Genotype by environment interactions for growth in Red Angus[1]

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ABSTRACT: Accuracy of sire selection is limited by how well animals are characterized for their environment. The objective of this study was to evaluate the presence of genotype × environment interactions (G×E) for birth weight (BiW) and weaning weight (WW) for Red Angus in the United States. Adjusted weights were provided by the Red Angus Association of America. Environments were defined as 9 regions within the continental United States with similar temperature–humidity indices. Mean weights of calves were determined for each region and for each sire's progeny within each region. A reaction norm (RN) for each bull was estimated by regressing the sire means on the region means weighted for the number of progeny of each sire. The range for BiW and WW RN was −1.3 to 4.0 and −1.7 to 2.8, respectively. The heritabilities of BiW and WW RN were 0.40 and 0.39, respectively. Phenotypic and genetic correlations between BiW and WW RN were 0.19 and 0.54, respectively. The phenotypic correlation of the progeny mean to the RN was −0.20 ($P < 0.05$) and suggests that sires with higher means are more stable in progeny performance across environments. Weights in different regions were considered separate traits and genetic correlations were estimated between all pairs of regions as another method to determine G×E. Genetic correlations < 0.80 indicate G×E at a level for concern, but existed for only 2 of 36 estimates for BiW and 12 of 36 estimates for WW. Genetic correlations between different regions ranged from 0.74 to 0.96 for BiW and 0.62 to 0.99 for WW and indicate that sires tend to rank similarly across environments for these traits.

Key words: beef cattle, genotype × environment interaction, growth, reaction norms, Red Angus

INTRODUCTION

Artificial insemination has made it possible to use the same bull across a wide variety of environments, yet no one bull may be optimal for all environments. If genotype × environment interaction (**G×E**) exists, choosing a sire based on its EPD estimated from performance measured largely in one environment may result in less than optimum performance in another environment. Burns et al. (1979) reported significant G×E for birth and weaning weights for cattle produced and reared in Florida versus Montana, highly divergent environments. Conversely, Tess et al. (1984) found little evidence for G×E for the same traits in cattle produced and reared in different locations within North Carolina, a more limited range of environments.

One approach to assessing G×E is the use of reaction norms (**RN**). The slope of a RN describes the change in performance of progeny as environmental quality changes (Falconer and Mackay, 1996). The average slope is expected to be 1.0, and a slope of less than 1 indicates that a bull produces progeny robust to changes in the environment whereas a slope

of greater than 1 indicates that a bull produces progeny that are responsive to changes in environmental quality. Following the model proposed by Eberhart and Russell (1966) for evaluating stability of performance of crop varieties, RN have been used to characterize beef cattle (Mattar et al., 2011; Cardoso and Tempelman, 2012), sheep (Pollott and Greeff, 2004), swine (Silva et al., 2014), and dairy cattle (Strandberg et al., 2009). An alternative to a RN is to consider a trait expressed in different environments as 2 traits and estimate the genetic correlation between them (Bertrand et al., 1987). A high genetic correlation (>0.80) indicates little evidence for G×E (Robertson, 1959). The objective of this study was to determine the magnitude of G×E for birth weight and weaning weight in Red Angus cattle produced across 9 regions determined by average temperature–humidity index.

MATERIALS AND METHODS

Field data from an existing database were used in this study and are therefore exempt from animal care and use committee approval.

Nine regions across the United States were modified from the map presented by Leighton et al. (1982) by using the first 3 digits of U.S. Postal Service ZIP Code associated with the mailing address of the herd owner (Leighton et al., 1982; Bertrand et al., 1987). Eastern Oklahoma and northeastern Texas were moved from the Southern region to the Lower Plains due to the minor use of fescue in these areas, and northwestern Louisiana was moved to the Gulf region (Fig. 1). Brown et al. (1997) showed G×E for cows grazing endophyte-infected tall fescue compared with cows grazing Bermuda grass, indicating a need to redraw these regions.

These regions were designated

1. Corn Belt,
2. Desert,
3. Gulf Coast,
4. Lower Plains,
5. Mountains,
6. Northeast,
7. Pacific,
8. South, and
9. Upper Plains.

The data set used for this study was provided by the Red Angus Association of America (Denton, TX) and included adjusted birth weight (**BiW**) and adjusted weaning weight (**WW**) on 1,355,873 calves. The BiW performance records were adjusted for age of dam and WW records were adjusted for age of dam

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

and age of calf at time or recording. Breed-specific adjustment factors for age of dam were applied during record adjustment. The data set was filtered for calves with recorded BiW and WW, birth and weaning dates, and age at weaning of 160 to 250 d. The data set was further filtered by setting the minimum and maximum BiW to 22.7 and 50.0 kg, respectively, and minimum and maximum WW to 159.1 and 409.1 kg, respectively. After applying these constraints, records on 946,695 calves remained in the data set.

Sires were required to have at least 150 calves, with at least 50 calves in a minimum of 2 regions and with calves in at least 6 regions. After edits, the final data set contained records on 67,122 calves born from 1972 to 2011 and sired by 105 bulls.

Reaction Norms

Mean adjusted weights for BiW and WW were calculated for each sire within a region and denoted as the progeny means. Mean weights were obtained for BiW and WW within each region and denoted as environmental means.

Reaction norms for BiW and WW were obtained by fitting a model to the sire means to a model weighted by for the number of progeny for each sire in each region:

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

$$y_i = \beta_{0i} + \beta_{1i} \text{RegAveWt}_j + e_{ij},$$

in which y_i is the estimate of the mean weight of the sire's progeny within a region, β_0 is the intercept, β_1 is the slope, and RegAveWt_j is the mean weight for the trait within a region, and e_{ij} iid. $\sim N(\mathbf{0}, \sigma_{ij}^2)$ is the error term.

Heritability of Birth Weight and Weaning Weight

The heritabilities of BiW and WW were estimated for each region and across all regions by using a univariate animal model in ASReml 4 (Gilmour et al., 2014). Maternal genetic effects were not considered in the evaluations. All variance components and functions thereof were from models that estimated only direct genetic effects. Three generations were included in the pedigree file. Birth and weaning weights on 67,122 calves were included in the analyses and the relationship matrix included 116,063 individuals. The following model determined the heritability of BiW and WW:

$$y_{ij} = \mu + \text{region}_j + \text{animal}_i + CG_k + e_{ijk},$$

in which y is the observation of the trait (BiW or WW), μ is the trait mean, region is fitted as a fixed effect and 1 of 9 regions where the data were reported, animal represent the random animal, **CG** is the random contemporary group for that trait (BiW or WW), and e is the error term.

Heritabilities of Reaction Norms

The heritabilities of the RN for BiW and WW were estimated with a bivariate animal model. Slopes were calculated as described above for 105 bulls. The relationship matrix included the sires, dams, and paternal and maternal grandsires of the 105 bulls included in this analysis.

Genetic Correlations between Regions

To evaluate G×E between regions, BiW (and, likewise, WW) was considered a different trait in each region. A genetic correlation was estimated between each pair of regions (36 genetic correlations) using the following model in ASReml 4. To estimate the genetic correlations between regions, the following 2-trait sire model analysis in ASReml 4 was used:

$$y_{ij} = \mu + \text{region}_j + \text{sire} \times \text{region}_{ij} + CG_k + e_{ijk},$$

in which y is the observation of the trait (BiW or WW), μ is the trait mean, region is fitted as a fixed effect and 1 of 9 regions where the data were reported, sire × region is the random sire × region interaction, CG = the random contemporary group for that trait (BiW or WW), and e is the error term.

Residual effects were assumed uncorrelated because calves were observed in only 1 environment.

RESULTS AND DISCUSSION

There were 105 sires of 67,122 calves in this data set. The Mountains and the Upper Plains regions contained all sires, whereas only 59 and 80 sires were represented in the Desert and the Gulf Coast regions, respectively (Table 1).

Calves were unevenly distributed across the regions, with 61.2% of the calves produced in the Mountains and the Upper Plains regions (23,491 and 17,593, respectively). Two Midwest regions, the Corn Belt and the Lower Plains, produced 20.3% of the calves, whereas 2 extreme southern regions (the Gulf Coast and the Desert) represented only 2.9% of the data set. The remaining regions (the Northeast, the Pacific, and the South) produced only 15.5% of the calves.

Overall mean weights (SD) and mean weights by region are presented in Table 2. Overall mean weights were 36.6 (4.6) and 268.3 (36.6) kg for BiW and WW, respectively. Mean BiW ranged from 33.9 to 37.2 kg. Two southern regions, the Gulf Coast and the South, had the lowest BiW, as expected, whereas the highest BiW were in the more northern regions of Upper Plains, the Mountains, and the Northeast, with BiW of 37.0, 37.0, and 37.2 kg, respectively.

Weaning weights ranged from 238.3 to 275.6 kg, with the smallest WW, likewise, in the southern regions and the larger WW in the northern regions. Mean WW in the Gulf Coast and the South regions were 238.3 and 258.0 kg, respectively. Mean WW in the Northeast, the Pacific, the Corn Belt, and the Mountains regions were 275.6, 275.6, 272.9, and 272.8 kg, respectively.

Heritability of Birth Weight and Weaning Weight

Heritabilities within each region were estimated using a univariate animal model, and results are shown in Table 3. The BiW h^2 range was 0.0 (the Gulf Coast) to 0.46 (the Upper Plains), with a national estimate of 0.43. The dramatic drop in h^2 was unexpected in the Gulf Coast and the Lower Plains regions (0.0 and 0.17, respectively). The estimates for BiW h^2 were slightly lower compared with Winder et al. (1990), who reported 0.47 and 0.46, respectively.

Heritability for WW ranged from 0.05 (the Gulf Coast) to 0.41 (the Desert), with a national estimate of 0.38 using the single-trait animal model (Table 3). The estimate for WW was similar to that of Winder et al. (1990) but much higher than that of Speidel et al. (2005). Williams et al. (2012b) reported heritability estimates of 0.28 and 0.26 for WW, with greater heritability in low altitudes. Heritability estimates tend to be lower in field data compared with designed studies

Table 1. Number of sires by region

Region	Number
Corn Belt	102
Desert	59
Gulf Coast	80
Lower Plains	100
Mountains	105
Northeast	99
Pacific	91
South	101
Upper Plains	105

Table 3. Heritability and phenotypic variance of birth and weaning weights by region

Region	Birth weight		Weaning weight	
	V_P	h^2 (SE)	V_P	h^2 (SE)
Corn Belt	14.1	0.24 (0.06)	669.8	0.12 (0.04)
Desert	13.6	0.30 (0.21)	535.4	0.41 (0.21)
Gulf Coast	13.5	0.00 (0.06)	465.7	0.05 (0.08)
Lower Plains	14.4	0.17 (0.05)	562.7	0.07 (0.03)
Mountains	16.5	0.37 (0.04)	578.2	0.27 (0.04)
Northeast	14.9	0.28 (0.09)	599.3	0.10 (0.06)
Pacific	13.9	0.30 (0.09)	691.6	0.37 (0.10)
South	15.6	0.33 (0.09)	634.0	0.21 (0.07)
Upper Plains	17.1	0.46 (0.05)	601.3	0.37 (0.05)
United States	16.4	0.43 (0.03)	623.1	0.38 (0.03)

due to uncontrolled environmental sources of variation (Bertrand et al., 1985).

Reaction Norms

The estimates for the mean RN in each region were expected to be close to 1.0 and were 1.0 and 1.03 for BiW and WW, respectively (Table 4). The range for BiW and WW RN was −1.3 to 4.0 and −1.7 to 2.8, respectively. The SD for BiW and WW RN was 0.72 and 0.86, respectively.

Overall intercepts and slopes were determined and for each sire for each trait were used to plot the RN for BiW and WW. The average RN for the 105 sires was 1.0 for BiW and WW. The RN of the sires (15 sires) with >1,000 calves are illustrated in Fig. 2 and 3 for BiW and WW, respectively. The average RN for these 15 most heavily used sires were 1.0 and 1.1 for BiW and WW, respectively.

Three sires stood out as having BiW RN different from others among the 15 most heavily used (Fig. 2). Two had relatively flat slopes (0.2 and 0.5) and a third was parallel to (0.9) but considerably below the remaining bulls. For WW RN, only 1 sire stood apart from the other with a very flat (0.2) slope (Fig. 3).

Heritability of Reaction Norms

The heritabilities of BiW and WW RN were 0.40 ± 0.28 and 0.39 ± 0.21, respectively. Mattar et al. (2011) reported that heritability estimates increased with increasing environmental performance. The phenotypic and genetic correlations between the slopes of the BiW and WW reactions norms were 0.19 ± 0.10 and 0.54 ± 0.40, respectively. These data indicate heritability for the RN is moderate and if information is available, producers should be able to select sires that respond to environmental improvement. Maricle (2008) also reported moderate heritabilities of RN and noted that expected progeny differences for RN could be calculated to facilitate selection of sires. In addition, the relatively high genetic correlation indicates similar genetic control of consistency of performance across environments for both traits.

Genetic Correlations between Regions

Genetic correlations between regions for BiW (Table 5) ranged from 0.74 between the South and the Desert regions to 0.96 between the Corn Belt and the Lower Plains, the Corn Belt and the Mountains, and the Corn Belt and the Upper Plains regions. The lowest correlations were associated with the Desert and the South regions, whereas the highest correlations were associated with the Corn Belt region. Only 2 correlations were in the range of concern (<0.80) and both were associated with the Desert region. This sug-

Table 2. Means (SD) for birth weight (BiW) and weaning weight (WW) by region

Region	No.	Mean BiW, kg	Mean WW, kg
Corn Belt	6,731	36.6 (4.4)	272.9 (42.7)
Desert	663	35.8 (4.5)	261.3 (41.3)
Gulf Coast	1,303	33.9 (4.5)	238.3 (36.1)
Lower Plains	6,920	36.2 (4.5)	264.4 (36.3)
Mountains	23,491	37.0 (4.6)	272.8 (35.7)
Northeast	2,705	37.2 (4.4)	275.6 (36.7)
Pacific	3,458	35.6 (4.4)	275.6 (40.8)
South	4,258	34.8 (4.5)	258.0 (37.2)
Upper Plains	17,593	37.0 (4.6)	264.3 (36.6)
United States	67,122	36.6 (4.6)	268.3 (37.8)

Table 4. Description of reaction norms (RN) for birth weight (BiW) and weaning weight (WW)

Trait, RN	Mean	SD	Minimum	Maximum
BiW	1.00	0.72	−1.3	4.0
WW	1.03	0.86	−1.7	2.8

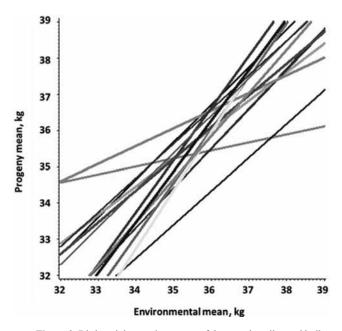**Figure 2.** Birth weight reaction norms of the most heavily used bulls.

Figure 3. Weaning weight reaction norms of the most heavily used bulls.

gests that across most of the country, sires are going to rank nearly the same for BiW, but it may be useful to take extra care in choosing sires for the Desert region.

Genetic correlations between regions for WW (Table 6) ranged from 0.62 between the Gulf Coast and the South regions to 0.99 between the Corn Belt and the Northeast regions. The lowest correlations were associated with the South region, whereas the highest correlations were associated with the Northeast region. The range in genetic correlations between regions for BiW was less than the genetic correlations between regions for WW. Although BiW genetic correlations were relatively low for the Desert and, to a lesser extent, in the South regions, low WW genetic correlations were more commonly associated with the South and, to a lesser extent, with the Desert and the Gulf Coast regions. Three correlations for the Desert and the Gulf Coast regions were <0.80, whereas all of the correlations associated with the South region were <0.80. These data suggest that Red Angus may rerank when used in cooler vs. hotter climates and even comparing hot, humid climates with hot, dry climates.
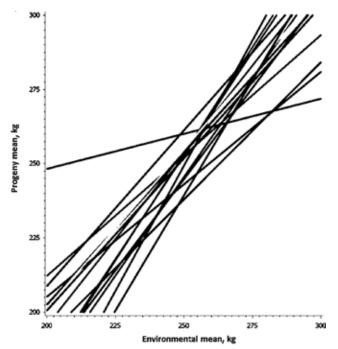
Bertrand et al. (1985) reported significant differences in sire × region effects in Polled Hereford field data (range from 0.39 to 1.0). Williams et al. (2012b) explored G×E between high and low altitudes and found a correlation of 0.74.

Buchanan and Nielsen (1979) analyzed Simmental and Maine-Anjou field data and reported significant sire × region effects. Nunn et al. (1978) did not find significant sire × region effects in Simmental for BiW but did for WW in most regions. However, Nunn et al. (1978) did not find significant sire × region effects comparing eastern and western Montana. Tess et al. (1979) reported no significant sire × region effects when comparing 3 regions (Montana, the Midwest, and Texas).

The low correlation of the southern regions (the South, the Desert, and the Gulf Coast) with the northern regions (the Mountains, the Northeast, the Pacific, and the Upper Plains) agrees with Williams et al. (2012a),

Table 5. Genetic correlations between geographic regions for birth weight

	Corn Belt	Desert	Gulf Coast	Lower Plains	Mountains	Northeast	Pacific	South	Upper Plains
Corn Belt		0.84	0.94	0.96	0.96	0.95	0.92	0.86	0.96
Desert			0.80	0.82	0.82	0.81	0.78	0.74	0.82
Gulf Coast				0.91	0.91	0.90	0.87	0.82	0.91
Lower Plains					0.93	0.92	0.89	0.84	0.94
Mountains						0.92	0.89	0.84	0.93
Northeast							0.88	0.83	0.92
Pacific								0.80	0.89
South									0.84
Upper Plains									

Table 6. Genetic correlations between geographic regions for weaning weight

	Corn Belt	Desert	Gulf Coast	Lower Plains	Mountains	Northeast	Pacific	South	Upper Plains
Corn Belt		0.87	0.82	0.87	0.96	0.99	0.92	0.74	0.96
Desert			0.73	0.78	0.85	0.88	0.82	0.65	0.85
Gulf Coast				0.74	0.82	0.83	0.78	0.62	0.81
Lower Plains					0.86	0.88	0.82	0.66	0.85
Mountains						0.97	0.91	0.72	0.94
Northeast							0.93	0.74	0.97
Pacific								0.69	0.90
South									0.72
Upper Plains									

who reported a low correlation (0.77) for southeastern region (**SoE**) winter-born Angus calves with northwestern region (**NW**) winter-born calves and a low correlation (0.69) of SoE winter-born calves with NW spring-born calves. The correlations for the other seasons (SoE fall-born and SoE winter-born calves [0.80], SoE fall-born and NW winter-born calves [0.82], SoE fall-born and NW winter-born calves [0.86], and NW winter-born and NW spring-born calves [0.93]) were of sufficient magnitude not to be of concern. These studies are not directly comparable but the data sets have similar characteristics. Contemporary groups are smaller in the Southeastern United States compared with the Northwestern United States and the calves born in the Northwestern United States are heavier compared with calves born in the Southeastern United States. Williams et al. (2012b) suggest the differences in weights observed between regions and seasons may be complex. For example, calves born in smaller contemporary groups in the Southeastern United States may perform better than expected due to increased care over calves from larger contemporary groups.

In another study, Williams et al. (2012a) compared Angus cattle at different altitudes and reported a genetic correlation of 0.74 for WW in Colorado. This is much lower compared with the result of this study, with a correlation of 0.94 for WW between the Upper Plains and the Mountains regions.

Conclusion

These data indicate G×E is of small magnitude for BiW and WW in Red Angus in the United States. Sires would be expected to rank similarly for offspring performance across most regions, with the possible exception of the Desert region for BiW and the South and the Gulf Coast regions for WW. When G×E is of concern, it might be addressed by including a RN along with the EPD and accuracy for that trait. Producer education would be required to maximize the value of the RN. A second option is to provide a genetic evaluation for each region wherein EPD for sires would be reranked through transformation using the RN. In practice, a producer would specify his environment to access the genetic evaluation for their specific region. Although many studies have found G×E for growth traits in beef cattle, there remains challenges in determining the appropriate boundaries for each environment and how best to use RN.

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