812. Building on Falconer's work on environmental sensitivity and scale

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Abstract

Reaction norms are popular for analysing the genetics of environmental sensitivity in animals. The slope of the reaction norm is directly used as a measure of sensitivity. However, some of the variation in slope might be due to differences in the scale of the genetic variance. This problem was considered in 1990 by Falconer in the context of phenotypic reaction norms. This paper extends his work into the current use of genetic random regression reaction norms. A simple post-hoc method to estimate breeding values for environmental sensitivity independent of scale effects while accommodating for higher-order polynomials is proposed. A small example is used for illustration.

Introduction

There are two classes of genotype by environment interaction (G×E). Rank-type G×E occurs when the ranking of genotypes change in different environments, while scale-type G×E occurs when the genetic variance changes in different environments. In the context of breeding programs, rank-type G×E is more important as it means selection candidates change depending on the environment. In contrast, the effect of scale-type G×E can be completely removed by using an appropriate transformation (Falconer and Mackay, 1996). Both types of G×E often act simultaneously in a population (Falconer, 1990).

Reaction norm models (RNMs) estimated via random regression capture both rank and scale-type G×E. This approach uses a covariate, such as the mean performance of a contemporary group, to measure the environmental quality for each animal. The breeding value of each animal is then calculated as a function of the covariate, using the performance of relatives in different environments to infer how it changes. A linear function is often used, resulting in estimated breeding values (EBVs) for the intercept and slope for each animal. It is popular to treat the slope as an EBV for how sensitive a genotype is to different environments i.e. it's environmental sensitivity (ES) (Knap, 2005). However, it could be important to consider that the variation in slope arises from both rank and scale-type G×E (Falconer, 1990).

Falconer (1990) noted that many traits have higher variances when the means are higher. The consequence of this in a reaction norm model is illustrated in Figure 1. As the environmental mean increases, the genotypes spread out. While the rankings of genotypes do not change, there is still variation in the slope of genotypes. In this case, does the slope represent the ES of a genotype? If we assume it does, we would note that animals with a larger intercept have a larger slope. This frequently results in the conclusion that higher performing animals are more sensitive (Rauw and Gomez-Raya, 2015). However, animals with negative intercepts of the same size have equivalently large slopes (i.e. equally as sensitive), just in the opposite direction. Also, a scale transformation that equalises the variance across the environments would completely remove the variation in slope. If we ascribe the correlation between intercept and slope (r_{IS} = ~0.99) to a scale effect, the variation in slope due to re-ranking would be ($1 - r_{IS}^2$) (Falconer, 1990), or effectively to zero.

Falconer did not offer a strong opinion on the treatment of scale in reaction norms, other than to say scale effects should be considered in the analysis of environmental sensitivity (Falconer, 1990). However in Falconer and Mackay (1996), it is recommended that by recognising a true scale effect, such as larger variances

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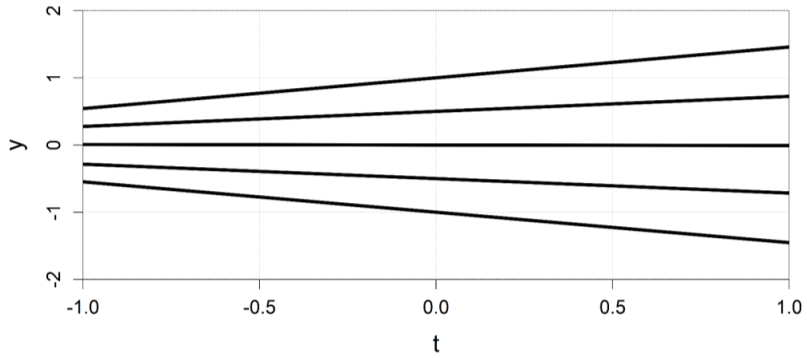

Figure 1. Reaction norm where the variance of y increases with t.

associated with higher body weights in mice, '… there is no need to look deeper into the genetic properties of the character for explanation.' This logic could be applied to the treatment of slope variance in Figure 1.

Hayes *et al.* (2003) accounted for scale in RNMs using a log transformation on phenotypic data. However, if the ratio of genetic and phenotypic variance changes across environments, the genetic variance might not be properly scaled this way (Falconer, 1990). Since random regression RNMs separate genetic and residual variance, a post-analysis focusing only on the genetic variance might be a better course of action. The following method corrects for heterogenous genetic variance on estimates of ES. Ordinary polynomials are used, although it can be easily modified for other polynomials such as Legendre.

Scale-correction method

Consider a random regression reaction norm model that estimates K, a $p \times p$ matrix containing the genetic variances and covariances between the intercept, slope and higher order regression coefficients up to p-1. This also model also estimates breeding values for the intercept (a_0), slope (a_1) and higher order coefficients for each animal. The EBV for animal i in environment j with score t is given by:

$$\boldsymbol{EBV_{i,j} = a_{0_i} + a_{1_i} \times t_j + \cdots + a_{p-1_i} \times t^{p-1}}$$

The genetic variance and covariance matrix (G) between j environments across the trajectory can be obtained by: $G = \Phi K \Phi'$, where Φ is an $j \times p$ matrix containing a vector of 1's in the first column and a vector of the j environmental scores in the second. The remaining p-2 columns of Φ are given by: $\Phi_{i,q-2} = (\Phi_{i,2})^q$, where q is the order of the polynomial. The diagonal of G gives the genetic variance for each environment. The EBVs for all animals can be standardised (SEBV) within environments based on the diagonal of G:

$$SEBV_{i,j} = \frac{EBV_{i,j}}{\sqrt{G_{j,j}}} \quad (1)$$

When plotted, the SEBVs preserve the points of reranking, but are not affected by scale effects. The SEBVs will not be linear with respect to $\boldsymbol{t}$ (even when using a linear reaction norm), so the average of the first derivative of the curve can be used to approximate the absolute change in SEBV:

$$ES_i = \frac{SEBV_{i,\max(t)} - SEBV_{i,\min(t)}}{\max(t) - \min(t)} \quad (2)$$

This can be interpreted as the 'real' environmental sensitivity (ES_i) of genotype i, representing the change in performance relative to its contemporaries in the absence of heterogenous genetic variance. Another advantage is that it permits higher-order reaction norms to be modelled while still capturing the ES into a single value. The average first derivative could also be explored over different segments of the trajectory.

Applied to a small example

Genetic reaction norms were simulated under zero, medium and high scale effects across environments (t) -1 to 1 units. The variance in intercept and slope was fixed to 1 and 0.4, while the correlation between them was 0, 0.5 and 0.95 for low, medium and high scenarios respectively. For each scenario, 1000 reaction norms were simulated and adjusted for scale following the scale-correction method. A subset of 5 genotypes were drawn from the population in the medium scenario and plotted in Figure 2a. This scenario represented a modest G×E interaction; the genetic correlation between environments -0.75 and 0.75 units was 0.62, while the genetic variance increased from 0.79 to 1.37. For a study with similar G×E levels, see (Madsen *et al.*, 2018). Equation 1 was applied to the population, which created Figure 2b. In this plot, the points of re-ranking were the same as in Figure 2a, however the variance of the SEBV was constant over t and the reaction norms were non-linear. The absolute change in SEBV was then calculated using Equation 2 and is illustrated in a sensitivity plot (Figure 2c). The sensitivity plot should not be interpreted directly as a reaction norm, as it is a linear approximation of the true reaction norm in Figure 2b. Rather, it is only used to visualise the sensitivity of each genotype.

Based on the original reaction norm, genotype 1 would be considered more robust than genotype 2, as it has a flatter slope. However, this is interpretation reverses after correcting for scale effects. This is best explained by looking at the standard deviation (SD) bands in Figure 2a. Genotype 1 is approximately 2.73 SDs above average when t=-1, but this reduces to 1.68 SDs when t=1. Therefore, its performance is relatively more sensitive compared to genotype 2, which is consistently 2.1 SDs above average across the environments. Despite a flat slope in the original reaction norm, genotype 5 improves in rank as t increases and therefore has a positive slope after correction. Meanwhile, genotypes 3 and 4 are not greatly affected by the scale correction, as the effect of scale is not as large closer to the mean.

The relationships between slope before and after correction under the three scenarios are plotted in Figure 3. The scale-correction did not affect the slope when there were no scale effects. As scale effects increased, the correlation between slope before and after correction decreased.

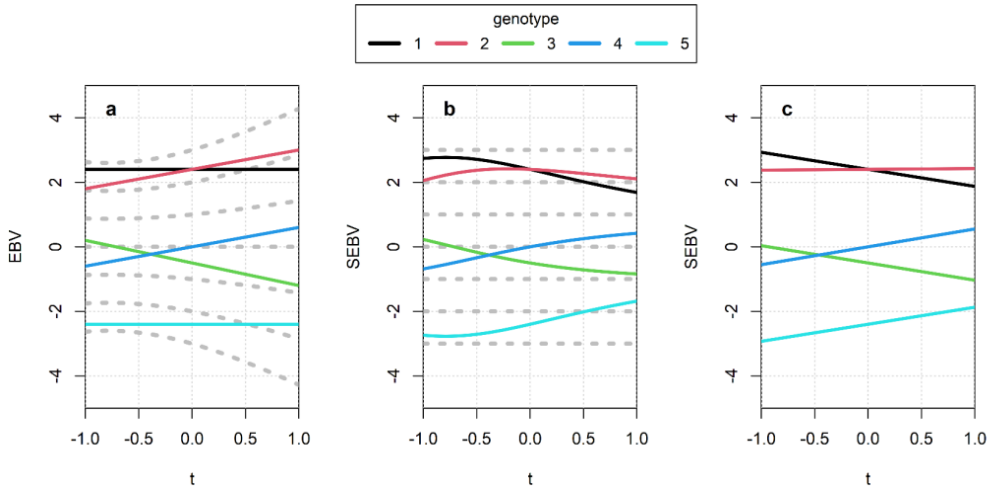

Figure 2. Reaction norms of 5 genotypes coloured individually, with ± standard deviation bands of EBVs given by the broken grey lines a: reaction norms before correction, b: reaction norms with variance standardised, c: sensitivity plot demonstrating change in slope.

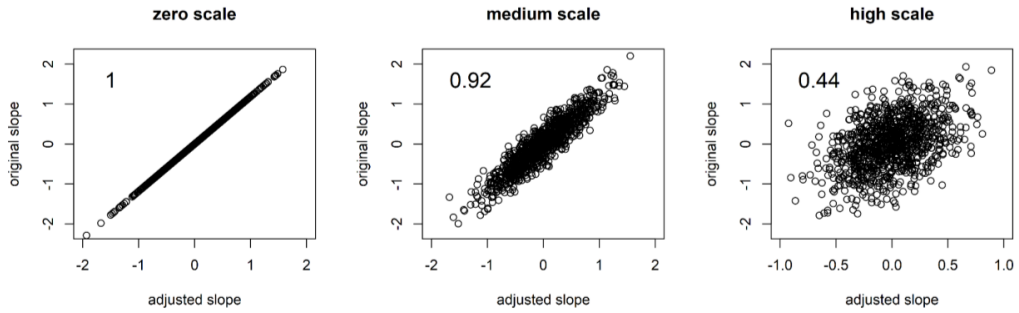

Figure 3. Scatterplot between slope EBVs before (original slope) and after (adjusted slope) being corrected for scale. The correlation is given in the top left.

The method could also be used in the analysis of longitudinal traits, where scale effects are very important. For instance, there is far less variation in weaning weights than in adult weights in livestock. In a linear random regression over time, this would bias the slope of high-weaning weight animals upward and low-weaning weight animals downward. Applying the scale correction would remove this bias and help identify animals that increase in ranking over time (i.e. faster growing animals).

Conclusions

To make progress in genetic selection, it is important to have a clear understanding of the trait being selected for. Environmental sensitivity derived from the slope of a reaction norm was previously not clearly defined, due to the impact of scale effects. A simple method for adjusting for scale effects is given. The resulting estimate of ES captured variation between genotypes in the degree of re-ranking, which could be used directly in breeding programs. The scale-correction could also be useful in longitudinal traits.

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