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Genotype-by-environment interaction for weaning weight in Angus cattle using principal component and multi-dimensional reaction norm analysis

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Introduction

Current animal breeding programs make selection and mating decisions based on estimated breeding values (EBVs) that are assumed to be constant across environments. However, this assumption may not always hold, as the breeding value of an animal may vary depending on the environmental conditions in which it is raised, leading to genotype-by-environment interaction (GEI). Recently, reaction norm models (RNM) have been used to assess GEI in beef cattle across several traits (Freitas *et al.,* 2021; Oliveira *et al.,* 2018**)**. The RNM regresses the phenotype on a continuous environmental gradient (EG), decomposing EBVs into environment-independent and environment-specific components. In animal breeding, RNM most commonly use a single covariate to estimate a set of genetic regression coefficients for each animal; here, we extend this framework to a multiple regression setting. Accordingly, two principal components (PC1 and PC2 scores) derived from standardized environmental variables summarizing herd environments were used as EG in a multi-dimensional reaction norm model (MRNM). Thus, the objective of this study was to investigate the presence and magnitude of GEI for weaning weight (WW) in Angus cattle using principal components and MRNM.

Materials & Methods

Adjusted WW records were obtained from the American Angus Association (AAA). The dataset comprised 364,319 WW records collected from 3,498 farms, and 36,968 contemporary groups (CGs). The CGs consisted of animals born in the same herd, year, season, sex, and common management from birth to weaning. Based on farm locations (zip code), soil, elevation, and weather data were extracted from NASA POWER (NASA POWER Data Access Viewer) and averaged to represent long-term mean environmental conditions. These environmental variables were standardized and subjected to principal component analysis (PCA). The first two principal components (PC1 and PC2 scores), which together explained the greatest proportion of environmental variability, were simultaneously used as EG in an MRNM. We fitted the following homoscedastic MRNM to evaluate GEI for WW in Angus cattle:

$$\mathbf{y}_{ij}=\mathbf{X\beta}+\beta_0+\boldsymbol{\beta}_1 PC1_j+\boldsymbol{\beta}_2 PC2_j+\mathbf{a}_{0i}+\mathbf{a}_{1i} PC1_j+\mathbf{a}_{2i} PC2_j+\mathbf{m}_{0i}+\mathbf{m}_{1i} PC1_j+\mathbf{m}_{2i} PC2_j+\mathbf{mpe}+\mathbf{e}_{ij} \quad (1)$$

where $\mathbf{y}_{ij}$ is the WW of animal i in a given environment j; $\boldsymbol{\beta}$ is the vector of fixed CG effects, with $\mathbf{X}$ as the corresponding incidence matrix; β_0 is the overall fixed intercept; $\boldsymbol{\beta}_1$ and $\boldsymbol{\beta}_2$ are the fixed regression coefficients describing the population level response of WW to $PC1_j$ and $PC2_j$, respectively; $\mathbf{a}_{0i}$, $\mathbf{a}_{1i}$ and $\mathbf{a}_{2i}$ are the vectors of direct additive genetic intercept and slopes of the reaction norms for $PC1_j$ and $PC2_j$, respectively; $\mathbf{m}_{0i}$, $\mathbf{m}_{1i}$ and $\mathbf{m}_{2i}$ represent the

corresponding maternal additive genetic intercept and slopes; **mpe** is a vector of maternal permanent environment effects assumed $N(0, \mathbf{I}_{nd}\sigma^2_{mpe})$, where $\mathbf{I}_{nd}$ is an identity matrix of dams with WW records; and **e** is a vector of random residual effects, assumed as $N(0, \mathbf{I}\sigma^2_e)$. The following co-variance structure was assumed for the estimation of additive (co)variance components:

$$\begin{bmatrix}\mathbf{a}_{0i}\\ \mathbf{a}_{1i}\\ \mathbf{a}_{2i}\end{bmatrix} \sim N\left(0, \begin{bmatrix}\sigma^2_{a_{0i}} & \sigma_{a_{0i,1i}} & \sigma_{a_{0i,2i}}\\ \sigma_{a_{0i,1i}} & \sigma^2_{a_{1i}} & \sigma_{a_{1i,2i}}\\ \sigma_{a_{0i,2i}} & \sigma_{a_{1i,2i}} & \sigma^2_{a_{2i}}\end{bmatrix} \otimes A\right) \quad (2)$$

where, $\sigma^2_{a_{0i}}$ is the additive genetic intercept variance; $\sigma^2_{a_{1i}}$ and $\sigma^2_{a_{2i}}$ are the corresponding additive genetic slope variances; and **A** is the additive genetic relationship matrix. Given estimate of random regression coefficients (co)variance matrix, covariance function was applied to estimate genetic variances and (co)variances at any locations across the two-dimensional PC1-PC2 EG. (Co)variance components were estimated using GIBBSF90+ programs (Lourenco *et al.,* 2022).

Results

(Co)variance components for WW using MRNM were estimated using pedigree-based BLUP in a Bayesian framework (Table 1). Relevant genetic parameters included direct additive genetic intercept and slope variances, heritability estimates, and genetic correlations evaluated across PC1-PC2 EG. A positive genetic covariance was observed between the direct additive genetic intercept and reaction norm slopes, with estimates of 0.85 ± 0.68 kg^2 for PC1 and 17.69 ± 0.85 kg^2 for PC2, indicating that animals with higher baseline genetic merit tended to exhibit greater environmental sensitivity, particularly along the PC2 gradient.

Table 1. (Co)variance components estimate for weaning weight (kg) using a multi-dimensional reaction norm model

Parameters	Estimate (standard deviation)
σ^2_{a0}	194.88 (8.40)
$\sigma_{a0,a1}$	0.85 (0.68)
σ^2_{a1}	0.55 (0.14)
$\sigma_{a0,a2}$	17.69 (0.85)
σ^2_{a2}	3.79(0.28)
$\sigma_{a1,a2}$	-0.25 (0.14)
$\sigma_{a0,m0}$	-45.98 (5.19)
σ^2_{mpe}	74.33 (3.08)
σ^2_e	374.33 (4.65)

σ^2_{a0} = intercept variances for direct additive genetic effect; σ^2_{a1} = direct additive genetic slope variances for PC1; σ^2_{a2} = direct additive genetic slope variances for PC2; $\sigma_{a0,m0}$ = genetic covariance between direct additive and maternal additive genetic effect; σ^2_{MPE} = maternal permanent environment variance; σ^2_e = residual variances

Direct heritability estimates described as a function of EG are shown across the PC1-PC2 plane (Figure 1-A). At an average environment (PC1 = 0 and PC2 = 0), we found a heritability estimate of 0.32, which is comparable to that reported by the AAA in their national genetic evaluation. However, heritability estimates varied strongly across the PC1-PC2 EG, with higher estimates observed toward positive PC1 and PC2 values. Higher heritability estimates were also observed at positive PC2 values even when PC1 was negative, indicating a stronger influence of PC2 on genetic variances. Overall, these results suggest that variation along the PC2 gradient contributes substantially to GEI for WW. The genetic correlation estimates for

WW across the PC1–PC2 EG ranged from 0.65 to 0.99, indicating the presence of GEI (Figure 1-B). Genetic correlations were high among similar environments, particularly when PC2 values were positive, even when PC1 differed in sign, but declined in contrasting environments—most notably when PC2 was negative and PC1 was positive—and were lowest when both PC1 and PC2 were negative, leading to environment-specific responses to selection.

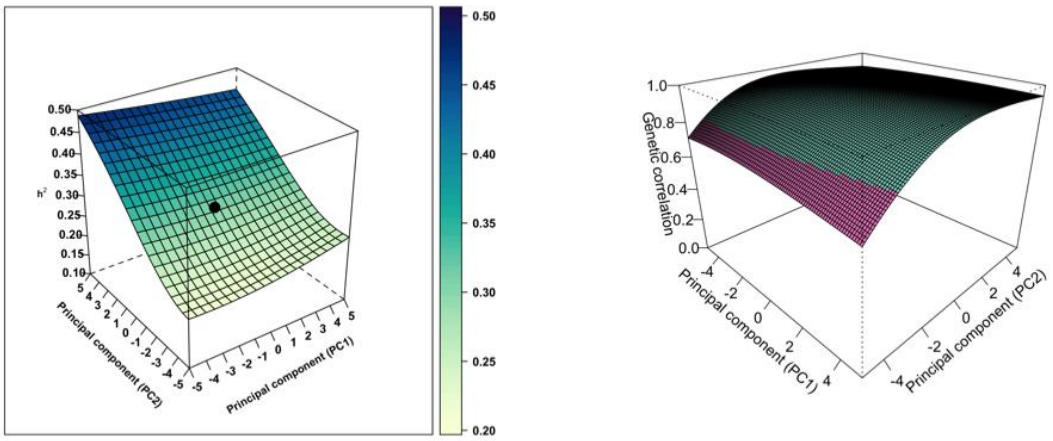

Figure 1-A. Direct additive heritability (h^2) of WW across the PC1-PC2 EG; the black dot marks the reference environment (PC1=PC2=0). **Figure 1-B.** Genetic correlation surface across the PC1–PC2 EG, with green indicating correlations >0.80 and pink indicating correlations <0.80.

Figure 2 shows reaction norms of the top 50 sires with the highest EBVs at the reference environment (PC1 = 0, PC2 = 0). When examining the reaction norm trajectories across PC1**,** while holding PC2 constant**,** reaction norms were largely flat with minimal re-ranking of sires, indicating limited environmental sensitivity along this gradient (Figure 2-A). In contrast, when reaction norms were evaluated across PC2, with PC1 held constant, the average EBV increases and substantial re-ranking of sires is observed, providing evidence of rank-type GEI (Figure 2-B).

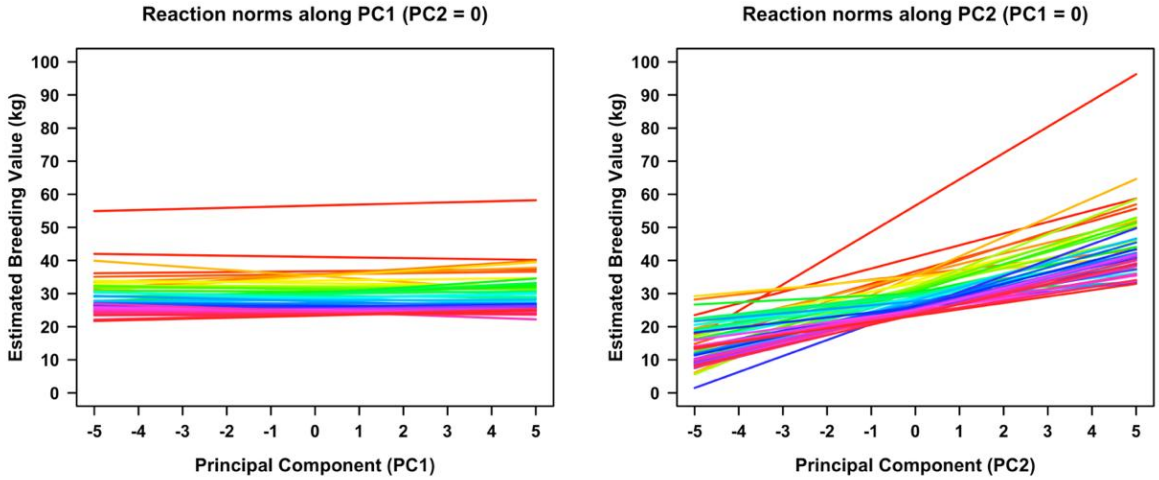

Figure 2. Reaction norms of EBVs for WW of top 50 Angus sires top ranked at the reference environment (PC1=PC2=0): **2-A** EBVs plotted along the PC1 EG with PC2 held constant at zero, and **2-B** EBVs plotted along the PC2 EG with PC1 held constant at zero.

Discussion

Our results revealed substantial variation in heritability estimates across PC-defined EG reflecting heterogeneity of variances across production environments. Consequently, expected response to selection for WW may differ across environments. Varying heritability estimates for weaning-related traits have also been widely reported in beef cattle (Cardoso and Tempelman, 2012; MacNeil *et al.,* 2017). Genetic correlations for WW across environmental PCs were generally high; however, correlations between contrasting environmental PCs significantly deviated from unity, indicating GEI. Reaction norms for sires further reinforced the existence of GEI across different levels of environmental PCs. Crossings of sire reaction norms occurred primarily along the PC2 gradient while PC1 was held constant, indicating substantial rank-type GEI. Within this context, the MRNM allows the genetic prediction of an individual across a multi-dimensional range of environments facilitating the simultaneous selection of animals with high WW and environmental robustness, thereby enabling precision, environment-specific breeding and management decisions.

Conclusions

This study shows that PCs (PC1 and PC2 scores) derived from standardized environmental variables can be used as covariables in an MRNM to account for GEI in cattle. Our study reveals that genetic variation exists in the response of animals across the PC1-PC2 EG, with a positive genetic covariance between the direct additive genetic intercept and reaction norm slopes, indicating that animals with a higher baseline genetic merit tended to exhibit greater environmental sensitivity. The genetic correlations across PC1-PC2 EG were different from unity, indicating that selection at different points along the PC1-PC2 EG affects sire performance across environments. Both scale- and rank-type GEI were detected through changes in genetic variance estimates, primarily along the PC2 EG. These findings underscore the importance of accounting for GEI in breeding programs and implementing environment-specific selection strategies to maximize production gains and enhance the sustainability of beef cattle production.

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