Genotype by environment interaction for stayability of Red Angus in the United States

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ABSTRACT: Bulls are used across a wide variety of environments through the use of artificial insemination. However, not all bulls rank the same for genetic merit in all environments. Sire selection could be more accurate via improved methods of characterization. The objective of this study was to evaluate the presence of genotype by environment (G×E) interaction for stayability in Red Angus in the United States. Environments were defined as nine regions within the continental United States with similar temperature-humidity indices. Stayability was defined as having a calf at age 4 given that the cow had a calf at

age 2. A probit sire model was used to determine the heritability on the underlying scale. The percentage of females that calved at age 2 that also calved at age 4 ranged from 32.9 to 58.5% across regions and was 55.0% for the national data set. The heritability of stayability ranged from 0.10 to 0.57 across regions and was 0.12 for the national data set. Genetic correlations were estimated for stayability between all pairs of regions. An estimate of less than 0.80 indicates G×E at a level for concern. Genetic correlations between regions ranged from 0.32 to 0.87 and were <0.80 for 29 of 36 region pairs.

Key words: beef cattle, genotype by environment interaction, reaction norms, Red Angus, stayability

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INTRODUCTION

Genotype by environment (G×E) interactions have been described as the reranking of sires when progeny performance is measured in different environments (Falconer, 1952). Some researchers have found significant G×E for weaning weight in beef cattle (Bertrand et al., 1985; Notter et al., 1992; Williams et al., 2012). Reproductive fitness is important to a beef cattle enterprise, tends to be low in heritability, and may be more affected by G×E compared to weight traits.

Two approaches to assessing G×E are by 1) considering a trait expressed in different environments

as two traits and estimating the genetic correlation between them (Dickerson, 1962; Bertrand et al., 1987), and 2) calculating the slope of the reaction norm (RN), which describes the change in performance of a genotype as environmental quality changes (Falconer and MacKay, 1996). The average RN slope is expected to be 1.0, a slope of less than one indicates stability of performance across changing environments, whereas a slope of greater than one indicates sensitivity to changes in environment (Mattar et al., 2011) and describes the response of a genotype or variety (Falconer and MacKay, 1996) to changes in environments. For a sensitive genotype performance may be excellent in an excellent environment, but performance drops quickly when the environment is less than ideal, as illustrated in swine by Knap and Su (2008).

Keeping cows in the breeding herd is important to the viability of a beef herd. Females are expected

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to calve at the age of two, breed back, and remain productive for many years as they are exposed to a wide variety of environmental conditions. Stayability has become the favored measure of this characteristic. If GxE for stayability is important, producers may benefit from genetic analyses that account for adaptation to local conditions. The objective of this study was to evaluate the presence of GxE for stayability in Red Angus in the United States.

MATERIALS AND METHODS

Field data from an existing database were used and thus Animal Care and Use Committee approval was not required.

Stayability has been defined as the probability a cow will remain in the herd until 6 yr of age given she first calved as a 2 yr old (Brigham et al., 2009). To increase the number of records in this analysis, stayability was defined as the probability of having a calf at age 4 (Brigham et al., 2009), given that the female had a calf at age 2. In addition, this younger age requirement could potentially reduce the concern that culling for nonreproductive reasons had occurred (Brigham et al., 2009). The females used for this analysis met the following requirements:

1. The females were born between 1 January 1993 and 30 June 2006.
2. Their calves were born in the appropriate age range (Table 2).
3. Calves were born in the same season of birth as the dam.
4. Dams must calve in the same season they were born.
5. The owner and the breeder were in the same region. This parameter was used to identify females that were born, raised, and produced in the same

region and also to avoid potential inaccuracies by assigning on owner's zip code only.

6. All sires were known, were 365 days of age at the time of conception of progeny and had qualifying daughters in more than one region.
7. Contemporary groups (CG) were defined as females born in the same herd in the same season of the same year. Each CG had at least five females with at least two sires represented and in which those sires had daughters in at least one other region.

In this data set, 365,133 calves were born to 115,408 females. After applying the requirements above, only 22,735 females were eligible for the analysis when using the traditional definition (6 yr of age). Brigham et al. (2009) estimated genetic correlations between traditional stayability compared to stayability at younger ages. The genetic correlations were 0.84 for 3–4 yr and 0.85 for 4–5 yr. Martinez et al. (2005) found similar results with correlations between 4 and 5 yr stayability of 0.85 and 4 and 6 yr of 0.86. Therefore, this analysis used females old enough to have three calves instead of five calves, which increased the number of females to 28,985.

Similar to the map presented by Leighton et al. (1982), nine regions were created by using the first three digits of U.S. Postal Service Zip Code associated with the herd owner's mailing address (Leighton et al., 1982; Bertrand et al., 1987). These regional boundaries contain similar climate that influence forage production and herd management practices. These are regional identifiers that denote production environments with similar names as used in other cartographic utilization, but do not have similar strict geographic boundaries. Data from the National Oceanic and Atmospheric Administration (Table 1) were used to confirm the climatic boundaries (NOAA, 2017).

Relative to the map from Leighton et al. (1982), and due to the relatively minor presence of fescue in these areas, Eastern Oklahoma and Northeastern Texas were moved from the Southern region to the Lower Plains, whereas Northwestern Louisiana was moved to the Gulf region (Figure 1). The Great Lakes were included in the Northeast. The ranking of cows grazing endophyte-infected tall fescue compared to cows grazing Bermuda grass illustrated GxE and a need to redraw these regions (Brown et al., 1997).

These regions were designated from northwest to southeast:

1. Pacific
2. Desert

Table 1. Average temperature and precipitation by region from 1975 to 2017

Region	Average	
	Temperature (deg. C)	Precipitation, ml
Corn belt	10.5	83.1
Desert	10.4	32.8
Gulf	18.7	114.6
Lower plains	14.5	58.7
Mountains	4.4	51.8
Northeast	6.6	82.8
Pacific	10.5	169.2
South	13.4	100.8
Upper plains	7.3	38.6

<https://www.ncdc.noaa.gov/cag/>.

3. (Rocky) Mountains
4. Upper (Great) Plains
5. Lower (Great) Plains
6. Corn Belt
7. Northeast (Including the Great Lakes)
8. South (including the Mid-Atlantic)
9. Gulf Coast (including the Lower Atlantic)

The females in this data set had 21,619 dams with 21,358 dams having calves in only one region, 250 dams with calves in two regions and three dams with calves in three regions. There were 1,051 sires with 18 sires having daughters in all 9 regions and 20 sires having daughters in 8 regions.

Variance components were estimated by fitting residual maximum likelihood linear sire models with the probit option for categorical data. These were estimated for the stayability benchmark of 4 yr of age. Dams were required to be at least as old as the defined benchmark to receive a stayability observation for a given endpoint and were required to have calved on an annual basis within a 60-d time period of the previous calving. A favorable designation (1) was given to dams that met these criteria (SUCCESS) and an unfavorable designation (0) was given to dams that did not meet these criteria (FAILURE).

Genetic Correlations Between Regions

Genetic correlations between regions were determined using a probit sire/maternal grand-sire model in ASReml 4 (Gilmour et al., 2015). SUCCESS was considered a different trait for each region. The following model was used:

$$y_{ij} = \mu + \text{region}_j + \text{sire} * \text{region}_{ij} + \text{CG}_k + e_{ijk}$$

where y was the observation of the trait (SUCCESS), μ = the trait mean, region = one of nine regions where the data were reported, $\text{sire} * \text{region}$ = the random sire by region interaction, CG = the random contemporary group for the trait (SUCCESS), and e = the error term.

Residual effects were assumed uncorrelated because most (98.8%) females were observed in only one environment.

Reaction norms. Region SUCCESS means and sire SUCCESS means were estimated in each region. The RNs for SUCCESS were obtained by fitting sire SUCCESS means to a model weighted for the number of progeny for each sire in each region:

$$y_i = \beta_0 + \beta_1 \text{RegAveStay}_j + e_{ij}$$

in which, y_i was the estimate of the mean SUCCESS of the sire's progeny within a region, β_0 was the intercept, β_1 was the slope, RegAveStay_j was the mean SUCCESS within a region, and $e_{ij} \sim N(0, \sigma_{ij}^2)$ was the error term.

Heritability of SUCCESS

Heritabilities of SUCCESS were estimated with a sire model with REGION as a fixed effect and a random CG in ASReml 4 (Gilmour et al., 2014). Maternal genetic effects were not considered. All variance components and functions were from

Figure 1. Climatic regions are defined as: (1) Pacific, (2) Desert, (3) (Rocky) Mountains, (4) Upper (Great) Plains, (5) Lower (Great) Plains, (6) Corn Belt, (7) Northeast (including the Great Lakes), (8) South (including the Mid-Atlantic), and (9) Gulf Coast (including the Lower Atlantic).

Table 2. Age at calving and calf requirements

Age of dam, yr	Age at calving, days		Required calves
	Min	Max	
2	670	790	1
3	1,035	1,155	2
4	1,400	1,520	3

models that estimated direct genetic effects only. The pedigree file contained three generations.

Stayability was analyzed as a univariate on the underlying scale using the model

$$y = X\beta + Zu + e$$

in which y was the vector of transformed observations on the underlying scale, X was a known design matrix relating fixed effects (REGION) to those individuals in vector y . Z was the design matrix relating the random additive genetic effects (sire) and random CG effects in u to the individuals in vector y , and e was a vector of random residual errors.

In addition,

$$\text{var} \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} \sigma_a^2 A & 0 \\ 0 & \sigma_e^2 I \end{bmatrix}$$

in which A was Wright's additive numerator relationship matrix, I was an identity matrix with order equal to the number of observations in Y . The additive and residual variances were σ_a^2 and σ_e^2 , respectively. The residual variances (σ_e^2) were forced to be equal to 1.

RESULTS AND DISCUSSION

Females in the hotter regions had reduced stayability compared to the more Northern regions (Table 3). Less than 40% of females were still in production in the Desert and Gulf regions at the age of four (had three calves) and greater than 55% of the females were still in production in the Corn Belt, Mountain, Northeast, and Upper Plains regions. These frequencies were similar to those reported by Snelling et al. (1995), who found frequencies of 75 and 39%, respectively, for a Red Angus herd, and 79 and 38%, respectively, for a black Angus herd, for females which had two and five calves, respectively, given she had calved once. Similarly, Martinez et al. (2005) found 53% of Herefords in northwest Nebraska had weaned three calves, given that they had weaned one calf.

The distribution of observations is shown in Table 3. Regions Mountain and Upper Plains have the majority of the observations (60.5%). Comparisons of SUCCESS by region showed all pairwise comparisons except Corn Belt with Mountain, Corn Belt with Northeast, Corn Belt with Upper Plains, Lower Plains with Pacific, Mountain with Northeast, and Northeast with Upper Plains to differ ($P < 0.05$). These regions, except Lower Plains, are located in the northern half of the United States and may offer some guidance for clustering regions for further analysis. The northern regions (Corn Belt, Mountains, Northeast and Upper Plains) have relatively high stayability and are similar to each other, whereas the Gulf, Desert, and Southeast are not only different from the northern regions, but differ from each other. The Lower Plains and Pacific were intermediate between the other groups. Interestingly, the northern regions appear to be similar from the Northeast to the Mountains, but that does not appear to be true for southern regions. Females in regions Gulf, Desert, Lower Plains, and Southeast may be exposed to environmental extremes which warrant further study. Extremes in heat, humidity, and differences in forages or other nutritional inputs among the southern regions may be important to explaining differences in SUCCESS.

One of the challenges of GxE studies is the need to define the environments. Many studies have used geographical regions (Nunn et al., 1978; Tess et al., 1979; Bertrand et al., 1985, 1987). Tess et al. (1979) examined GxE for weaning weights of Simmental-sired calves in Montana, the Midwest, and Texas. In that study, it was reported that interactions between sires and herds appeared to be much more important than sire $\times$ region interactions. Notter et al. (1992) defined environment as the herd and reported on sire $\times$ herd interactions for weaning weight. Although significant interactions were found, these authors suggested accommodations in the genetic analysis may be needed but did not suggest there was a compelling case for the development of a herd specific breeding value. Speidel et al. (2007) used body condition as an indicator of environmental conditions, whereas Vercoe and Frisch (1992) defined environments as different diet quality and level of parasite control.

Stayability generally decreased in each region from 1993 to 2006 (Figure 2). Possible explanations may include a year effect or changes in genetics or management. Females born in Desert and Gulf were lower than the national average (55%) in all years, whereas females born in Mountain exceeded

50% each year and females born in Corn Belt and Upper Plains exceeded 50% every year except one (Table 2). Females born in 2005 and 2006 failed to exceed the national average, which may be due to significant environmental challenges. The range across years in percentage of females that stayed in the herd was greatest in Southeast (49%) and Gulf (43%) while the smallest range was Mountain (15%) and Upper Plains (19%), indicating that adaption is better to Mountains and Upper Plains environments and/or the environment is more similar from year-to-year in the Mountain and Upper Plains compared to the Southeast and Gulf.

The heritability of SUCCESS on the underlying scale for the national data set was 0.12 ± 0.02 (Table 4). Within region h^2 ranged from a low of 0.10 ± 0.06 in region Corn Belt to a high of 0.57 ± 0.35 in region Gulf. Heritabilities were considerably higher in Desert and Gulf compared to other studies, but the estimates for these regions were accompanied by large SE, as a result of very small data sets in these regions. Overall, h^2 were similar in this analysis compared to Snelling et al. (1995), but lower to those reported by Van Melis et al. (2007) and Martinez et al. (2005).

Snelling et al. (1995) estimated heritabilities of 0.09, 0.10, 0.07, and 0.20 for stayability on the underlying scale defined as having 2, 5, 8, and 11 calves, respectively, given the females had calved at the age of two in a Red Angus herd. Van Melis

et al. (2007) estimated heritabilities of stayability of Nellore cows using age definitions of 5, 6, or 7 yr. Their estimates were 0.25, 0.22, and 0.28 for ages 5, 6, and 7, respectively. Martinez et al. (2005) estimated heritabilities of stayability of Hereford cows of 0.24, 0.25, 0.19, 0.19, and 0.18, for ages 2, 3, 4, 5, and 6, respectively. Barreto et al. (2017) estimated the heritability of stayability of Nellore cows of 0.11 when using A matrix (pedigree) and 0.14 using H matrix (pedigree information and SNP data). In this study, new candidate regions for stayability were detected with most related to reproductive, immunological, and central nervous system functions.

Figure 3 illustrates the RNs of the 10 most heavily used sires across different environments. Most of the sires exhibit RNs as expected and are similar to each other. However, one sire has a much flatter slope. The flatter slope indicates the daughters perform similarly across different regions and those daughters may be superior to other sire's daughters when the environment becomes more challenging. Conversely, this sire's daughters do not perform as well as daughters of other sires when the environment is less challenging. Sires with slopes significantly different than one might provide information related to physiology or about the use of those sires across the United States.

Bertrand et al. (1987) used genetic correlations to describe GxE and following Robertson (1959) suggested that a high genetic correlation (>0.80) between environments indicates little evidence for

Figure 2. Stayability by year.

Table 3. Count and percentage of stayability to age 4 by region and year

		Corn belt	Desert	Gulf	Lower plains	Mountain	Northeast	Pacific	Southeast	Upper plains	Total
1993	Count	81	19	7	40	645	28	114	71	371	1,376
	Percentage	72.8	52.6	28.6	77.5	65.4	71.4	74.6	64.8	62.0	65.8
1994	Count	107	21	11	62	626	41	130	70	377	1,445
	Percentage	57.9	33.3	54.5	64.5	65.2	73.2	53.8	71.4	67.6	64.2
1995	Count	129	15	21	58	704	55	88	98	422	1,590
	Percentage	69.0	33.3	47.6	75.9	59.8	72.7	43.2	48.0	66.1	61.2
1996	Count	142	24	29	82	673	51	84	128	431	1,644
	Percentage	57.7	45.8	41.4	61.0	53.5	52.9	54.8	44.5	65.2	56.3
1997	Count	173	33	15	94	736	33	88	114	407	1,693
	Percentage	59.0	36.4	46.7	50.0	53.1	66.7	56.8	60.5	61.9	56.2
1998	Count	184	21	13	178	777	38	99	107	361	1,778
	Percentage	61.4	47.6	46.2	55.6	50.2	52.6	71.7	57.9	64.5	56.5
1999	Count	207	37	29	204	751	73	109	136	446	1,992
	Percentage	47.3	32.4	48.3	46.6	52.9	67.1	39.4	52.9	57.6	52.1
2000	Count	269	46	31	263	834	115	85	177	532	2,352
	Percentage	53.5	30.4	32.3	53.2	51.6	57.4	34.1	57.1	53.2	51.7
2001	Count	276	27	49	266	878	115	86	181	521	2,399
	Percentage	60.5	37.0	28.6	49.2	55.4	63.5	58.1	53.0	55.7	54.9
2002	Count	294	48	28	316	746	127	113	245	520	2,437
	Percentage	56.8	45.8	32.1	50.9	63.3	61.4	38.9	47.3	61.3	57.0
2003	Count	323	39	41	233	820	120	85	224	557	2,442
	Percentage	56.0	46.2	22.0	53.6	60.5	63.3	60.0	33.9	64.5	57.0
2004	Count	319	19	29	237	837	206	85	233	627	2,592
	Percentage	57.7	52.6	31.0	52.7	53.5	49.5	50.6	49.4	55.2	53.3
2005	Count	388	28	36	250	856	168	106	247	787	2,866
	Percentage	54.9	25.0	11.1	39.6	51.9	54.2	36.8	34.0	48.7	47.6
2006	Count	412	21	11	227	684	251	69	83	621	2,379
	Percentage	51.2	52.4	27.3	41.9	53.2	46.2	44.9	22.9	50.9	49.0
Total count		3,304	398	350	2,510	10,567	1,421	1,341	2,114	6,980	28,985
Percentage		56.7 ^{af}	39.9 ^b	32.9 ^a	51.1 ^d	56.1 ^e	57.0 ^{ef}	51.5 ^d	47.8 ^c	58.5 ^f	55.0

^{abcdef}Values with no superscript in common differ ($P < 0.05$).

Table 4. Heritability of SUCCESS by region

Region	Phenotypic		h^2	SE
	Variance	SE		
Corn belt	1.24	0.04	0.10	0.06
Desert	1.36	0.14	0.36	0.27
Gulf	1.77	0.23	0.57	0.35
Lower plains	1.41	0.06	0.26	0.10
Mountains	1.25	0.03	0.14	0.03
Northeast	1.23	0.06	0.17	0.10
Pacific	1.28	0.07	0.12	0.09
Southeast	1.47	0.07	0.18	0.08
Upper plains	1.35	0.05	0.19	0.05
United States	1.30	0.02	0.12	0.02

GxE. Falconer and MacKay (1996) stated a low genetic correlation means that genotypes react differently to different environments and have regression lines with different slopes. Increased sensitivity appears to increase the environmental variance and reduce the heritability.

Figure 3. SUCCESS reaction norms of the most heavily used bulls.

Table 5. Genetic correlations between geographic regions for stayability

	Corn belt	Desert	Gulf	Lower plains	Mountain	Northeast	Pacific	Southeast	Upper plains
Corn belt		0.75	0.87	0.62	0.58	0.74	0.75	0.74	0.55
Desert			0.87	0.58	0.82	0.78	0.82	0.74	0.79
Gulf				0.70	0.70	0.82	0.82	0.80	0.70
Lower plains					0.40	0.60	0.46	0.50	0.32
Mountain						0.70	0.68	0.60	0.69
Northeast							0.72	0.65	0.58
Pacific								0.78	0.69
Southeast									0.58
Upper plains									

SUCCESS was considered a separate trait in each region and correlations estimated between each region (Table 5). Genetic correlations <0.80 indicate GxE at a level for concern and existed for 29 of 36 estimates. Correlations ranged from 0.87 to 0.32. The highest correlations were between the Gulf and Corn Belt (0.87), Gulf and Desert (0.87), Gulf and Northeast (0.82), Gulf and Pacific (0.82), Desert and Mountain (0.82), and Gulf and Southeast (0.80). The lowest correlations were between the Lower Plains and the Upper Plains (0.32), Lower Plains and Mountain (0.40), Lower Plains and Pacific (0.46), and Lower Plains and Southeast (0.50).

Given the economic importance of stayability, a more in-depth study is justified to determine appropriate groupings for GxE analysis. Environments might be determined by the level of performance within each CG, such that high, medium, and low levels of performance of a trait lead to more accurate RNs, correlations, and genetic evaluations.

CONCLUSIONS

This study showed GxE exists for Stayability in Red Angus in the United States. Possible methods to accommodate for GxE might include regional adjustment of EPDs or the use of RNs in genetic evaluation.

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