± 0.01 (reported with the largest standard error). This heritability estimate was lower than a previous estimate using a sire model in Red Angus cattle of 0.17 ± 0.01 (McAllister et al., 2011). For STAY, the heritability estimate was 0.10 ± 0.01 (reported with the largest standard error). Traditionally, heritability estimates for STAY have varied from population to population, as well as differences in trait definition. In Hereford cattle, Martinez et al. (2005) reported a heritability estimate of 0.30 ± 0.14 , for the ability of a female to remain in the herd until 6 yr of age, and a heritability estimate of 0.35 ± 0.13 for the ability of a female to have 5 consecutive calves. Comparing the STAY heritability estimates to those reported by Snelling et al. (1995), which ranged from 0.11 to

0.23 for the ability of a female to have 5 consecutive calves on 2 farms using marginal maximum likelihood and Method R techniques (Reverter et al., 1994), variability of estimates is evident. For both HPG and STAY, estimates in the current analysis were lower than the results presented in previous research. However, the low heritability estimate for these traits is not unreasonable given the low heritability estimates that are commonly associated with reproductive traits (Cammack et al., 2009).

Heritability estimates for HPG and STAY were similar in magnitude irrespective of the production trait that they were evaluated with. For all production traits, direct heritability estimates were generally moderate to high (0.22 to 0.71). Maternal heritability estimates for Pre-WG, WW, and YW were low in magnitude (<0.11). For the analyses conducted with HPG, the direct and maternal genetic correlations for Pre-WG, WW, and YW were -0.31 ± 0.03 , -0.29 ± 0.03 , and 0.02 ± 0.05 , respectively. Similarly, the direct and maternal correlations for Pre-WG, WW, and YW for the analyses conducted with STAY were -0.32 ± 0.03 , -0.30 ± 0.03 , and 0.07 ± 0.05 , respectively. Estimates of direct and maternal correlations were consistent with ranges established in previous research (Meyer, 1992). For both Pre-WG and WW, the amount of variance accounted for by permanent environmental effects reported with largest standard error was 0.14 ± 0.01 in HPG analyses and 0.13 ± 0.004 for

Table 5. Summary statistics for fertility and production traits used for variance component estimation in Red Angus cattle

Trait		Heifer pregnancy	Stayability
Heifer pregnancy	<i>n</i>	29,322	
	Mean	0.77	
	SD	0.42	
Stayability	<i>n</i>		43,328
	Mean		0.28
	SD		0.45
Birth weight, kg	<i>n</i>	141,436	159,204
	Mean	36.08	36.14
	SD	5.46	5.31
Preweaning gain, kg	<i>n</i>	134,202	144,198
	Mean	220.07	219.27
	SD	38.00	38.90
Weaning weight, kg	<i>n</i>	134,202	144,198
	Mean	256.19	255.36
	SD	40.16	41.09
Postweaning gain, kg	<i>n</i>	101,916	92,842
	Mean	160.00	169.06
	SD	63.84	64.11
Yearling weight, kg	<i>n</i>	103,334	90,536
	Mean	418.51	430.94
	SD	83.64	86.39
Scrotal circumference, cm	<i>n</i>	20,389	15,185
	Mean	35.34	34.99
	SD	2.77	6.67
Rib eye area, cm ²	<i>n</i>	2,372	1,676
	Mean	81.51	82.26
	SD	9.40	9.42
Backfat, mm	<i>n</i>	2,404	1,717
	Mean	14.01	14.22
	SD	4.03	4.32
Marbling score	<i>n</i>	2,234	1,459
	Mean	5.44	5.51
	SD	1.08	1.09
Hot carcass weight, kg	<i>n</i>	2,409	1,721
	Mean	369.96	371.77
	SD	39.74	38.15
Ultrasound rib eye area, cm ²	<i>n</i>	39,227	29,406
	Mean	71.06	70.97
	SD	13.43	12.84
Ultrasound backfat, mm	<i>n</i>	39,274	29,477
	Mean	5.60	5.84
	SD	2.24	2.29
Ultrasound intramuscular fat, %	<i>N</i>	39,113	29,269
	Mean	3.56	3.64
	SD	0.97	1.01
Teat score	<i>n</i>		2,483
	Mean		5.38
	SD		2.03
Udder suspension score	<i>n</i>		2,483
	Mean		4.94
	SD		2.02
Mature weight, kg	<i>n</i>		30,599
	Mean		537.49
	SD		90.21
Body condition score	<i>n</i>		30,646
	Mean		5.15
	SD		0.99

Table 6. Estimates of parameter variance, phenotypic variance, heritability ($h^2 \pm SE$), and permanent environment effects ($c^2 \pm SE$) for heifer pregnancy and production traits in Red Angus cattle

Trait	Parameter variance	Phenotypic variance	h^2	c^2
HPG _D	0.14 ²	1.14 ²	0.12 ± 0.01 ²	
BWT _D	27.25	46.65	0.58 ± 0.01	
Pre-WG _D	360.09	1,431.13	0.25 ± 0.01	
Pre-WG _M	151.15	1,431.13	0.11 ± 0.01	
Pre-WG _{PE}	199.72	1,431.13		0.14 ± 0.01
WW _D	442.35	1,508.69	0.29 ± 0.01	
WW _M	154.30	1,508.69	0.10 ± 0.01	
WW _{PE}	212.53	1,508.69		0.14 ± 0.004
Post-WG _D	344.49	1,532.42	0.22 ± 0.01	
YW _D	987.04	3,056.03	0.32 ± 0.01	
YW _M	166.38	3,056.03	0.05 ± 0.01	
SC _D	2.43	5.25	0.46 ± 0.02	
REA _D	3.56	9.74	0.37 ± 0.07	
BF _D	0.14	0.52	0.27 ± 0.06	
MARB _D	0.32	0.80	0.40 ± 0.06	
HCW _D	482.69	1,969.41	0.25 ± 0.06	
UREA _D	3.33	8.19	0.41 ± 0.01	
UBF _D	0.03	0.10	0.35 ± 0.01	
UIMF _D	0.18	0.50	0.38 ± 0.01	

¹HPG_D = heifer pregnancy direct (%); BWT_D = birth weight direct (kg); Pre-WG_D = Prewaning gain direct (kg); Pre-WG_M = Prewaning gain maternal (kg); Pre-WG_{PE} = Prewaning gain permanent environment of the dam (kg); WW_D = weaning weight direct (kg); WW_M = weaning weight maternal (kg); WW_{PE} = weaning weight permanent environment if the dam (kg); Post-WG_D = post weaning gain direct (kg); YW_D = yearling weight direct (kg); YW_M = yearling weight maternal (kg); SC_D = scrotal circumference direct (cm); REA_D = rib eye area direct (cm²); BF_D = backfat direct (mm); MARB_D = marbling score direct; HCW_D = hot carcass weight direct (kg); UREA_D = ultrasound rib eye area direct (cm²); UBF_D = ultrasound backfat direct (mm); UIMF_D = ultrasound intramuscular fat direct (%).

²Reported as the average of heritability estimates and largest SE of all 2-trait analyses between heifer pregnancy and production traits.

STAY analyses. For udder traits, permanent environmental effects did not explain any of the variation for these traits. This might be a result of the limited number of repeated records used in the evaluation. Of the 2,432 records used in this study, only 28% of females had multiple observations and 42% were the same score across years. In addition, 79% of the data were within 1 SD of the mean. Permanent environment effects accounted for 0.16 ± 0.02 of the variance of MW and 0.18 ± 0.01 of the variation of BCS. These estimates result in repeatability estimates of 0.73 ± 0.01 for MW and 0.45 ± 0.01 for BCS.

Heifer Pregnancy

Table 8 summarizes the estimated genetic and residual covariance as well as the genetic and residual correlations between HPG and production traits. The genetic correlation with the highest magnitude was between HPG and Pre-WG_D at 0.24 ± 0.08 . Although previous estimates of genetic correlations between the traits were not available, Roberts et al. (2009) showed on the phenotypic level that increases of 0.1 kg/d in preweaning average daily gain increased the percentage

of heifers achieving puberty during a postweaning treatment of restricted and ad libitum control diets by 11.6 ± 2.6 percentage points. Additionally, multiple studies from the 1950s through the 1970s suggested that preweaning growth had a greater influence on age of puberty (AOP) than postweaning growth rate (Wiltbank et al. 1966; Swierstra et al. 1977). Perry et al. (1991) reported that heifers that have the ability to reach puberty at younger ages have the opportunity to have multiple ovulation cycles before the breeding season with later cycles being more fertile than the pubertal estrus. Therefore, it is not unreasonable to assume that the benefits of higher Pre-WG would extend to the HPG phenotype as well.

Genetic correlations between HPG and WW_D and YW_D were low and positive at 0.18 ± 0.08 and 0.21 ± 0.07 , respectively. Fortes et al. (2012) examined both REML and genomic correlations for HPG and weight traits in Brangus cattle. The authors found the REML correlations to be -0.28 ± 0.38 for 205-d weight and -0.14 ± 0.35 for 365-d weight. Additionally, genomic correlations were calculated using an associated weight matrix. These genomic correlations between HPG, and 205-d weight and 365-d weight were found to be

Table 7. Estimates of parameter variance, phenotypic variance, heritability ($h^2 \pm SE$), and permanent environment effects ($c^2 \pm SE$) for stayability and production traits in Red Angus cattle

Trait	Parameter variance	Phenotypic variance	h^2	c^2
STAY _D	0.11	1.11	0.10 ± 0.01^2	
BWT _D	24.62	43.71	0.56 ± 0.01	
Pre-WG _D	342.41	1408.54	0.24 ± 0.01	
Pre-WG _M	146.39	1408.54	0.10 ± 0.01	
Pre-WG _{PE}	189.66	1408.54		0.13 ± 0.004
WW _D	422.33	1564.44	0.27 ± 0.01	
WW _M	158.06	1564.44	0.10 ± 0.01	
WW _{PE}	202.91	1564.44		0.13 ± 0.004
Post-WG _D	408.75	4414.32	0.24 ± 0.01	
YW _D	1097.07	3234.75	0.34 ± 0.01	
YW _M	212.46	3234.75	0.07 ± 0.01	
SC _D	2.64	5.45	0.49 ± 0.03	
REA _D	2.55	10.00	0.26 ± 0.08	
BF _D	0.15	0.64	0.24 ± 0.07	
MARB _D	0.24	0.80	0.30 ± 0.08	
HCW _D	496.18	1941.06	0.26 ± 0.07	
UREA _D	3.02	7.86	0.38 ± 0.02	
UBF _D	0.04	0.10	0.40 ± 0.02	
UIMF _D	0.22	0.56	0.39 ± 0.02	
TS _D	2.07	2.93	0.71 ± 0.02	
TS _{PE}	0.00	2.93		0.00 ± 0.00
US _D	2.16	3.09	0.70 ± 0.02	
US _{PE}	0.00	3.09		0.00 ± 0.00
MW _D	3606.96	6375.24	0.57 ± 0.02	
MW _{PE}	1017.38	6375.24		0.16 ± 0.02
BCS _D	0.14	0.54	0.27 ± 0.02	
BCS _{PE}	0.10	0.54		0.18 ± 0.01

¹STAY = stayability; BWT = birth weight; Pre-WG = preweaning gain; WW = weaning weight; Post-WG = postweaning gain; YW = yearling weight; SC = scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

²Reported as the average of heritability estimates and largest SE of all 2-trait analyses between stayability and production traits.

0.17 and 0.10, respectively. The differences between the current study and previous literature may arise from the relatively small sample size ($n = 835$) used in the study of Fortes et al. (2012). Moreover, *Bos indicus* cattle, traditionally, achieve puberty at a later age, which might also bias these estimates and cause a nonzero correlation.

Genetic correlations among HPG, UBF, and UREA were low but positive in nature. In Brangus cattle, positive correlations were also estimated between UREA and UBF (Fortes et al., 2012). All carcass traits and UIMF also showed to have little to no genetic relationship with HPG. For Red Angus cattle, McAllister et al. (2011) found a stronger positive correlation (0.13 ± 0.09) between HPG and UIMF using a sire model. Although the estimate in the current study is lower in magnitude, both estimates were within the range of the standard errors.

Generally, correlations between HPG and BWT, Post-WG, and SC were near zero or had standard errors that encompassed zero. These results suggest that little genetic relationship exists between the traits. To the best of our knowledge, there were no published genetic correlations between BWT and HPG. The current estimate suggests a relationship between HPG and BWT such that heifers that were born with heavier birth weights have a lower chance of conceiving during their first breeding season. Nonetheless, Cushman et al. (2009) showed that heifers with higher birth weights had a greater antral follicle count and higher HPG rates ($P = 0.05$). Although our results revealed that postweaning gain had a negligible genetic relationship with HPG, previous research showed that a phenotypic increase in heifer's PWG can help reduce the AOP (Wiltbank et al., 1969). This was then developed into various heifer development programs.

Table 8. Estimates of genetic covariance, residual covariance, genetic correlation, and residual correlation between heifer pregnancy (HPG) and production traits in Red Angus cattle

Trait	Genetic covariance with HPG	Residual covariance with HPG	Genetic correlation with HPG	Residual correlation with HPG
BWT _D	-0.08	0.02	-0.06 ± 0.05	0.01 ± 0.01
Pre-WG _D	1.12	0.79	0.24 ± 0.08	0.04 ± 0.01
Pre-WG _M	0.00	0.79	0.00 ± 0.09	0.04 ± 0.01
WW _D	0.94	0.80	0.18 ± 0.08	0.04 ± 0.01
WW _M	0.07	0.80	0.02 ± 0.09	0.04 ± 0.01
Post-WG _D	0.30	0.59	0.06 ± 0.07	0.03 ± 0.01
YW _D	1.46	1.53	0.21 ± 0.07	0.14 ± 0.03
YW _M	0.01	1.53	0.00 ± 0.11	0.14 ± 0.03
SC _D	-0.03	0.00	-0.06 ± 0.09	
REA _D	0.37	0.00	0.21 ± 0.21	
BF _D	-5.54	0.00	-0.08 ± 0.23	
MARB _D	-0.17	0.00	-0.08 ± 0.19	
HCW _D	-0.16	0.00	-0.03 ± 0.25	
UREA _D	0.27	0.16	0.16 ± 0.08	0.03 ± 0.01
UBF _D	0.05	0.17	0.14 ± 0.08	0.01 ± 0.01
UIMF _D	0.01	0.01	0.06 ± 0.08	0.02 ± 0.01

¹BWT_D = birth weight direct (kg); Pre-WG_D = Prewaning gain direct (kg); Pre-WG_M = Prewaning gain maternal (kg); WW_D = weaning weight direct (kg); WW_M = weaning weight maternal (kg); WW_{PE} = weaning weight permanent environment (kg); Post-WG_D = postweaning gain direct (kg); YW_D = yearling weight direct (kg); YW_M = yearling weight maternal (kg); SC_D = scrotal circumference direct (cm); REA_D = rib eye area direct (cm²); BF_D = backfat direct (mm); MARB_D = marbling score direct; HCW_D = hot carcass weight direct (kg); UREA_D = ultrasound rib eye area direct (cm²); UBF_D = ultrasound backfat direct (mm); UIMF_D = ultrasound intramuscular fat direct (%).

The objective of the development programs was to feed heifers so that they can achieve weights that are 65% of their MW at the start of the breeding season (Patterson et al., 1992). Although a phenotypic relationship may exist between AOP and Post-WG, this relationship does not extend to the genetic relationship of HPG and Post-WG in these data.

SC has also been a suggested tool to improve reproductive performance. Brinks et al. (1978) showed that the genetic correlation between SC and AOP was negative. More recently, however, the relationship between SC and HPG has been disputed, in which multiple studies have found negligible genetic relationship between the traits (Evans et al., 1999; McAllister et al., 2011). This could be a result of selection and changes in performance in the intervening period. In the current study, a slight negative association between these traits was estimated; however, this estimate was not different from zero. This may partially be explained by the fact that if all heifers reach puberty at an age before breeding, then heifers that reach this point earlier have no advantage because all females are successfully cycling at the beginning of the breeding season (Martin et al., 1992).

Overall residual correlations between HPG and the production traits were positive and weak. The strongest correlation was between HPG and YW (0.14 ± 0.03). These results suggest that an

environment that promotes a higher YW will also increase the probability of a female to become pregnant during their first breeding season. The effect of the previously mentioned heifer development programs may be seen through this correlation.

Stayability

Table 9 presents genetic and residual covariance as well as genetic and residual correlation estimates between STAY and each of the production traits. Maternal genetic components of Pre-WG, WW, and YW were strongly correlated with STAY. Culbertson (2014) examined the relationship between milk production and STAY, in Red Angus cattle, and determined that the relationship was nonlinear. Conversely, Rogers et al. (2004) found that as milk EPD increased, the risk ratio of a cow being culled also increased. This might be due to the environment the cows in that study were housed in, where they may over-produce given environmental resources because of inadequate accumulation of fat reserves. However, in dairy cattle, as milk production increased the relative culling rate decreased (Vukasinovic et al., 2001). This can be attributed to that the highest producing cows are the most beneficial in a dairy herd and nutrition is generally not a problem within these herds. Maternal traits again offer little advantage to more traditional methods

Table 9. Estimates of genetic covariance, residual covariance, genetic correlation, and residual correlation between stayability (STAY) and production traits in Red Angus cattle

Trait	Genetic covariance with STAY	Residual covariance with STAY	Genetic correlation with STAY	Residual correlation with STAY
BWT _D	-0.04	-0.09	-0.03 ± 0.04	-0.03 ± 0.01
Pre-WG _D	0.01	-0.33	0.00 ± 0.06	-0.02 ± 0.01
Pre-WG _M	1.54	-0.33	0.54 ± 0.05	-0.02 ± 0.01
WW _D	-0.13	-0.44	-0.03 ± 0.06	-0.02 ± 0.01
WW _M	1.64	-0.44	0.55 ± 0.05	-0.02 ± 0.01
Post-WG _D	-0.40	-0.19	-0.09 ± 0.05	-0.01 ± 0.01
YW _D	-0.55	-0.61	-0.07 ± 0.06	-0.06 ± 0.03
YW _M	1.20	-0.61	0.36 ± 0.07	-0.06 ± 0.03
SC _D	0.03	0.00	0.04 ± 0.08	
REA _D	0.01	0.00	0.01 ± 0.21	
BF _D	0.34	0.00	0.53 ± 0.20	
MARB _D	0.06	0.00	0.40 ± 0.20	
HCW _D	0.67	0.00	0.14 ± 0.21	
UREA _D	0.27	0.06	0.19 ± 0.07	0.01 ± 0.02
UBF _D	0.13	0.01	0.37 ± 0.07	0.01 ± 0.02
UIMF _D	0.00	0.00	-0.01 ± 0.07	0.01 ± 0.02
TS _D	0.14	0.00	0.30 ± 0.11	
US _D	0.11	0.00	0.23 ± 0.11	
MW _D	0.17	1.91	0.01 ± 0.06	0.07 ± 0.02
BCS _D	0.01	0.00	0.05 ± 0.07	

¹STAY = stayability; BWT = birth weight; Pre-WG = preweaning gain; WW = weaning weight; Post-WG = postweaning gain; YW = yearling weight; SC = scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

of measuring STAY. This is because in order for a sire to gain added accuracy for maternal traits his daughters must produce calves to model genetic differences for maternal effects.

Carcass and ultrasound traits showed varying degrees of genetic relationships with STAY. The traits REA, HCW, and UIMF all had large SE that encompassed 0 suggesting minimal genetic relationships between the traits. The genetic correlation between STAY and MARB was moderate and positive, whereas the correlation with UIMF was near 0. This may be due to the limited marbling score phenotypes used in the analysis or to the imperfect genetic relationship between MARB and UIMF. Generally, correlations between MARB and UIMF are high (>0.7), so the conflicting results were unexpected (Crews et al., 2003; McAllister et al., 2011). Correlations between STAY and both BF and UBF were positive and moderate to high in magnitude. These results suggest that cattle with a genetic predisposition to deposit a higher amount of subcutaneous fat also have a higher chance to rebreed. Subcutaneous fat phenotypes offer an advantage as an indicator trait for STAY because they can be collected at younger ages on both males and females, especially via ultrasound backfat measures. These

are generally collected at 1 yr of age and before a female enters the breeding herd. Within this analysis, 7,470 females had both a STAY and UBF phenotype. Short and Adams (1988) described a priority list for available energy in beef cattle. Among this list initiation, maintenance of pregnancy ranks above the formation of excess energy reserves. The correlation between BF and UBF may be early indicators of a female's genetic potential to produce excess energy reserves in successive years.

Genetic relationships were negligible between STAY and BWT, Pre-WG_D, WW_D, Post-WG, YW_D, SC, REA, HCW, UIMF, MW, and BCS. The additive genetic correlations between weight traits (BWT, Pre-WG, WW, Post-WG, and YW) and STAY were negative and weak in magnitude, whereas the genetic correlation between STAY and MW was positive. In Chanchim beef cattle, Buzanskas et al. (2010) reported weak genetic correlation between 420-d weight and STAY. Conversely, Eler et al. (2014) estimated a moderate positive genetic correlation between Post-WG and STAY. Alternatively, in the current study, a weak negative genetic association between STAY and Post-WG was estimated. The different results may be attributed to the fact that, in previous research, results were drawn on

B. indicus females that generally experience puberty at later age. Rogers et al. (2004), using a survival regression analysis of *Bos Taurus* composite cattle, showed that birth weight and 365-d BWT did not significantly ($P > 0.1$) affect the length of the productive life in a cross-bred population.

In the current study, mature cow traits were not strongly correlated with STAY. The results of the low genetic correlation between BCS and STAY were unexpected given that earlier in life measurements of external fat (UBF, BF) estimated stronger genetic relationships with STAY. Beckman et al. (2006) also estimated genetic correlations between STAY and BCS at ages 2, 3, and 4 yr and reported they were not different from 0 in Red Angus cattle. Even though BCS is commonly promoted as a tool to diagnose the nutritional status of cattle in order to prepare them for breeding, the discrete nature and distribution of both BCS and STAY present challenges for determining the genetic relationship between the traits. Additionally, BCS are used to adjust feeding strategies so that all animals are in adequate condition at the beginning of the breeding season, and if this goal is accomplished, this may explain why there is no relationship between the traits.

Moderate positive correlations were estimated between TS and US and STAY. The highest achievable score of 9 would be considered very tight for suspension and very small for teats (BIF, 2011) both of which are considered an ideal score (Bradford et al., 2015). A positive correlation between the traits would signify that cows with less pendulous udders are more likely to remain in the herd, because females with larger and more pendulous udders can have a higher chance of issues with calves being able to nurse (Ventorp and Michanek, 1992). However, in terms of decreasing the age of measurement of phenotypes, udder traits offer little advantage over using calving data at younger ages, because observations are taken at the birth of a calf (BIF, 2011). A possible future solution for these traits that are measured later in life is the use of genomic information. However, future studies need to be performed to identify QTL for these traits.

In summary, genetic relationships between HPG or STAY and other production traits were low to moderate in magnitude. For HPG including Pre-WG as a correlated trait has the potential to improve accuracy. Preweaning gain lends itself to be an ideal indicator trait because it can be easily and cheaply recorded, measured on both sexes, and occurs before culling decisions are made, maximizing the amount of data that is available

for the evaluations and improving predictions by reducing the effect of the traditional culling bias of the data. An additional outcome of this study is that selection for improving weight and carcass traits should not have a negative effect on the ability of a female to become pregnant during her first breeding season. The trait that offers the best opportunity as an indicator trait for STAY is UBF. The inclusion of this trait into STAY genetic evaluation will add information from both males and females at approximately a year of age. This is a full 2 yr before observations are taken for even multiple trait STAY (Brigham et al., 2007). This will allow increasing STAY accuracy of prediction for young sires by using both phenotypes to make STAY genetic predictions.

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