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Macro- and micro-genetic environmental sensitivity of yearling weight in Angus beef cattle

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ABSTRACT

Australian beef cattle experience variable conditions, which may give rise to genotype-by-environment interactions depending on the genotypes' macro- and/or micro-genetic environmental sensitivity (**GES**). Macro-GES gives rise to genotype-by-environment interactions across definable and shared environments, while micro-GES causes heritable variation of phenotypes, e.g., the performance of progeny from one sire may be more variable than other sires. Yearling weight (**YW**) is a key trait in Australian Angus cattle that may be impacted by both macro- and micro-GES. Current models for genetic evaluation of YW attempt to account for macro-GES by fitting sire-by-herd interactions (**S** × **H**). Variation in micro-GES had not yet been estimated for YW in Australian Angus. The aim of this study was to estimate genetic variation due to macro- and micro-GES in YW of Australian Angus cattle. A reaction norm with contemporary group effects as the environmental covariate was fitted either as an alternative to or in combination with a random S × H effect to account for macro-GES. Double hierarchical generalised linear models (**DHGLM**), fitted as sire models, were used to estimate the genetic variance of the dispersion as a measure of micro-GES. Variation due to both macro- and micro-GES were found in YW. The variance of the slope of the reaction norm was 0.02–0.03 (SEs 0.00), while the S × H variance accounted for 7% of the phenotypic variance in all models. Results showed that both a random S × H effect and a reaction norm should be included to account for both macro-GES and the additional variation captured by an S × H effect. The heritability of the dispersion on the measurement scale ranged from 0.06 to 0.10 (SEs 0.00) depending on which model was used. It should therefore be possible to alter both macro- and micro-GES of YW in Australian Angus through selection. However, care should be taken to ensure an appropriate data structure when including sire-by-herd interactions in the mean part of a DHGLM; otherwise, it can cause biased estimates of micro-GES.

Implications

Genotype-by-environment interactions across environments can have considerable impacts on genetic gain in large-scale breeding programs, while within environments genotype-by-environment interactions can decrease product uniformity. This study compared multiple models for the estimation of genotype-by-environment interactions across and within environments and reports estimates of variance components for yearling weight in Australian Angus. It was shown that estimation of genotype-by-environment interactions across and within environments was possible for this dataset. The estimation of genotype-by-environment interactions can be replicated with other traits for which considering genotype-by-environment interactions are relevant.

Introduction

Genotype-by-environment (**G** × **E**) interactions can present challenges for accurately predicting genetic gain in large-scale livestock breeding programs. The underlying cause of G × E is a difference in environmental sensitivity between genotypes. Animals with high genetic environmental sensitivity (**GES**) respond more to environmental differences than animals with low GES; thus, they are more sensitive to environmental changes. The GES can be categorised into two classes, macro- and micro-GES. The first class, macro-GES, is the sensitivity of a genotype to identifiable environments termed macro-environments (i.e., locations, management, feeding type) (Falconer and Mackay, 1996). The second class, micro-GES, is the sensitivity of a genotype to the environ-

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mental conditions that are experienced by the individual animal, known as a micro-environment (Hill and Mulder, 2010). While variance in both macro- and micro-GES causes G × E, the two types have different impacts on breeding programs.

Genotype-by-environment interactions due to macro-GES have been studied in a wide range of populations (Kolmodin et al., 2002; Mulder et al., 2013; Chu et al., 2019). Macro-GES can result in changes in genetic variance (scale type) or re-ranking of animals across macro-environments. Re-ranking due to macro-GES often has a larger impact on the breeding program than scale-type macro-GES because it results in suboptimal selection decisions when animals perform across different macro-environments (Falconer and Mackay, 1996). However, scale-type G × E can result in re-ranking of animals when traits with this form of G × E are included in a composite index (Namkoong, 1985). Both re-ranking and scale-type G × E can impact genetic gain in a breeding program if not considered.

In contrast to macro-GES, micro-GES does not cause re-ranking across environments, but it affects consistency in phenotypes. Animals with large micro-GES have offspring with more variable phenotypes than low micro-GES animals (Rönnegård et al., 2013). Genetic variation in micro-GES has been found for multiple traits in different livestock species. Heritabilities estimated from previous studies have ranged from 0 to 0.23 with the majority being below 0.05 (see e.g., the reviews by Hill and Mulder (2010) and Iung et al. (2020)). Studies of micro-GES in beef cattle are limited, and current publications are on micro-GES in Nellore beef cattle (Neves et al., 2011; Neves et al., 2012; Iung et al., 2017). This may be due to the data structure and recording methods of most beef cattle production systems.

The challenges of estimating micro-GES in beef cattle are related to the way micro-GES is estimated. Because micro-GES is the genetic variance of the variability of phenotypes, it requires many records from the same animal or closely related animals to estimate the genetic variance due to micro-GES (Mulder et al., 2013; Madsen et al., 2021). In beef production, the number of repeated records on the same animal for a routinely recorded trait is limited. Records from many closely related animals are therefore required. Madsen et al. (2021) showed that with average sire family sizes of 20 offspring per sire, 500 sire families were required for accurate estimation of micro-GES when using a double hierarchical generalised linear model (**DHGLM**). DHGLMs were originally developed by Lee and Nelder (2006) and later adapted by Rönnegård et al. (2010) and Felleki et al. (2012) for the estimation of micro-GES in livestock. Such models can also include a term to estimate macro-GES.

Macro-GES can have substantial impacts on beef cattle production systems, as these are typically dispersed across large areas that experience a range of environmental conditions. In an attempt to remove variation due to macro-GES, it is common to include a sire-by-herd interaction (**S** × **H**) term in the model when analysing traits in beef cattle (Graser et al., 2005). However, it has been noted that factors other than macro-GES may contribute to variation due to S × H, such as differential non-random mating between herds and errors in contemporary group (**CG**) definitions (Notter et al., 1992; Graser et al., 2005). Furthermore, sires used exclusively within a single herd can result in biased estimates of additive genetic variance when including an S × H term (Meyer, 2003). Alternative models to capture macro-GES have been suggested. These models include reaction norm models that regress performance across a continuous macro-environmental variable, e.g., temperature, humidity, or the average performance of cohorts in a macro-environment.

In the Australian Angus breed, yearling weight (**YW**) is routinely recorded by most breeders such that an appropriately structured dataset can be created to examine both macro- and micro-GES. Furthermore, YW is a predictor of growth and an early indicator of mature weight and carcass weight, and it is therefore relevant to investigate both macro- and micro-GES of YW. The aims of this study were to estimate the genetic variance due to macro- and micro-GES in YW for Australian Angus beef cattle and evaluate the best model to simultaneously estimate macro- and micro-GES of YW in Australian Angus.

Material and methods

Data

The data used in this study consisted of YW records measured on live animals. As per Angus Australia's definition of YW (also known as 400-day weight) animals had to be between 301 and 500 days of age (Angus Australia, 2021). To ensure this study related to the current modern Angus population, only animals measured since 2015 were retained. All records in the dataset had known mating type (natural or artificial insemination), birth type (natural or embryo transfer), date of birth, date of observation, sex, sire and dam.

A concatenation herd, year, observation date and breeder-defined management group was used as CG definition as described by Graser et al. (2005), with the exception that the sex was omitted from the CG definition. Instead, the sex effect was fitted separately in the statistical models. This was done based on linear regression analysis conducted in R (R Core Team, 2019) showing the necessity of including sex as a separate fixed effect. Records deviating more than 3 SD from the phenotypic mean of the CG were excluded. For animals with repeated measurements, only the record from the largest CG was kept.

Editing was done to ensure an appropriate data structure existed for the estimation of both macro- and micro-GES. Records from sires with less than five offspring, records from CGs with less than 60 animals or with offspring from less than five sires were removed from the final dataset.

The final dataset contained 100 612 records with an average YW of 400.40 kg (SD 79.49 kg) and a range of YW of 118–740 kg. Descriptive statistics for the data structure of the final dataset can be found in Table 1.

Two pedigrees were constructed based on either animals with records or sires of animals with records, to be used in animal and sire models, respectively. Both pedigrees were traced three generations back from the focal individuals, excluding animals without phenotyped descendants. The offspring-based pedigree contained 196 157 animals and the sire-based pedigree contained 13 076 animals.

Statistical analysis

To examine whether either macro- and/or micro-GES exists for yearling weight in Angus beef cattle, six statistical models were used. Three were animal models used to assess the different meth-

Table 1
Number of sires, dams and contemporary groups (CGs) along with the average (SD) number of records and the range in number of records in each category for yearling weight in a population of Australian Angus cattle.

Item	Count	Number of records	
		Average (SD)	Range
Sires	2 520	39.93 (102.38)	5–1 836
Dams	54 677	1.84 (1.87)	1–102
CGs	830	121.22 (71.57)	60–758

ods for estimating macro-GES, and three were DHGLMs fitted as sire models for the estimation of micro-GES.

Macro-genetic environmental sensitivity models

The three animal models differed in how they accounted for macro-GES. Macro-GES was fitted either as an S × H interaction or as a reaction norm with contemporary group effect on phenotype as environmental covariate (**EC**), or as both effects.

The first animal model included an S × H term (**A-SH**). This model was used to represent the current model used to estimate macro-GES in beef cattle in BREEDPLAN, Australia (Graser et al., 2005).

$$y = Xb + Za + Lsh + e_a \quad (\mathrm{A-SH})$$

where y contained the measured phenotype (YW), the vector b contained the fixed effects of sex and CG and a fixed regression on age at measurement for y, the vector a was the random genetic animal effect, sh was a vector of random sire S × H effects, and e_a was the vector of residuals of y. X, Z, and L were the design matrices for b, a and sh, respectively.

The distribution assumption for the random genetic animal effect was $a\ N(0, \sigma_a^2 \mathrm{A}_a)$, where A_a was the numerator relationship matrix based on the full pedigree. The distribution of the random S × H effect and residuals were $sh\ N(0, \mathrm{I}\sigma_{sh}^2)$ and $e_a\ N(0, \mathrm{I}\sigma_{e_a}^2)$, respectively, where I was an appropriate identity matrix.

The second animal model included a linear reaction norm to estimate macro-GES (A-RN), to examine if this method of macro-GES estimation performs better than the S × H effect.

$$y = Xb + [Z_{int} \quad Z_{sl}] \begin{bmatrix} a_{int} \\ a_{sl} \end{bmatrix} + e_a \quad (\mathrm{A-RN})$$

Compared to A-SH, the genetic animal effect in A-RN was regressed on an environmental covariate using a first-order polynomial, resulting in an intercept (a_{int}) and a slope (a_{sl}), with corresponding design matrices Z_{int} and Z_{sl}, respectively, and the distribution assumption of $\begin{bmatrix} a_{int} \\ a_{sl} \end{bmatrix} N\left(0, \begin{bmatrix} \sigma_{a_{int}}^2 & \sigma_{a_{int,sl}} \\ \sigma_{a_{int,sl}} & \sigma_{a_{sl}}^2 \end{bmatrix} \otimes \mathrm{A}_a\right)$. Z_{sl} contained the estimated CG effect which was used as the environmental covariates of the reaction norm. The estimated CG effect associated with y_i was obtained from $y = Xb + Za + Ccg + e_a$, with b only including sex while the CG effect was fitted as the random effect cg with a distribution following $cg\ N\left(0, \sigma_{cg}^2 \mathrm{I}\right)$, such that the average macro-environment was placed at 0. The estimated CG effects, and consequently EC, ranged from −201.23 to 163.59 kg with a maximum SE of prediction of 6.54 kg. The remaining effects in A-RN were the same as in A-SH, omitting the S × H term.

The third animal model included both a linear reaction norm and an S × H effect (**A-RNSH**). This was motivated by the hypothesis that other factors than just macro-GES can contribute to S × H in which case it may be necessary to include both effects in the model to accurately account for macro-GES.

$$y = Xb + [Z_{int} \quad Z_{sl}] \begin{bmatrix} a_{int} \\ a_{sl} \end{bmatrix} + Lsh + e_a \quad (\mathrm{A-RNSH})$$

where the genetic animal effects were as described for A-RN and the remaining effects were as described for A-SH.

To facilitate the comparison between the animal models and the DHGLMs (see next section), the residual variance was assumed to be homogenous across macro-environments.

Micro-genetic environmental sensitivity models

Three DHGLM models were used to estimate micro-GES. Each of the three DHGLMs were implemented as sire models to avoid biased estimates of variance components because of having one record per animal (Mulder et al., 2013). Each DHGLM was a direct extension of the sire model version of each of the animal models, such that the distribution of the residual variance followed $e_s\ N(0, V)$, where $\log(V) = X_d b_d + Z_d s_d$, to model the micro-GES in yearling weight.

The first DHGLM was a DHGLM with an S × H (**D-SH**). This model extended the current model for macro-GES estimation to also estimate micro-GES of YW in beef cattle.

$$\begin{bmatrix} y \\ y_d \end{bmatrix} = \begin{bmatrix} X & 0 \\ 0 & X_d \end{bmatrix} \begin{bmatrix} b \\ b_d \end{bmatrix} + \begin{bmatrix} Z & 0 \\ 0 & Z_d \end{bmatrix} \begin{bmatrix} s \\ s_d \end{bmatrix} + \begin{bmatrix} L & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} sh \\ 0 \end{bmatrix} + \begin{bmatrix} e_s \\ e_{s_d} \end{bmatrix} \quad (\mathrm{D-SH})$$

where y contained the measured phenotype (YW) for the mean part (trait 1) and y_d was the calculated phenotype based on the residuals of the measured phenotype (see Eq. (5) below) for the dispersion part (trait 2). The vector b contained the fixed effects of sex and CG for y, and b_d contained the population mean for y_d. The vectors s and s_d referred to the random genetic sire effect on y and y_d, respectively. The vector sh was the random sire S × H effect. The vectors e_s and e_{s_d} contained the residuals of y and y_d, respectively. X, X_d, Z, Z_d and L were the design matrices for b, b_d, s, s_d and sh, respectively.

The distribution assumptions for the random genetic sire effects were $\begin{bmatrix} s \\ s_d \end{bmatrix} N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_s^2 & \sigma_{s_d,s} \\ \sigma_{s,s_d} & \sigma_{s_d}^2 \end{bmatrix} \otimes \mathrm{A}_s\right)$, where A_s were the numerator relationship matrix based on the sire pedigree. The distribution of the random S × H effect was $sh\ N(0, \mathrm{I}\sigma_{sh}^2)$, where I was an appropriate identity matrix. The distribution of the residuals followed $\begin{bmatrix} e_s \\ e_{s_d} \end{bmatrix} N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \mathrm{I}\begin{bmatrix} W_s^{-1}\sigma_{\epsilon_s}^2 & 0 \\ 0 & W_{s_d}^{-1}\sigma_{\epsilon_{s_d}}^2 \end{bmatrix}\right)$, where $\sigma_{\epsilon_s}^2$ and $\sigma_{\epsilon_{s_d}}^2$ were scaling variances and W_s and W_{s_d} were weights.

The weight for the residual variances were

$$W_s = diag\left(\widehat{y_d}\right)^{-1} \quad (1)$$

$$W_{s_d} = diag\left(\frac{1-h}{2}\right) \quad (2)$$

where h was a vector of the diagonal elements of the hat-matrix of y ($\widehat{y} = \mathrm{H}y$) also known as the leverage (Hoaglin and Welsch, 1978). Due to the weights already containing the reciprocal of the residual variances per observation, $\sigma_{\epsilon_s}^2$ and $\sigma_{\epsilon_{s_d}}^2$ were expected to equal 1, however, estimating them allows for more flexibility in the model (Mulder et al., 2013). The residual variances ($\sigma_{e_s}^2$ and $\sigma_{e_{s_d}}^2$) were then

$$\sigma_{e_s}^2 = \frac{\sigma_{\epsilon_s}^2}{\frac{tr(W_s)}{n}} \quad (3)$$

$$\sigma_{e_{s_d}}^2 = \frac{\sigma_{\epsilon_{s_d}}^2}{\frac{tr(W_{s_d})}{n}} \quad (4)$$

where n is the total number of records.

The phenotypes used to estimate micro-GES (y_d) were calculated as

$$y_{di} = \frac{\widehat{e}_i^2}{1-h_i} \quad (5)$$

where $\widehat{e}_i^2$ was the squared estimated residual of observation i and h_i was the leverage of observation i estimated in the mean part of the model (Rönnegård et al., 2010).

The second DHGLM included a linear reaction norm (**D-RN**). Reaction norms were first included in the mean part of a DHGLM

by Mulder et al. (2013). This model represented the alternative model for macro-GES estimation, extended to also estimate micro-GES.

$$\begin{bmatrix} y \\ y_d \end{bmatrix} = \begin{bmatrix} X & 0 \\ 0 & X_d \end{bmatrix} \begin{bmatrix} b \\ b_d \end{bmatrix} + \begin{bmatrix} Z_{int} & Z_{sl} & 0 \\ 0 & 0 & Z_d \end{bmatrix} \begin{bmatrix} s_{int} \\ s_{sl} \\ s_d \end{bmatrix} + \begin{bmatrix} e_s \\ e_{s_d} \end{bmatrix} \quad (\mathrm{D-RN})$$

Compared to D-SH, the genetic sire effect on y in D-RN was obtained similarly to the genetic animal effect in the A-RN and A-RNSH, resulting in an intercept (s_{int}) and slope (s_{sl}) of the additive genetic sire effect. The estimated CG effect used as the environmental covariate was here obtained from a sire model ($y = Xb + Zs + Ccg + e_s$) rather than the animal model as for A-RN and A-RNSH. The range of the EC was −200.88 to 165.50 kg with a maximum SE of prediction of 6.64 kg. The distribution assumptions for the additive sire effects were $\begin{bmatrix} s_{int} \\ s_{sl} \\ s_d \end{bmatrix} N\left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma^2_{s_{int}} & \sigma_{s_{sl},s_{int}} & \sigma_{s_d,s_{int}} \\ \sigma_{s_{int},s_{sl}} & \sigma^2_{s_{sl}} & \sigma_{s_d,s_{sl}} \\ \sigma_{s_{int},s_d} & \sigma_{s_{sl},s_d} & \sigma^2_{s_d} \end{bmatrix} \otimes \mathrm{A}_s \right)$. The remaining effects were as for D-SH, omitting the S × H term.

The third DHGLM was a DHGLM with both a linear reaction norm and an S × H effect.

$$\begin{bmatrix} y \\ y_d \end{bmatrix} = \begin{bmatrix} X & 0 \\ 0 & X_d \end{bmatrix} \begin{bmatrix} b \\ b_d \end{bmatrix} + \begin{bmatrix} Z_{int} & Z_{sl} & 0 \\ 0 & 0 & Z_d \end{bmatrix} \begin{bmatrix} s_{int} \\ s_{sl} \\ s_d \end{bmatrix} + Wsh + \begin{bmatrix} e_s \\ e_{s_d} \end{bmatrix} \quad (\mathrm{D-RNSH})$$

where the genetic sire effects were as described for D-RN and the remaining effects were as described for D-SH.

All models were analysed using DMU (Madsen and Jensen, 2013). For the DHGLMs, the following algorithm was implemented:

1. Initialise model by running the mean part as a univariate model on y with homogeneous residual variance.
2. Calculate y_d from Eq. (5) and W_{s_d} from Eq. (2) based on the residuals and leverages estimated in step 1.
3. Run the dispersion part as a univariate generalised linear mixed model on y_d.
4. Calculate W_s from Eq. (1) based on the predicted dispersion phenotypes estimated in step 3.
5. Run the bivariate model on y and y_d.
6. Update W_s, y_d and W_{s_d} based on the predicted dispersion phenotypes, residuals and leverages estimated in step 5.
7. Iterate steps 5–6 until converged or the algorithm has run 50 iterations.

Convergence was said to occur when the difference between the estimated genetic covariance matrix from run t and run $t-1$ was less than 10^{-4}. If the algorithm ran 50 iterations, the model was considered as not converged and the results were discarded.

Postanalysis corrections and heritabilities

To facilitate the comparison of estimated genetic variances across models, the estimated sire variance of the DHGLMs was converted to the animal level. The additive genetic sire variance is $¼\sigma^2_a$ and the remaining $¾\sigma^2_a$ is included in the estimated residual variance. For the mean part of D-SH, D-RN and D-RNSH, the additive genetic variances (σ^2_a, $\sigma^2_{a_{int}}$ and $\sigma^2_{a_{sl}}$) were obtained by multiplying the genetic sire variances (σ^2_s, $\sigma^2_{s_{int}}$ and $\sigma^2_{s_{sl}}$) by 4. For A-RN, A-RNSH, D-RN and D-RNSH, the additive genetic variance was calculated for EC j following:

$$\sigma^2_{aj} = \sigma^2_{a_{int}} + 2 * \sigma_{a_{int,sl}} * EC_j + \sigma^2_{a_{int}} * EC^2_j \quad (6)$$

For A-SH, A-RN, A-RNSH and the mean part of D-SH, D-RN and D-RNSH, the heritabilities (in the average macro-environment), denoted h^2, were then calculated as the ratio of the additive genetic variance (of the intercept) to the phenotypic variance (in the average macro-environment). For A-SH, A-RNSH, D-RN and D-RNSH, the phenotypic variance included the S × H variance. For A-RN, A-RNSH, D-RN and D-RNSH, the heritability was also calculated for EC j as the ratio of σ^2_{aj} to σ^2_{Pj}, where σ^2_{Pj} was the phenotypic variance in EC j. The heritabilities of A-RN, A-RNSH, D-RN and D-RNSH were plotted across −2 to 2 SD of the EC (Fig. 1).

For the dispersion part of D-SH, D-RN and D-RNSH, the additive genetic variance was corrected as well. This correction considered the inclusion of $¾\sigma^2_a$ in the residual of the mean part when they were used to calculate the dispersion phenotype, as described in Madsen et al. (2021):

$$\sigma^2_{a_d} = 4\sigma^2_{s_d}\left(\frac{\sigma^2_{e_s}}{\sigma^2_{e_s} - 3\sigma^2_s}\right)^2 \quad (7)$$

The heritability of the dispersion on the estimated scale (log-scale, h^2_d) was then the ratio of the additive genetic variance to phenotypic variance of the dispersion.

The additive genetic variance of the dispersion obtained from the DHGLMs were converted from the log scale to the measurement scale following Mulder et al. (2009).

$$\sigma^{2\,*}_{a_d} = 2\left(\sigma^2_{e_s} - 3\sigma^2_s\right)^2 h^2_d \quad (8)$$

The heritability of the dispersion part of the D-SH on the scale of measurement was

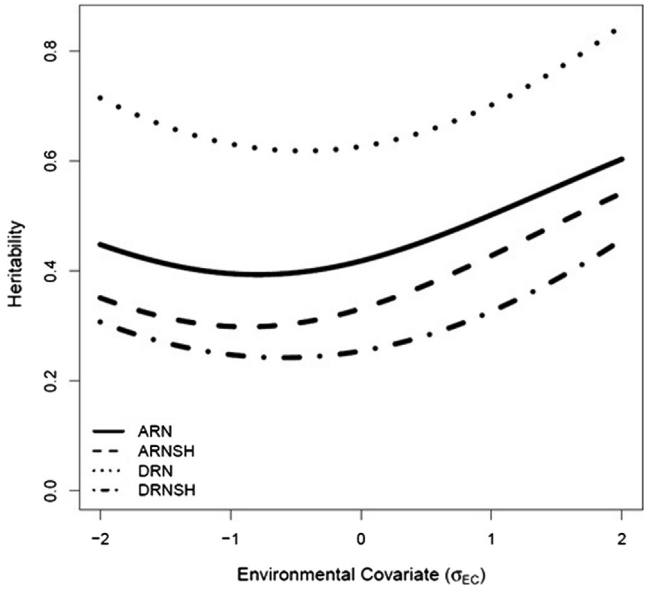

Fig. 1. The heritability of the animal model with a reaction norm (A-RN, solid line), the animal model with a reaction norm and a sire-by-herd interaction (A-RNSH, dashed), the double hierarchical generalised linear model with a reaction norm (D-RN, dotted) and the double hierarchical generalised linear model with a reaction norm and sire-by-herd interaction term (D-RNSH, dashed and dotted) across the environmental covariate from −2 to 2 SD of the environmental covariate (σ_{EC}) for yearling weight in a population of Australian Angus cattle.

$$h_d^{2^*} = \frac{\sigma_{a_d}^{2\ *}}{2\sigma_P^4 + 3\sigma_{a_d}^{2\ *}} \quad (9)$$

where σ_P^4 was the squared phenotypic variance of the mean part of the model (Mulder et al., 2007).

For YW, the measurement unit was kg and the variances of the animal models and the mean part of the DHGLMs therefore had the unit of kg^2. The dispersion part of DHGLMs were estimating a variance of the residual variance from the mean part of the models and the unit on the measurement scale was therefore kg^4. To make comparison between the mean and dispersion part of DHGLMs more straightforward, the genetic SD of the dispersion on the measurement scale were calculated as

$$\sigma_{a_d}^{*} = \sqrt{\sigma_{a_d}^{2\ *}} \quad (10)$$

The calculations were conducted in R (R Core Team, 2019), and approximate SEs were obtained using the deltaMethod function of the car package (Fox and Weisberg, 2019).

Model evaluation

To assess which of the animal models or DHGLMs had the best fit in the current dataset, Akaike information criterion (**AIC**) and Bayesian information criterion (**BIC**) were calculated. These criteria were used instead of a log-likelihood ratio test because AIC and BIC account for the number of parameters and BIC also considers the amount of data used for estimation.

For the animal models, the AIC and BIC were calculated via

$$AIC = 2k - 2\ln\left(\widehat{L}\right) \quad (11)$$

$$BIC = k\ln(n) - 2\ln\left(\widehat{L}\right) \quad (12)$$

where k was the number of parameters estimated by the model, $\widehat{L}$ was the estimated likelihood of the model obtained from DMU and n was the number of records analysed.

For the DHGLMs, the likelihood obtained from DMU needs to be adjusted for the use of squared residuals as observations for the dispersion part of the model. This is done by using the adjusted profile h-likelihood (Lee and Nelder, 2006; Rönnegård et al., 2010; Mulder et al., 2013).

$$APHL = -2\ln\left(\widehat{L}\right) - \sum\frac{w_{di}}{\sigma_{\epsilon_d}^2} - \sum\frac{\ln\left(\sigma_{\epsilon_d}^2\right)}{w_{di}} \quad (13)$$

The adjusted profile h-likelihood was then used in place of $-2\ln\left(\widehat{L}\right)$ in Eqs. (10) and (11) to calculate AIC and BIC.

The three animal models were nested models, as were the three DHGLMs, and the AIC and BIC of two different model types could therefore be compared within model type. For AIC, the comparison criterion was the relative likelihood of model x ($x \in$ A-SH, A-RN, A-RNSH or D-SH, D-RN, D-RNSH) compared to the model with the lowest AIC value of the nested models (Burnham and Anderson, 2004).

$$pAIC_x = \exp\left(\frac{AIC_{min} - AIC_x}{2}\right) \quad (14)$$

where AIC_{min} was the minimum AIC value for the comparable models and AIC_x was the AIC value of the model for which pAIC was to be calculated. The preferred model had a pAIC value of 1.

The difference between model x and the model among the nested models with the lowest BIC was assessed by calculating ΔBIC

$$\Delta BIC = BIC_x - BIC_{min} \quad (15)$$

Results

Genetic variance of macro-GES was found in all models, while the genetic variance of micro-GES was found in all three DHGLMs (D-SH, D-RN and D-RNSH) (Table 2). All estimates of additive genetic variance for macro- and micro-GES were significant based on the 95% confidence intervals of the raw estimates (Supplementary Table S1). The S × H term accounted for approximately 7% of the phenotypic variance in all models including the term (A-SH, A-RNSH, D-SH and D-RNSH).

In the animal models, variance components were primarily impacted by the presence or absence of the S × H term. The A-SH and A-RNSH had similar (≤5% difference) variance components and heritabilities. Meanwhile, A-RN had 21–25 and 5% higher additive genetic variance of the intercept and slope, 4–8% less residual variance and 26–27% higher heritability than the other animal models.

The same pattern was observed for the mean part of the DHGLMs, but with larger differences between the models with and without an S × H term. The additive genetic variances were consistent for the D-SH and D-RNSH. The D-RN had 2.5–2.6 times larger additive genetic variance of the intercept and 42% higher additive genetic variance of the slope, 42% less residual variance and 2.4–2.5 times larger heritability than the other DHGLMs.

The heritability changed considerably across the range of −2 to 2 SD of the EC for all reaction norm models (Fig. 1). The minimum heritabilities over the range were 0.39 (at $-0.80\sigma_{EC}$), 0.30 ($-0.90\sigma_{EC}$), 0.62 ($-0.45\sigma_{EC}$) and 0.24 ($-0.60\sigma_{EC}$) for the A-RN, A-RNSH, D-RN and D-RNSH, respectively. The heritability was 0.03–0.09 larger at $-2\sigma_{EC}$ than the heritability of the intercept (at $0.00\sigma_{EC}$) and 0.19–0.22 larger at $2\sigma_{EC}$.

The variance components of the dispersion part of the DHGLMs also differed considerably more between the model without the S × H term and the other two models than between the two DHGLMS with an S × H term. The D-SH and D-RNSH had consistent estimates (difference ≤ 1%) of all variances and heritabilities. The D-RN had 3.1 and 2.6–2.7 times higher additive genetic variance and heritability of the dispersion on the log-scale, 20 and 40% less additive genetic SD and heritability of the dispersion on the measurement scale than the other two DHGLMs.

Comparing the variance components estimated with the D-SH and D-RNSH to those estimated with the A-SH and A-RNSH, respectively, the DHGLMs had 30% lower additive genetic variance (of the intercept), 47% lower additive genetic variance of the slope, 8–9% lower S × H variance and 11–20% lower heritability then their animal model counterparts. The D-RN had 45% higher and 28% lower additive genetic variance of the intercept and slope, respectively, 38% lower residual variance and 50% higher heritability than the A-RN.

The genetic correlations between intercept and slope were low to moderate and had a 95% confidence interval including 0 for D-RN (Table 3). Meanwhile, all the genetic correlations including the dispersion were low. Only the correlation between mean and dispersion in D-SH and between the intercept and dispersion in D-RNSH had 95% confidence intervals not including 0.

For the estimation of macro-GES, without considering micro-GES, the pAIC and ΔBIC indicated that A-RNSH was the best-fitting model of A-SH, A-RN and A-RNSH (Table 4). For the simultaneous estimation of macro- and micro-GES, pAIC and ΔBIC indicated that D-RN was superior to D-RNSH and D-SH for the current dataset.

Discussion

The current study examined the levels of genetic variance due to macro- and micro-GES in YW in Australian Angus using multiple

Table 2
Estimated variances and heritabilities from the animal model with a sire-by-herd interaction term (A-SH), a reaction norm (A-RN) or both (A-RNSH) and the double hierarchical generalised linear model with sire-by-herd interactions (D-SH), a reaction norm (D-RN) or both (D-RNSH) for yearling weight in a population of Australian Angus cattle.

Item	A-SH	A-RN	A-RNSH	D-SH	D-RN	D-RNSH
σ^2_a	435.08 (15.79)			306.14 (30.64)		
$\sigma^2_{a_{int}}$		526.33 (14.94)	421.59 (15.48)		763.29 (35.24)	296.03 (30.12)
$\sigma^2_{a_{sl}}$		0.033 (0.002)	0.032 (0.002)		0.024 (0.004)	0.017 (0.003)
$\sigma^2_{a_d}$				0.93 (0.08)	2.86 (0.38)	0.92 (0.08)
$\sigma^*_{a_d}$				557.52 (13.98)	461.48 (16.01)	558.32 (13.98)
σ^2_{sh}	92.54 (4.51)		89.92 (4.49)	85.05 (4.83)		82.10 (4.79)
$\sigma^2_{e_a}$	799.72 (10.67)	732.26 (10.18)	760.37 (10.55)	779.90 (23.45)	454.97 (27.08)	785.01 (23.06)
$\sigma^2_{e_{a_d}}$				2.29 (0.03)	2.28 (0.03)	2.29 (0.03)
h^2	0.33 (0.01)	0.42 (0.01)	0.33 (0.01)	0.26 (0.03)	0.63 (0.02)	0.25 (0.02)
h^2_d				0.32 (0.03)	0.84 (0.09)	0.31 (0.02)
$h^{2^*}_d$				0.09 (0.004)	0.06 (0.004)	0.10 (0.004)

σ^2_a = additive genetic variance, $\sigma^2_{a_{int}}$ and $\sigma^2_{a_{sl}}$ = additive genetic variance of the intercept and slope of the reaction norm, $\sigma^2_{a_d}$ = additive genetic variance of the dispersion on the logarithmic scale. $\sigma^*_{a_d}$ = genetic SD of the dispersion on the measurement scale, σ^2_{sh}, $\sigma^2_{e_a}$ and $\sigma^2_{e_{a_d}}$ = sire-by-herd variance and residual variance of the mean and dispersion. h^2, h^2_d and $h^{2^*}_d$ = heritability of the mean and dispersion on the logarithmic and measurement scale.

Table 3
Estimated genetic correlations from the animal model with a reaction norm (A-RN) or a reaction norm model and a sire-by-herd interaction (A-RNSH) and the double hierarchical generalised linear model with sire-by-herd interactions (D-SH), a reaction norm (D-RN) or both (D-RNSH) for yearling weight in a population of Australian Angus cattle.

Model	A-RN	A-RNSH	D-SH	D-RN	D-RNSH
$r_{int,sl}$	0.31 (0.02)	0.38 (0.02)		0.12 (0.07)	0.22 (0.10)
$r_{m,d}$			0.13 (0.06)		
$r_{int,d}$				0.03 (0.04)	0.14 (0.06)
$r_{sl,d}$				0.12 (0.08)	0.13 (0.10)

$r_{int,sl}$ = genetic correlation between intercept and slope, $r_{m,d}$ = genetic correlation between mean and dispersion. $r_{int,d}$ = genetic correlation between intercept and dispersion. $r_{sl,d}$ = slope and dispersion.

Table 4
Model selection criteria for the animal model with sire-by-herd interactions (A-SH), a reaction norm (A-RN) or both (A-RNSH) and the double hierarchical generalised linear model with sire-by-herd interactions (D-SH), a reaction norm (D-RN) or both (D-RNSH) for yearling weight in a population of Australian Angus cattle.

Item	A-SH	A-RN	A-RNSH	D-SH	D-RN	D-RNSH
k	3	4	5	6	8	9
AIC	805 900	806 588	805 413	−540 678	−542 169	−540 440
BIC	805 929	806 626	805 461	−540 621	−542 093	−540 355
pAIC	0	0	1	0	1	0
ΔBIC	468	1 165	0	1 473	0	1 738

k = number of estimated parameters. AIC = Akaike information criterion. BIC = Bayesian information criterion. pAIC = relative probability of AIC $\left(pAIC_x = \exp\left(\frac{AIC_{min} - AIC_x}{2}\right)\right)$. ΔBIC = delta BIC ($\Delta BIC = BIC_x - BIC_{min}$).

models. Both animal models and DHGLMs showed the presence of variation in macro-GES of YW either captured in the S × H term or as the slope of the reaction norm. All DHGLMs showed variation due to micro-GES of YW.

Genetic environmental sensitivity of yearling weight

The S × H effect accounted for 7% of the phenotypic variance, regardless of whether the model included a reaction norm, even though the variance of the S × H effect was slightly reduced when a reaction norm was included. This indicated that in addition to macro-GES, other factors contributed to the estimated S × H effects. Differential non-random mating among herds has been shown to contribute approximately a third of the variance captured by the S × H term in weaning weight in Australian Angus (Notter et al., 1992). The impact of differential non-random mating among herds in the current dataset was not directly quantified; however, it is likely to have some impacts as producers select specific sires to breed their cows to. In addition, 76% of sires and 99% of dams had offspring exclusively within one herd, meaning that the herd effect may be confounded with sire and/or dam. Meyer (2003) concluded that single-herd sires could lead to biased estimates of additive genetic variance when using animal models due to the S × H term picking up too much additive genetic variance. In the current study, confounding between genetic effects and the herd is a likely contributor to the S × H variance. Including

the reaction norm separates G × E across CGs from the other contributors to the S × H variance, allowing for a clearer understanding of the impact of macro-GES on YW in Angus cattle.

Due to the low genetic variance of slope found in the current study, reaction norm models may be considered overly complex relative to the gain in accuracy of estimates. Similarly, previous studies have shown YW in Angus cattle to be minimally affected by macro-GES (Meyer, 1995; Jeyaruban et al., 2009; Bradford et al., 2016). However, the additive genetic variance of the slope cannot be taken out of the context of the EC. The heritabilities of the reaction norm models changed considerably across the EC (Fig. 1). However, the curvature of the heritabilities was forced to be convex as the reaction norms were linear and the residuals were assumed homogeneous across the macro-environments. Fig. 1 showed that even the small estimated variance of the slope found in the current study can have a considerable impact on the heritability of YW in Australian Angus reared over a wide range of macro-environments.

Of the animal reaction norms, the A-RNSH was a better fit for the data, even when considering the increased complexity of the model as done when using pAIC and ΔBIC as selection criteria. A-RNSH also yielded the most reasonable estimated heritability in the average macro-environment. A-RN had a heritability in the average environment well above the heritabilities of 0.19–0.40 previously reported in literature (Carter et al., 1990; Robinson, 1996; Arthur et al., 2001; Torres-Vázquez et al., 2018). In contrast, the A-RNSH had heritabilities in line with the values previously reported. These results show that both effects should be included when analysing macro-GES of YW in Australian Angus.

The same pattern of larger heritability of YW, when the model did not contain an S × H term, was observed for the D-RN, though in these models the difference was considerably larger. The additive genetic variance of the intercept in the D-RN was larger than in any other model. This may have occurred primarily due to the DHGLMs being sire models, and not directly due to the estimation of micro-GES. Sire models do not account for the genetic merit of dams, thus attributing all resemblance between half-sibs to sires though some resemblance would be caused by relationships between dams. The resemblance of half-sibs caused by their dams should in theory impact all the DHGLMs similarly. However, the DHGLM with an S × H term (D-SH and D-RNSH) had lower estimates of additive genetic variances of the mean compared to their animal model counterparts (A-SH and A-RNSH). In these models, the S × H variance may capture some of the bias the dam relationships caused in the D-RN because of the high proportion of dams that are confounded with herd. Additionally, because the D-SH and D-RNSH are sire models, the models may not be able to correctly assign variance due to confounding between some sires and herd, as 76% of the sires were single-herd sires. These single-herd sires are essentially fitted twice in the DHGLMs with a S × H term. As a result, both the additive genetic variances and the S × H variance were reduced in D-SH and D-RNSH compared to the animal versions.

In the sire model versions of the animal models (results not shown), the same pattern of reduced additive genetic and S × H variance was observed, but in these models, the residual variance was increased considerably compared to the animal models. The increase in residual variance remained after removing the ¾ additive genetic variance expected to be included in the residual variance of a sire model. This means that the residual variance of the sire models with an S × H term likely includes more genetic variance than the expected ¾. This indicates that a larger than expected part of the residual variance in the D-SH and D-RNSH may in reality be genetic. This could explain why the D-SH and D-RNSH had larger genetic SD and heritability of the dispersion on the measurement scale than the D-RN. The heritability of the dispersion on the measurement scale was slightly larger than the heritability of YW from the mean part of the models in the D-SH and D-RNSH, and considerably larger for the D-RN. Furthermore, the models including an S × H term had larger genetic SD of the dispersion on the measurement scale than the genetic variance of the mean part of the models.

Due to the limited number of studies reporting genetic variance due to micro-GES in YW of beef cattle, it is hard to determine if the results of the different DHGLMs in the current study are in line with expectations. Genetic variance due to micro-GES of YW has been studied in Nellore cattle from Brazil and Paraguay with a two-step approach by Neves et al. (2012) and using DHGLMs by Iung et al. (2017). The heritabilities on the measurement scale in the current study were higher than those reported by Iung et al. (2017). However, it is not clear whether Iung et al. (2017) corrected the additive genetic variance of the dispersion on the log-scale for the additional genetic variance it would contain when using a sire model (see Eq. (6)). Comparisons of variances and heritabilities of the dispersion between the present study and the study by Iung et al. (2017) should therefore be done with caution. Aside from the correction for the use of sire models, breed differences may have contributed to the differences in heritabilities observed between the current study and the study by Iung et al. (2017). However, this seems unlikely when considering that the heritabilities on the measurement scale were similar to the heritability up to 0.06 reported by Neves et al. (2012) for Nellore beef cattle. The two-step approach used by Neves et al. (2012) was implemented on the animal level, and the comparison is therefore not affected by the need for corrections of the micro-GES variance. The estimate of micro-GES obtained from the D-RN therefore seems reasonable, while the estimates of micro-GES on the measurement scale from the D-SH and D-RNSH were considerably larger than those reported previously. As a result, the D-RN is the suggested model for estimating micro-GES in the current dataset, despite the heritability of YW being considerably larger than previously reported in the literature. The model selection criteria likewise indicated that the D-RN was the best fit for the data out of the tested DHGLMs.

Clearly, care must be taken when implementing DHGLM for datasets on single recorded traits with a high proportion of single-herd sires. For the time being, the S × H effect should be omitted when using DHGLMs fitted on the sire level to avoid overestimating the genetic variance due to micro-GES.

Selection on macro- or micro-genetic environmental sensitivity

Both the genetic variance of the slope in the models with reaction norms and the genetic variance of the dispersion from the DHGLMs showed that selection should be possible on both macro- and micro-GES of YW in Australian Angus.

An important consideration when selecting on a trait is the expected direct response. Direct response depends in part on the heritability and the genetic SD of the trait (Falconer and Mackay, 1996). For micro-GES, the heritability of the dispersion was low to moderate, but the genetic SD was considerable, showing that progress can be made. Divergent selection experiments on micro-GES of birth weight in mice have successfully established high and low micro-GES lines with heritabilities of the dispersion of 0.008 in the initial generation (Formoso-Rafferty et al., 2016). It should therefore be possible to select on micro-GES of YW.

It could be argued that, due to the low genetic variance of the slope, selection on macro-GES may not be efficient and the reaction norm can be omitted from the model in order to reduce the complexity of the model even if the fit of the model is also reduced. However, as stated previously, the EC covered a wide range and macro-GES can therefore have substantial impacts on the esti-

mated breeding values and selection responses across the range of macro-environments.

Based on the findings in the current study, both macro- and micro-GES may be considered lowly heritable traits. There are tools available to improve the response to selection of lowly heritable traits. Increased selection accuracy has been achieved by using genomic selection rather than pedigree-based selection for lowly heritable traits across a variety of livestock and aquaculture species (Mulder, 2017). For selection to reduce macro-GES, it has been shown that genomic selection is superior to traditional sib or progeny testing schemes, provided the reference population is reared across the entire EC (Mulder, 2017). A reference population for estimating micro-GES would require multiple records of closely related animals. Because micro-environments are specific to each of the animals, they are contained within macro-environments. As a result, the reference population should have multiple close relatives reared in the same macro-environments to facilitate micro-GES estimation. However, the reference population should also cover many macro-environments, such that micro-GES can be accurately estimated across macro-environments, thus, ensuring accurate selection on both macro- and micro-GES.

Another important aspect of the selection on new traits, such as macro- or micro-GES of a trait, is the possible correlated response in other traits. The correlated response in one trait to the selection on another trait is dependent in part on the genetic correlation between the two traits (Falconer and Mackay, 1996). The genetic correlations including the dispersion were not significantly different from zero in any of the DHGLMs, and correlated responses in micro-GES to selection on the mean or macro-GES are therefore not expected. The genetic correlation between intercept and slope was found to be lowly to moderately positive in all models including a reaction norm. This indicated that selection without considering macro-GES may result in increased levels of macro-GES in future. Even in the absence of a genetic correlation between intercept and slope, selection of the best-performing animals can alter macro-GES. If selection is based on the best-performing sires without regard to their macro-GES and the macro-environment improves across generations, macro-GES can increase even if the genetic correlation between intercept and slope were zero in the base population (Kolmodin et al., 2002). With this in mind, it is important to consider or at least account for macro-GES when selecting sires, e.g., high-performing sires could be selected among the sires with low macro-GES. Given the low to moderate genetic correlations between intercept and slope found here, it would be possible to identify animals with high YW and low macro-GES, thus allowing for selection to increase YW without negatively impacting macro-GES and *vice versa*.

The direction of selection on micro-genetic environmental sensitivity

The direction of selection on micro-GES would depend on where in the breeding program the selection is aimed. In the selection of production animals, the aim of the selection is primarily improved performance. Reducing micro-GES in these animals could increase uniformity, potentially increasing profitability. Mulder et al. (2007) showed that reducing micro-GES was of economic value in traits with an intermediate optimum based on profit functions. However, reducing micro-GES can be beneficial in most traits due to reducing the animals' overall sensitivity to minor disturbances in their surroundings and bio-economic modelling may be better suited to derive the profitability of reducing micro-GES in production animals (Rönnegård et al., 2013). For these reasons, reducing micro-GES may be beneficial in production animals, where increased production uniformity can ensure consistent quality for the consumers and consistent profits for the producers.

In the nucleus, however, the aim is to improve the genotypes that can be selected as parents of the following generation. In the nucleus, maintaining or even increasing micro-GES may be beneficial. If micro-GES were to be reduced in the breeding nucleus, it may result in a loss of the diversity required to identify top animals to be parents of the future generation. It has been shown through selection experiments that lines with low micro-GES have less selection response per generation than the high micro-GES lines (Formoso-Rafferty et al., 2016; Blasco et al., 2017). For mice selected for high or low micro-GES of birth weight, the selection had a substantially correlated response in birth weight itself in the high line, but not the low line, despite genetic correlations of 0.15–0.73 between birth weight and its micro-GES across seven generations of selection (Formoso-Rafferty et al., 2016). Based on these results, one might believe that selection to reduce micro-GES could potentially result in animals without the necessary variability of genotypes to continue selection. However, it may also be that after three generations of divergent selection variance parameters, like the genetic correlation, should be estimated within lines rather than across the full population. The observed 'lack' of correlated response in birth weight in the low line may have been due to a within line genetic correlation closer to zero.

Conclusions

Variation due to both macro- and micro-GES were present in YW of Australian Angus cattle showing that selection to alter GES of YW is possible in Australian Angus beef cattle. Multiple models were tested to identify the best-fitting methods for estimating macro-GES alone and along with micro-GES. For simultaneous estimation, the sire DHGLM with a reaction norm in the mean part of the model was the best-fitting model for this dataset.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.101068.

Ethics approval

Data used in this study were provided by the Angus Society of Australia and were collected as part of routine commercial animal management and, therefore, were not subject to animal care and animal ethics committee approval.

Data and model availability statement

The data/models were not deposited in an official repository. Inquiries should be made to the corresponding author.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

The authors declare that they have no competing interests.

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