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MACRO- AND MICRO-GENETIC ENVIRONMENTAL SENSITIVITY FOR 400 DAY WEIGHT IN AUSTRALIAN ANGUS

M.D. Madsen[1], J.H.J. van der Werf[1], V. Börner[2] and S. Clark[1]

[1] School of Environmental and Rural Science, University of New England
[2] Animal Genetics and Breeding Unit, University of New England

SUMMARY

Genotype by environment interactions can be caused by both macro- and micro-genetic environmental sensitivity (GES). In the current study, 400 day weight (400DW) measured on Australian Angus was analysed using a variability model and a reaction norm model to obtain estimates for genetic variation due to macro- and micro-GES. The results showed additive genetic variance for both macro- and micro-GES. Over the range of contemporary group means the macro-GES impacted the genetic variance and ranking of sires across environments. The presence of micro-GES indicated the possibility of selecting to reduce the variability of phenotypes, but further investigation into the consequences is needed.

INTRODUCTION

Genotype by environment interactions (G×E) occur when the phenotypes of different genotypes respond unequally to different environments. The genetic control of G×E is called genetic environmental sensitivity (GES). The environmental differences may be definable, such as temperature, location etc. These environments are termed macro-environments and are typically experienced by a cohort of animals (Falconer and Mackay 1996). Macro-environments are numerous in most livestock populations. Within macro-environments are micro-environments, which are experienced by individual animals and can be observed via differences in variation among progeny (Hill and Mulder 2010). Animals can exhibit GES in response to changes in both macro- and micro-environments, and GES is thus split into macro- and micro-GES.

The aim of this study was to estimate the levels of genetic variation due to macro- and micro-GES for 400 day weight in Australian Angus data.

MATERIALS AND METHODS

Data. Angus Australia provided 400 day weight (400DW) measured in kg on live animals. Contemporary groups (CGs) were constructed by concatenating herd, year, observation date and breeder defined management group for each record (see Graser *et al*. (2005)). The records were then cleaned in four stages. Firstly, all records had to be measured at 301-500 days of age, from animals with known sex, sire and dam and the recorded weight could not be more than 3 standard deviations from the phenotypic mean of its CG. Secondly, repeated measurements were removed by keeping the record belonging to the largest CG out of the available records for that animal. Thirdly, records from animals born prior to 2015 were removed. Lastly, animals with less than 4 paternal half-sibs and animals belonging to CGs with less than 60 animals or to single sire CGs were removed in an iterative procedure, which ensured all 3 criteria were met in the final data set. The final data contained 52,446 400DW records (mean 393.15kg; SD 74.83kg) from 1370 sires (mean number of offspring 38.3; SD 79.2) and 33,201 dams (1.58; 1.43) distributed over 443 CGs (mean number of records 118.39; SD 81.67). The animals were reared across the temperate Australia. The pedigree spanned 13 generations.

Statistical analysis. Micro-GES was investigated using a two-step approach described in Mulder *et al*. (2009) where step 1 is a traditional animal model and step 2 is a variability model where the *ln*-transformed squared residual form step 1 was used as the phenotype (Mulder *et al*. 2009). The

animal model (step 1) was also used to obtain the estimated environmental effect of CGs, which were used as environmental covariate in a linear reaction norm model to examine macro-GES (Falconer and Mackay 1996).

Animal model.

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e} \quad (1)$$

where **Y** was a vector containing the 400DW records, **b**, **a**, **c** and **e** were vectors of fixed effects (age at observation and sex), additive genetic animal effects, random effect of CGs and random residuals, respectively. **X**, **Z,** and **W** were design matrices linking records to fixed effects, animals and CGs, respectively. The distribution assumptions were $\mathbf{a} \sim N(\mathbf{0}, \sigma_a^2 \otimes \mathbf{A})$, $\mathbf{c} \sim N(\mathbf{0}, \sigma_c^2 \mathbf{I_c})$ and $\mathbf{e} \sim N(\mathbf{0}, \sigma_e^2 \mathbf{I_e})$, where **A** was the numerator relationship matrix and $\mathbf{I_c}$ and $\mathbf{I_e}$ were identity matrices of appropriate dimensions.

Variability model.

$$\mathbf{ln(e^2)} = \mathbf{X_v b_v} + \mathbf{Z_v a_v} + \mathbf{e_v} \quad (2)$$

where $\mathbf{ln(e^2)}$ was the *ln*-transformed squared residuals from the animal model, $\mathbf{b_v}$ contained the fixed effects of age at observation and sex, $\mathbf{a_v}$ and $\mathbf{e_v}$ were the additive genetic variance and random residuals of the variability of 400DW. $\mathbf{X_v}$ and $\mathbf{Z_v}$ were design matrices linking records to fixed effects and animals, respectively. The distribution assumptions were $\mathbf{a_v} \sim N(\mathbf{0}, \sigma_{a_v}^2 \otimes \mathbf{A})$ and $\mathbf{e_v} \sim N(\mathbf{0}, \sigma_{e_v}^2 \mathbf{I_e})$. The genetic variance estimated in this model ($\sigma_{a_v}^2$) was on the scale of the natural logarithm and thus a conversion was done to obtain the genetic variance of the additive genetic effect contributing to the residual variance $\sigma_{a_R}^2 = \sigma_{a_v}^2 \left(\sigma_{a_v}^2 + \sigma_{e_v}^2\right)^{-1} 2(\sigma_e^2)^2$ (Mulder *et al*. 2009).

Reaction norm model.

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Za_{int}} + \mathbf{Ha_{sl}} + \mathbf{Wc} + \mathbf{e} \quad (3)$$

where $\mathbf{a_{int}}$ and $\mathbf{a_{sl}}$ were the additive genetic animal effects for the intercept and slope, respectively, of the reaction norm and **H** contained the estimated CG effects. The distribution assumption of the additive genetic effect was $\begin{bmatrix} \mathbf{a_{int}} \\ \mathbf{a_{sl}} \end{bmatrix} \sim N\left(\mathbf{0}, \begin{bmatrix} \sigma_{a_{int}}^2 & \sigma_{a_{int}a_{sl}} \\ \sigma_{a_{sl},a_{int}} & \sigma_{a_{sl}}^2 \end{bmatrix} \otimes \mathbf{A}\right)$. The remaining effects and distribution assumptions were as in equation 1.

All analysis was performed in ASReml v4.1 (Gilmour et al., 2015).

Heritabilities. The heritability for the animal model was $h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$. The heritability of the residual was $h_R^2 = \frac{\sigma_{a_R}^2}{3\sigma_{a_R}^2 + 2\left(\sigma_a^2 + \sigma_e^2\right)^2}$ (Mulder *et al*. 2009). The heritability of the reaction norm model was only calculated for the average environment, i.e. replacing σ_a^2 with $\sigma_{a_{int}}^2$ in the formula given for the animal model.

RESULTS AND DISCUSSION

Results in Table 1 show additive genetic variance due to both macro- and micro-GES. The variation due to macro-GES (slope of reaction norm) were relatively low when compared to the intercept. However, while it is often assumed that breeding stock is exposed to similar environmental conditions across cohorts, we found that the mean value of CGs ranged from -149 to 173kg. The variation due to CG (σ_c^2) was 2399kg^2 and thus the standardised estimated range of CG effects were -3.04–3.52σ_c. Over a given environmental range it is commonly assumed that the bulk of the data is present in non-extreme environments, resulting in low accuracy of estimated environmental effects. While the bulk of CGs have effects in non-extreme environments (Figure 1), the data filtration in the current study has resulted in a significant number of animals in all environments, ensuring accurate estimation of CG effects across the full range. Across a large range of environmental effects even a low genetic variance due to macro-GES can have significant impacts

on the additive genetic variation across environments (Figure 2). The presence of macro-GES can result in scaling effects and/or re-ranking (Falconer and Mackay 1996). Scaling effects are differences in variance across macro-environments, which is of statistical concern and should be accounted for during analysis e.g. by using a reaction norm model. Re-ranking is of more practical concern since it occurs when animals are superior to others in one environment, but not in another. The estimated breeding values (EBVs) of the five most influential sires estimated with the reaction norm model show both scaling and re-ranking effects across environments (Figure 3). The sire represented by the grey line is the second poorest performer in the -3.0σ_c environment and the best in the 3.5σ_c environment, while the red sire performs consistently better than the black, blue, and green sires. If these sires were evaluated without consideration to macro-GES the red sire would be considered the best of the 5 sires (legend of Figure 3).

Table 1. Additive genetic variance (SE) from the animal model (σ^2_a) and the variability model ($\sigma^2_{a_v}$) and the additive genetic variance of intercept ($\sigma^2_{a_{int}}$) and slope ($\sigma^2_{a_{sl}}$) from the reaction norm model

Model*	σ^2_a	$\sigma^2_{a_v}$	$\sigma^2_{a_R}$	$\sigma^2_{a_{int}}$	$\sigma^2_{a_{sl}}$	$\sigma_{a_{sl},a_{int}}$	h^2	h^2_v	h^2_R
Animal	509.07 (19.26)	-	-	-	-	-	0.43	-	-
Variability	-	0.59 (0.05)	96937.08	-	-	-	-	0.11	0.03
Reaction norm	-	-	-	473.65	0.12 (0.00)	0.44 (0.13)	0.45	-	-

*the units for σ^2_a, $\sigma^2_{a_{int}}$, and $\sigma^2_{a_{sl}}$ were kg^2, for $\sigma^2_{a_v}$ the unit was kg^4, and the unit for $\sigma_{a_{sl},a_{int}}$ was kg.

The genetic correlation between intercept and slope was only 0.06 meaning there was little association between the breeding value for the level and the macro-GES. It should thus be possible to select animals with high EBV for intercept and low EBV for slope. This would be relevant if breeders wish to breed for high producing, robust animals, i.e. animals that are less sensitive to changes in macro-environments and thus performs similarly in all environments. However, if a breeder is consistently providing a superior environment for their animals it may be relevant to select on environmental specific EBVs to ensure maximum profit.

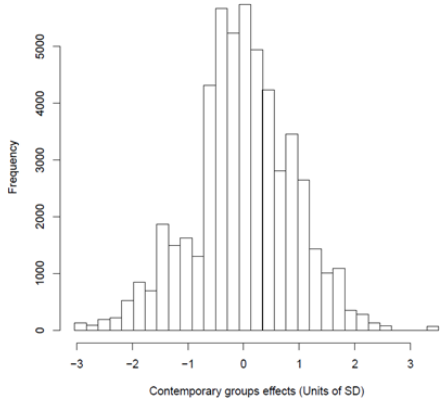

Figure 1. Frequency of the contemporary group effects (standardised)

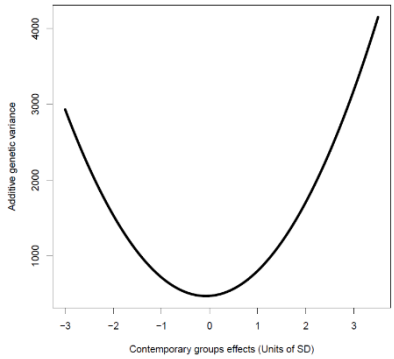

Figure 2. Additive genetic variance across the contemporary group effects (standardised)

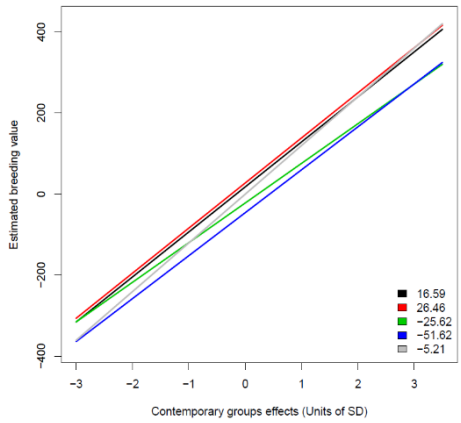

Figure 3. Estimated breeding values (EBVs) of the 5 most influential sires. Lines represent EBVs from the reaction norm model plotted across the contemporary group effects (standardised). Legend shows the corresponding EBVs from the animal model

Micro-GES affects the variability of phenotypes within macro-environments. A ten generation divergent selection experiment on litter size in rabbits have shown that selection to alter the variability of phenotypes is possible (Blasco et al., 2017). Thus, reducing micro-GES could reduce the variability and ensure more uniform production. This is especially relevant for traits, such as body weight in broilers, where the final product is penalised for falling outside a desired range (Mulder et al., 2009), i.e. traits with a non-linear profit margin. While 400DW itself does not have a non-linear profit margin it is an indicator trait for mature body weight and carcass weight, both of which may be penalised as slaughterhouses are not able to handle very small or overly large animals. The relatively high estimated variation due to micro-GES in 400DW showed that it should be possible to reduce the variation around the population mean for this trait, thus reducing the risk of the animals falling outside of the desired range for mature weight and carcass weight.

It has been shown that the variability model used in the current study has lower prediction ability than a double hierarchical generalised linear model (DHGLM) for estimation of micro-GES. Iung et al. (2017) observed lower accuracies of EBVs, partly because a DHGLM allows for estimation of the genetic correlation between σ^2_a and $\sigma^2_{a_v}$. However, Iung et al. (2017) did not find significant differences between estimated variances. A DHGLM was not fitted in the current study due to the

more stringent data structure requirements compared to variability models, but further research will be done to try and apply the DHGLM to the data and examine the difference between the two models.

CONCLUSION

In conclusion, the analysis showed evidence of macro-GES in 400 d weight in Australian Angus causing re-ranking across environments amongst the five most influential sires. It would therefore be possible to select on macro-GES to either reduce the overall impacts of changes in macro-environments or to ensure high performance in specific macro-environments. Considerable levels of micro-GES were also present in 400 day weight, showing the potential to increase uniformity, but further research is needed to improve the analysis and investigate the outcomes of selection on micro-GES.

REFERENCES

Blasco, A., M.-Á. Marina, G. Maria-Luz, I.-E. Noelia, and A. María-José. (2017) *Genet. Sel. Evol*. **49(1)**:1.

Falconer, D. S., and T. F. C. Mackay. (1996) Introduction to quantitative genetics. Pearson Education Limited, Essex, United Kingdom.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. (2015) ASReml User Guide Release 4.1 Functional Specification,. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK

Graser, H. U., B. Tier, D. J. Johnston, and S. A. Barwick. (2005) *Anim. Prod. Sci*. **45(8)**:913.

Hill, W. G., and H. A. Mulder. (2010) *Genet. Res*. **92(5-6)**:381.

Iung, L. H. S., H. H. R. Neves, H. A. Mulder, and R. Carvalheiro. (2017) *J Anim. Sci.* **95(4)**:1425.

Mulder, H. A., W. G. Hill, A. Vereijken, and R. F. Veerkamp. (2009). *Animal* **3(12)**:1673.