Assignment 2 Monday January 30 2017

Single trait selection on a reaction norm trait

Aim: In this exercise you investigate the consequences of selection on a single trait for response in level and slope of the reaction norm. The focus is on the degree of GxE-interaction depending on the reaction norm parameters, and on how response depends on the selection environment. The trait is milk yield in dairy cattle, which has a population average value of $\bar{x}$ = 8000kg. Herd-average milk yield in the population ranges from 5000kg to 11000kg.

Notation: Throughout, *scalars* are in *italics*, **MATRICES** are in **UPPERCASE BOLD**, **vectors** are in **lower case bold**.

Reaction norm: Consider a single trait determined by a linear reaction norm. The breeding value of individual *i* in environment *x* is given by $g_i(x) = g_{0,i} + g_{1,i}(x - \bar{x})$. Hence, g_0 is the breeding value for level and g_1 is the breeding value for slope, and the level (*i.e.*, the intercept) is defined in the mean environment $\bar{x}$. The environmental value, *x*, denotes the average milk yield in the environment of interest. (Hence, this is as in Finlay-Wilkinson regression). The selection environment is denoted with subscript s, and selection is on own performance for milk yield. Hence, selection is on $P(x_s)$. (For the sake of simplicity, here we ignore that there are two sexes.)

The phenotype is given by $P(x) = \bar{P} + g(x) + e$, where $\bar{P} = 8000$. In the lecture, we have largely ignored *e*, but usually both var(*e*) and var(*P*) increase with the trait level. In other words, herds with higher milk yield usually have higher phenotypic variance as well. In this exercise, therefore, phenotypic variance is given by the following function of herd-average milk yield:

$$\mathrm{var}(P) = 0.1\bar{P}^2 - 1536.75\bar{P} + 6\,894\,000$$

Where $\bar{P}$ is herd-average milk yield.

(Non-essential info that may be useful for further understanding: You may assume that the initial mean of the breeding values is zero for the level, $\bar{g}_0 = 0$, and one for the slope $\bar{g}_1 = 0$. As a consequence, the mean phenotype in environment *x* equals *x*, which agrees with the definition of *x* in FW-regression. In other words, $\bar{P}(x) = \bar{P} + \bar{g}_1(x - \bar{x}) = 8000 + 1(x - 8000) = x$.)

Selection: Selection is on the phenotype in the selection environment, $P_i(x_s) = \bar{P} + g_{0,i} + g_{1,i}(x_s - \bar{x}) + e$, which is a function of the breeding values for level and slope of the individual. The $\bar{P}$ is the same for everyone, and may be dropped. Hence, this may be interpreted as selection on an index $I_i = g_i(x_s) + e = (1 \quad x_s - \bar{x})\begin{pmatrix} g_{0,i} \\ g_{1,i} \end{pmatrix} + e = \mathbf{b}'\mathbf{g}_i + e$, where the vector of index weights is given by $\mathbf{b} = \begin{pmatrix} 1 \\ x_s - \bar{x} \end{pmatrix}$, and the vector of breeding values for level and slope of individual *i* is given by $\mathbf{g}_i = \begin{pmatrix} g_{0,i} \\ g_{1,i} \end{pmatrix}$. Thus the index is given by $I_i = \mathbf{b}'\mathbf{z}_i + e$. The e does not contribute to the G-matrix.

Response in level and slope: Interest is in response to selection in level and slope, $\Delta\bar{\mathbf{g}} = \begin{pmatrix} \Delta\bar{g}_0 \\ \Delta\bar{g}_1 \end{pmatrix}$, where $\Delta\bar{g}_0$ denotes response in level and $\Delta\bar{g}_1$ denotes response in slope. Hence, response to selection follows from regression of **g** on *I*, using the standard selection index expression:

$$\Delta\bar{\mathbf{g}} = \begin{pmatrix} \Delta\bar{g}_0 \\ \Delta\bar{g}_1 \end{pmatrix} = \mathbf{G}'\mathbf{b}\frac{\imath}{\sigma_I},$$

where $\imath$ denotes the intensity of selection. With mass selection, the standard deviation of the index is the square-root of phenotypic variance (given above).

With mass selection, **G** is symmetric, and is the variance-covariance matrix of the breeding values;

$$\mathbf{G} = \mathrm{cov}(\mathbf{g}, \mathbf{g}) = \begin{pmatrix} \sigma^2_{g_0} & \sigma_{g01} \\ \sigma_{g01} & \sigma^2_{g_1} \end{pmatrix}.$$

Response in phenotype: Interest is not only in response in level and slope, but also (or mainly) in response in phenotype in a response environment, say x_R, denoted as $\Delta\bar{g}(x_R)$. Since $g_i(x) = g_{0,i} + g_{1,i}(x - \bar{x})$, response in environment x_R can simply be obtained from the responses in level and slope, $\Delta\bar{g}(x_R) = \Delta\bar{g}_0 + \Delta\bar{g}_1(x_R - \bar{x})$.

Inputs: The following inputs are given: $\sigma^2_{g_0} = 550^2$ kg^2, $\sigma^2_{g_1} = 0.01$, $r_{g01} = 0.3$. Selection intensity $\imath = 1$.

A number of Equations has been implemented in the R-script entitled “univariate reaction norm milk yield.R.”

1. Plot the average reaction norm (i.e., before any selection has taken place, can be done by hand).
2. Plot the phenotypic and genetic variance (or sd) and the heritability as a function of the environment *x*, where *x* ranges from 5,000 to 11,000kg. Observe that the linear reaction norm enforces the variances to be a quadratic function of the environment.
3. Magnitude of GxE-interaction: Calculate the genetic correlation between the trait in the average environment (*x* = 8000) and in the highest (11,000kg) and lowest (5000kg) environments. Change the genetic variance in slope to see how the degree of GxE is affected.

4. Calculate the degree of GxE-interaction (i.e. the genetic correlation) between the lowest and the highest environment. What do you observe when you strongly increase the genetic variance in the slope?
5. Set values back to their defaults. Calculate response to selection in level and slope, when selecting in: 1. The average environment, 2. The lowest environment, 3. The highest environment. How does the change in environmental sensitivity depend on the selection environment?
6. Calculate the average reaction norm when you would select 5 generations in the high environment, and also when you would select 5 generations in the low environment. Does the difference between average milk yield in the high and low environment change?
7. Calculate response to selection in milk yield in the low environment when either: 1. Selection is in the low environment, 2. Selection is in the high environment.
8. Calculate correlated response in the low environment when selecting in the high environment, using the genetic correlation (*i.e.*, rather than the above equations) and compare with results of the above equation.