

Genetic variance in macro-environmental sensitivity in growth rate in Danish Duroc pigs

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Summary

The globalization of animal breeding programs means that selecting for animals that maintain high productivity across varying environments may be beneficial. One way this can be achieved is through selection for lower environmental sensitivity. Reaction norm models can be used to estimate environmental sensitivity caused by measurable differences in environment (macro environments). The aim of this study was to investigate the magnitude of macro-environmental sensitivity in average daily body weight gain in Danish Duroc pigs. The heterogeneity of residual variance across herds was also examined. Genetic parameter estimation was done in a Bayesian setting, for simultaneous estimation of the environmental values and covariates, considering heterogeneous residual variance. A univariate reaction norm model was developed for males and females separately. Significant macro-environmental sensitivity was found for both males and females. The posterior mean for additive genetic variance and heritability increased with increased environmental deviation. The posterior mean for the correlation between the additive genetic variance at different environmental gradients decreased with increasing deviations between the environments. Using the reaction norm model enables selection for animals with lower macro-environmental sensitivity.

Keywords: macro-environmental sensitivity, reaction norm, Bayesian analysis, heterogeneous residual variance

Introduction

Due to the high level of globalization in animal breeding programs, it can be beneficial to breed animals that maintain high and constant production levels across a wide range of environments. One approach to do this is to select animals that have limited environmental sensitivity. Previous studies have shown that environmental sensitivity (ES) is under genetic control (Falconer & Mackay, 1996). This suggests that we can select for animals that are robust across environmental gradients. Traditional estimation of additive genetic variance uses the linear animal model: $\mathbf{y} = \boldsymbol{\mu} + \mathbf{b} + \mathbf{a} + \mathbf{e}$, where \mathbf{y} is the vector of phenotypes, $\boldsymbol{\mu}$ is the mean, \mathbf{b} is fixed effects, \mathbf{a} is the additive genetic effect, and \mathbf{e} is the residuals. \mathbf{A} and \mathbf{I} are incidence matrices and $\mathbf{1}$ is a vector of ones (Mrode, 2014). However, this model does not account for ES, and thus no information is gained about the genetic variation in

response to different environments.

Macro-ES (ES caused by definable differences in environments) can be handled by treating observations for different environments as different traits. However, this is not feasible if there are many different environments. A more parsimonious model is a reaction norm model, where macro-ES is modelled as a random regression on an environmental gradient (Falconer & Mackay, 1996). This method requires a continuous covariate describing the difference between environments. In a Bayesian setting, Su *et al.* (2006) has developed a reaction norm model with unknown environmental covariate, where an environmental effect in the model is used as the environmental gradient. The general form of the reaction norm model is: $y = \mathbf{a} + \mathbf{a}^* \mathbf{H} \mathbf{e}$, where \mathbf{a} and \mathbf{a}^* are vectors of the intercept and slope of the additive genetic reaction norm, respectively. \mathbf{H} is a matrix with environmental gradient covariates, which is estimated during the analysis. The remaining variables are as described above.

The aim of this study was to investigate the magnitude of genetic variation in macro-ES in average daily body weight gain (ADG) in male and female Danish Duroc pigs. The analysis was done in a Bayesian setting, following Su *et al.* (2006) for simultaneous estimation of the environmental values and covariates. The heterogeneity of residual variance due to herds will also be examined.

Methods

Data

Data for this study were supplied by SEGES, Pig Research Centre, and were part of the routine Danish pig breeding program recording. ADG in the weight interval 30 kg to 100 kg for 75021 Duroc pigs (32297 males from 19 herds and 42724 females from 16 herds) was used. The pedigree for the animals with records was traced back 3 generations and included 91141 animals.

Statistical analyses

ADG has previously been shown to have different genetic variance in male and female broilers (Mebratie, *et al.*, 2017) and a study in pigs have found similar results (Nielsen *et al.*, 2017, pers.com). Therefore, to account for differences in genetic variance of ADG for male and female pigs, a univariate reaction norm model with herd specific residual variance was fitted separately for males and females. This results in 19 and 16 residual variance estimates for males and females, respectively.

(1)

where \mathbf{y} was a vector of ADG observations for either males or females, \mathbf{b} was a vector of fixed effect of year of birth and fixed regression on start body weight (SBW), \mathbf{a} corresponded to the additive genetic intercept, while \mathbf{a}^* was the slope, of the additive genetic reaction norm. \mathbf{h} , \mathbf{p} and \mathbf{l} were vectors of the random effects of herd-year-month (HYM), pen and litter, respectively. \mathbf{e} was a vector of the residuals of the model fitted for ADG of male or female pigs with heterogeneous residual variance in 19 and 16 classes, respectively. \mathbf{X} relates observations to the fixed effect of year of birth and SBW, \mathbf{Z} relates records to animals, and \mathbf{W} , \mathbf{V} and \mathbf{L} relates observations to HYM, pen and litter effects, respectively. \mathbf{H} contains the environmental covariate, which was updated in each

round of the Gibbs sampler based on the sampled \mathbf{h} vector,

The vectors \mathbf{h} , \mathbf{p} and \mathbf{l} were assumed to be mutually independent and normally distributed, and \mathbf{e} was assumed independent, normally distributed for herd 1 to m , where m was 19 in males and 16 in females. \mathbf{a} and \mathbf{a}^* was assumed correlated and normally distributed.

Bayesian estimation method via Gibbs sampling was used to sample location and dispersion parameters. This Bayesian reaction norm method allows inferring the population parameters and the environmental covariate in the model simultaneously, and accounting for heterogeneous residual variance. The prior probability distributions were inverse χ^2 with prior degree of freedom of 5 for the additive genetic variance and 3 for the remaining variance parameters. Estimates from a traditional REML model with homogeneous residual variance was used as scale parameters. The Gibbs sampling was performed for 2.5M rounds with the first 500k considered as burn-in and every 200th sample saved, resulting in 10k samples (i) for posterior analysis. The `boa` package (Smith, 2016) for R was used to evaluate convergence to the posterior distribution of the (co)variance parameters. The reaction norm analysis under a Bayesian setting described by Su *et al.* (2006) is implemented in DMU software (Madsen & Jensen, 2013), which was used in this study.

The additive genetic variance was evaluated for values of the environmental gradient from -3 to 3:

(2)

where \mathbf{k}_i was a 7×2 matrix with a column of ones for the intercept and a column of environmental gradient in standard deviation units of the HYM effect (\mathbf{e}) for each sample i , and $\sigma^2_{\mathbf{a}}$ was the additive genetic variance of the intercept and slope of the reaction norm for sample i , respectively, and $\sigma^2_{\mathbf{a}^*}$ was the covariance between the intercept and slope of sample i .

Heritability of ADG at environmental gradient j in a herd h can then be calculated for sample i , using:

(3)

where $\sigma^2_{\mathbf{a}}$ was the additive genetic variance at environment gradient j , and $\sigma^2_{\mathbf{p}}$ and $\sigma^2_{\mathbf{e}}$ were the variances of pen-effects, litter-effects and the residual variance of herd h , respectively, from sample i .

Results and discussion

In this study, the magnitude of genetic variation in macro-ES for ADG in male and female pigs was investigated using the reaction norm model with unknown covariates developed by Su *et al.* (2006) considering heterogeneous residuals for each herd. This method estimates the environmental values and genetic parameters simultaneously, which minimizes bias and maximizes accuracy of prediction of breeding values (Su *et al.*, 2006).

The posterior means of the distribution for the additive genetic variance for intercept and slope are presented in Table 1, along with the posterior mean for the genetic correlation between these. Posterior means and highest posterior density intervals for genetic variances and co-variances derived for 7 different values of the environmental gradient are presented in Table 2 for males and Table 3 for females. The posterior means of the distribution for heritability expressed with environmental gradient zero and residual variances in each h is presented in Table 4. Figure 1 displays the heritability in the herds with the lowest and highest residual variance, along with the heritability calculated using the average residual, for both males and females.

Genetic parameters of ADG

The posterior mean for heritability in the average herd with environmental gradient zero was 29% and 17% lower for males and females, respectively, than the heritability of 0.24 reported by Shirali *et al.* (2017) for ADG in Duroc using a traditional model jointly for males and females. However, the posterior mean for heritability increases as the environmental deviation increases (Figure 1) for both males and females and surpasses the 0.24 reported by Shirali *et al.* (2017) even in the herd with the highest residual variance (and consequently the lowest heritability).

The posterior mean of the additive genetic variance for intercept was 29% and 34% lower, for males and females, respectively, than the additive genetic variance of 2008 reported by Shirali *et al.* (2017) for ADG in Duroc from a traditional model across gender. The posterior mean of the additive genetic variance for slope was significantly different from zero for both males and females. The significant slope means that the additive genetic variance varies with environment. The posterior mean of the additive genetic variance was 98% and 42% higher in the -3 environment for males and females respectively, compared to values reported by Shirali *et al.* (2017). In the 3 environment, the increase was 52% and 67% for males and females, respectively, compared to Shirali *et al.* (2017).

The posterior mean for additive genetic correlations between ADG in different environments decrease when the environmental difference increased. The posterior mean for the correlations between the environments deviating five standard units from each other were not significantly different from zero for neither males nor females, neither was the correlations between the most extreme environments (-3 and 3) for females. The correlation between the most extreme environments for males were significantly different from zero, with an upper limit of the higher posterior density interval of -0.01.

The presence of significant slopes of the additive genetic variance and the low genetic correlation between the additive genetic variance in the 3 and -3 environments shows that it is possible to select for less macro-ES in Duroc pigs.

ADG in males and females

The posterior mean for heritability in the average herd was 15% lower for males than females. The posterior mean for intercept of the additive genetic variance was 7% larger in male than female. The posterior mean for slope of the additive genetic variance was 17% lower for males than females. The genetic correlation between intercept and slope were negative low in males and positive low in females. The additive genetic variance was higher in males than females when the environment did not deviate from zero or deviated negatively. When the environment deviated positively the females had higher additive genetic variance than the males. These differences indicate that treating ADG as one trait for males and females might violate model assumptions.

The residual variance was significantly larger in males than females in 10 of the 15 herds that rear animals of both sexes. The presence of significant differences in the residual variances between males and females, confirm that treating ADG as one trait with the same genetic variance for both males and females might violate model assumptions.

The model used in this analysis was univariate, meaning the correlation between ADG in the two sexes was not estimated. A multivariate reaction norm model, with homogeneous residuals (results not shown), estimated the correlation between the traits at 0.90 (SE 0.02).

Conclusion

A univariate reaction norm model with unknown covariates considering heterogeneous residual variance was developed for ADG in male and female Danish Duroc pigs. The reaction norm was found to explain the variation in genetic variance due to the environmental effect of HYM. The posterior mean of the distribution for heritability and additive genetic variance of ADG increased with increasing environmental deviation. The residual variance between herds were different suggesting that heterogeneity in residual variance should be considered. Furthermore, the analysis showed different heritability, additive genetic and residual variances for ADG in males and females. The reaction norm method with heterogeneous residual variance is feasible for explaining differences in residual variances between different herds and in identifying the amount of genetic variance existing in macro-ES. Results further suggest that it is possible to select for/against macro-ES.

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Table 1. Posterior means and highest posterior density (HPD) of the additive genetic variance of the intercept (and slope, and the posterior mean for the genetic correlation between intercept and slope of average daily body weight gain for males and females.

Trait	(HPD.)	(HPD)	(HPD)
male	1421 (1125-1720)	0.05 (0.04-0.07)	-0.14 (-0.29-0.02)
female	1327 (1128-1527)	0.06 (0.04-0.08)	0.09 (-0.04-0.22)

Table 2. Posterior mean and highest posterior density intervals for the genetic variance (diagonal), covariance (below diagonal) and correlation (above diagonal) in the environmental range for males.

	-3	-2	-1	0	1	2	3
-3	3991 (2968-5018)	0.98 (0.98-0.99)	0.91 (0.88-0.93)	0.70 (0.61-0.78)	0.36 (0.20-0.51)	0.04 (-0.14-0.23)	-0.19 (-0.37-(-0.01))
-2	3214 (2474-4052)	2669 (2085-3332)	0.97 (0.95-0.98)	0.81 (0.75-0.87)	0.52 (0.38-0.65)	0.21 (0.03-0.39)	-0.02 (-0.21-0.18)
-1	2436 (1869-3039)	2144 (1661-2615)	1812 (1428-2209)	0.93 (0.91-0.96)	0.72 (0.63-0.81)	0.46 (0.31-0.61)	0.24 (0.06-0.42)
0	1658 (1218-2093)	1579 (1222-1973)	1500 (1175-1825)	1421 (1125-1720)	0.92 (0.89-0.95)	0.74 (0.66-0.82)	0.57 (0.45-0.69)
1	880 (474-1307)	1034 (684-1386)	1188 (891-1511)	1342 (1049-1642)	1497 (1176-1812)	0.95 (0.93-0.96)	0.85 (0.80-0.89)
2	102 (-450-623)	489 (35-892)	876 (532-1229)	1264 (936-1582)	1651 (1283-2019)	2038 (1564-2488)	0.97 (0.96-0.98)
3	-676 (-1387-50)	-56 (-515-495)	565 (147-998)	1185 (812-1556)	1805 (1375-2248)	2425 (1857-3019)	3046 (2299-3817)

Table 3. Posterior mean and highest posterior density intervals for the genetic variance (diagonal), covariance (below diagonal) and correlation (above diagonal) in the environmental range for females.

	-3	-2	-1	0	1	2	3
-3	2845 (2176-3543)	0.98 (0.97-0.98)	0.86 (0.83-0.90)	0.62 (0.53-0.71)	0.31 (0.15-0.44)	0.04 (-0.13-0.21)	-0.14 (-0.31-0.02)
-2	2296 (1781-2806)	1944 (1552-2342)	0.95 (0.94-0.96)	0.77 (0.71-0.83)	0.50 (0.38-0.63)	0.26 (0.10-0.42)	0.08 (-0.10-0.25)
-1	1747 (1392-2124)	1593 (1293-1898)	1438 (1210-1690)	0.93 (0.91-0.95)	0.74 (0.66-0.82)	0.54 (0.41-0.66)	0.38 (0.23-0.52)
0	1198 (928-1483)	1241 (1010-1483)	1284 (1079-1493)	1327 (1128-1527)	0.94 (0.92-0.96)	0.81 (0.75-0.86)	0.69 (0.61-0.77)
1	649 (346-949)	889 (644-1136)	1130 (913-1342)	1370 (1155-1579)	1611 (1372-1861)	0.96 (0.95-0.97)	0.90 (0.87-0.93)
2	100 (-318-517)	538 (218-861)	976 (719-1224)	1413 (1176-1660)	1851 (1555-2154)	2289 (1899-2690)	0.98 (0.98-0.99)
3	-449 (-1061-92)	186 (-258-951)	821 (506-1134)	1456 (1170-1739)	2091 (1716-2453)	2726 (2237-3258)	3361 (2690-4030)

Table 4. Posterior means and highest posterior density interval (HPD) of the heritability (h^2) with environmental gradient zero and residual variance for average daily body weight gain for males and females in each herd and average across herds.

Herd	Male		Female	
	h^2 (HPD)	(HPD)	h^2 (HPD)	(HPD)
1	0.15 (0.12-0.18)	6265 (5836-6720)	0.19 (0.16-0.21)	4627 (4351-4880)
2	0.18 (0.15-0.22)	4680 (4329-5036)	0.22 (0.19-0.25)	3487 (3258-3713)
3	-	-	0.18 (0.15-0.20)	5010 (4729-5283)
4	0.19 (0.15-0.23)	4425 (3959-4871)	0.21 (0.18-0.24)	3846 (3549-4137)
5	0.17 (0.14-0.21)	5078 (4730-5426)	0.21 (0.18-0.24)	3724 (3476-3964)
6	0.19 (0.15-0.23)	4513 (4109-4953)	0.21 (0.18-0.24)	3654 (3391-3915)
7	0.17 (0.13-0.20)	5351 (4981-5727)	0.20 (0.17-0.23)	4000 (3762-4234)
8	0.16 (0.13-0.19)	5828 (5258-6374)	0.18 (0.15-0.21)	4803 (4402-5199)
9	0.17 (0.13-0.20)	5455 (5062-5827)	-	-
10	0.15 (0.12-0.18)	6524 (5906-7130)	0.16 (0.13-0.18)	6026 (5584-6478)
11	0.15 (0.12-0.19)	6207 (5743-6732)	0.17 (0.15-0.20)	5171 (4826-5495)
12	0.15 (0.12-0.18)	6427 (5723-7132)	0.17 (0.14-0.19)	5359 (4874-5842)
13	0.16 (0.13-0.20)	5699 (5122-6275)	0.19 (0.16-0.21)	4621 (4185-5062)
14	0.17 (0.12-0.21)	5468 (3911-7072)	-	-
15	0.22 (0.15-0.28)	3634 (2064-5512)	0.28 (0.22-0.34)	2322 (1540-3128)
16	0.18 (0.15-0.22)	4680 (4229-5187)	0.21 (0.18-0.25)	3712 (3267-4175)
17	0.15 (0.10-0.21)	6547 (3913-9614)	-	-
18	0.18 (0.14-0.22)	4893 (4149-5659)	0.24 (0.20-0.27)	3048 (2746-3350)
19	0.17 (0.13-0.20)	5415 (4715-6097)	0.18 (0.14-0.22)	4745 (3572-5989)
20	0.16 (0.11-0.21)	5816 (3823-7871)	-	-
Mean	0.17 (0.13-0.21)	5416 (4609-6274)	0.20 (0.17-0.23)	4260 (3844-4693)

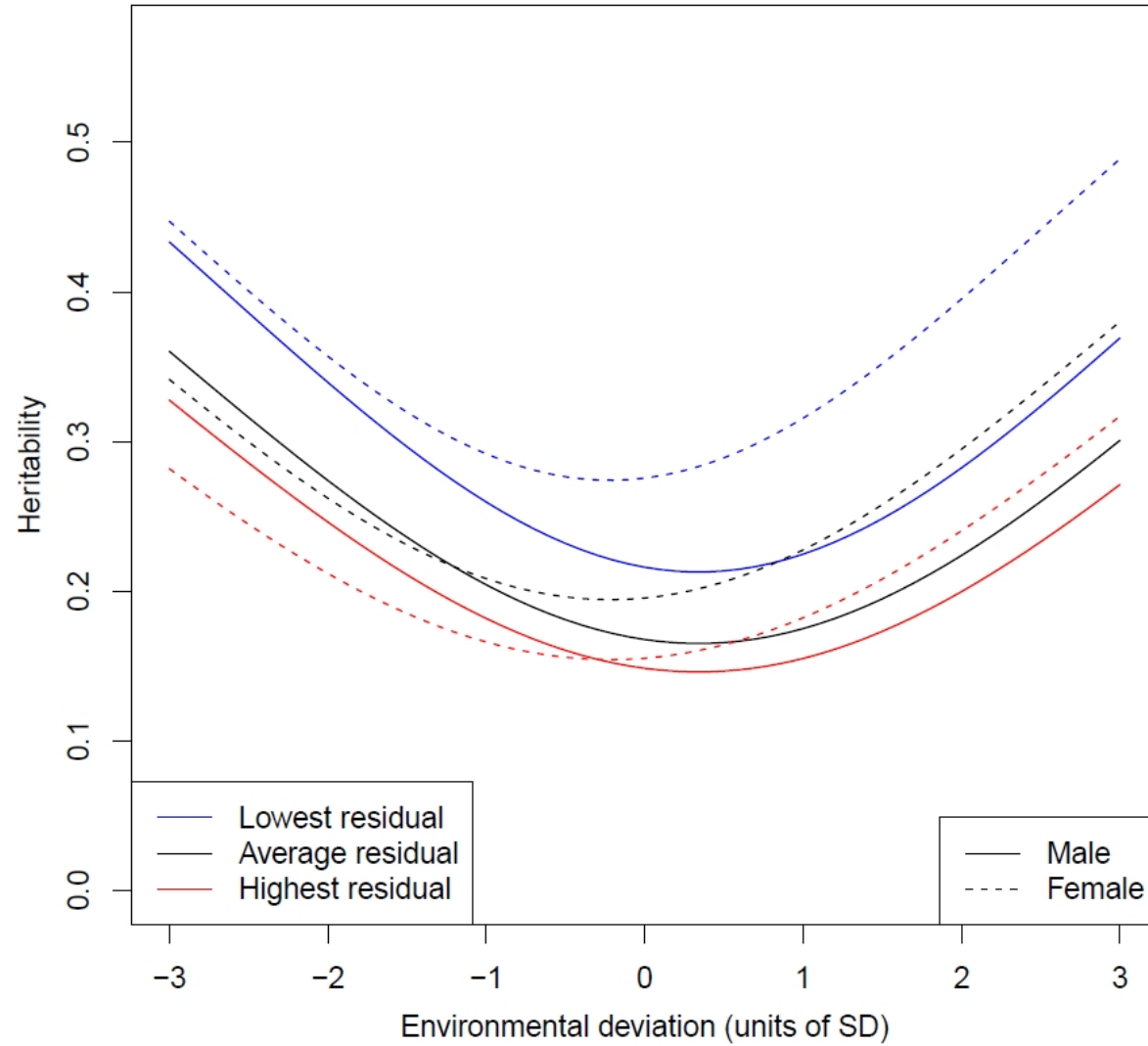


Figure 1. The heritability estimated in the average herd (black) and in the herd with the lowest (blue) and highest (red) residual variance for male (solid line) and female (broken line) Danish Duroc pigs.