American Society of Animal Science

The Scientific Voice of Animal Agriculture

Bayesian analysis of the linear reaction norm model with unknown covariate

Journal:	*Journal of Animal Science*
Manuscript ID:	E-2005-517
Manuscript Type:	Animal Genetics
Date Submitted by the Author:	14-Sep-2005
Complete List of Authors:	Su, Guosheng; Danish institute of Agricultural Sciences, Genetics and biotechnology Madsen, Per; Danish institute of Agricultural Sciences, Genetics and biotechnology Lund, Mogens; Danish Institute of Agricultural Sciences, Genetics and Biotechnology Sorensen, Daniel; Danish INstitute of Agricultural Sciences, Genetics & Biotechnology Korsgaard, Inge Riis; Danish Institute of Agricultural Sciences, Genetics and Biotechnology Jensen, Just; Danish Institute of Agricultural Sciences, Genetics and Biotechnology
Key Words:	G x E interaction, Environmental sensitivity, Reaction norm model, Environmental value, Gibbs sampler, Genetic parameters

Reaction norm model, unknown covariate

(**Section:** Animal Genetics -- Quantitative Genetics)

Bayesian analysis of the linear reaction norm model

with unknown covariate[1]

G. Su[2], P. Madsen, M. S. Lund, D. Sorensen , I. R. Korsgaard, J. Jensen

Danish Institute of Agricultural Sciences, Department of Genetics and Biotechnology,

DK-8830, Tjele, Denmark

[2] Correspondence: Dept. of Genetics and Biotechnology, Danish Institute of Agricultural Sciences, DK 8830, Tjele, Demark (phone: (45) 89 99 12 67; fax: (45) 89 99 13 00; email: guosheng.su[a]agrsci.dk)

1   **ABSTRACT** The reaction norm model is becoming a popular approach for the analysis of G x E

2   interactions. In a classical reaction norm model, the expression of a genotype in different

3   environments is described as a linear function (a reaction norm) of an environmental gradient or

4   value. A common environmental value is defined as the mean performance of all genotypes in the

5   environment, which is typically unknown. One approximation is to estimate the mean phenotypic

6   performance in each environment, and then treat these estimates as known covariates in the model.

7   However, a more satisfactory alternative is to infer environmental values simultaneously with the

8   other parameters of the model. This study describes a method and its Bayesian MCMC

9   implementation that makes this possible. Frequentist properties of the proposed method are tested in

10   a simulation study. Estimates of parameters of interest agree well with the true values. Further,

11   inferences about genetic parameters from the proposed method are similar to those derived from a

12   reaction norm model using true environmental values. On the other hand, using phenotypic means

13   as proxies for environmental values results in poor inferences.

14

15   Keywords: G x E interaction, Environmental sensitivity, Reaction norm model, Environmental

16   value, Gibbs sampler, Genetic parameters.

17

Introduction

19   The reaction norm model (Falconer and Mackay, 1996) is attractive to describe genotype by

20   environment interactions (G × E) partly because it can accommodate a very large number of

21   environmental levels with few parameters. In its standard version, it requires that covariates are

22   known (e.g., Karan et al., 1999; Ravagnolo and Misztal, 2000, Kingsolver, et al., 2004). However,

23   in animal breeding applications one may postulate a linear relationship between the phenotypic

24   expression of a given genotype and a particular environmental effect (e.g., herd effect). In this setup

25   the covariate (i.e., herd effect) is unknown. One approximation reported in the literature is to

26   compute the mean phenotypic performance in the appropriate environment and to use such an

27   estimate in lieu of the unknown covariate in the model (e.g., Calus et al, 2002; Kolmodin et al,

28   2002; Calus and Veerkamp, 2003).

29   Including a function of the data as a covariable in the sampling model for the data is clearly

30   unsatisfactory. Apart from the understatement of uncertainty due to treating phenotypic means as

31   known parameters, one can imagine situations that would lead to misleading representations of

32   environmental values using this approach. An example would be the presence of genetic trend.

33   Since in the reaction norm model a breeding value is defined as a function of the environmental

34   gradient, biased estimates of environmental values may result in incorrect ranking based on

35   predicted genetic values.

36   It is therefore important to find more appropriate methods to account for unknown covariates in

37   a reaction norm model. An alternative is to infer the environmental values simultaneously with the

38   other parameters of the model. The objectives of this study are (1) to describe a method and its

39   Bayesian MCMC implementation that makes this possible, and (2) using a simulation study, to test

40   the expectation that the proposed method leads to more satisfactory inferences about genetic

41   parameters than the approximate method mentioned above.

42

43   **Model and methods**

44   *Model*

45   When both genetic and non-genetic environmental sensitivities are taken into consideration, a

46   reaction norm model can be written as

47    $$\mathbf{y} = \mathbf{Xb} + \mathbf{Eh} + \mathbf{Z}_u\mathbf{u}_0 + \mathbf{H}_u\mathbf{u}_h + \mathbf{Z}_a\mathbf{a}_0 + \mathbf{H}_a\mathbf{a}_h + \mathbf{e} \tag{1}$$

48   where $\mathbf{y}$ is the data vector (order n), $\mathbf{b}$ is the vector of fixed effects (order n_b), $\mathbf{h}$ is the vector of

49   environmental values (order n_h), $\mathbf{u}_0$ is the vector of intercepts (order n_u), $\mathbf{u}_h$ is the vector of slopes of

50   reaction norms for non-genetic random effects (e.g., permanent effects, of order n_u), $\mathbf{a}_0$ is the vector

51   of intercepts (order n_g), $\mathbf{a}_h$ is the vector of slopes of additive genetic reaction norms (order n_g), and $\mathbf{e}$

52   is the vector of residual effects (order n). $\mathbf{X}$, $\mathbf{E}$, $\mathbf{Z}_u$, $\mathbf{H}_u$, $\mathbf{Z}_a$ and $\mathbf{H}_a$ are the incidence matrices. The ith

53   row of the matrices **X**, **E**, **Z**$_u$, and **Z**$_a$ has exactly one element equal to one, and the remaining

54   elements equal to zero. When the covariate associated to the reaction norm is treated as unknown,

55   the ith row of the matrices **H**$_u$ and **H**$_a$ has exactly one element equal to the effect of the environment

56   (h$_j$ or a function of h$_j$) where the observation is recorded, and the others equal to zero.

57   In principle **h** can be treated as a fixed or a random vector. Here it is treated as random in order

58   to better meet identifiability requirements. In the present model identifiability is a complex topic.

59   We limit ourselves to making the statement that the functions of the parameters that are estimated

60   and reported below are identifiable.

61   The conditional distribution of **y** is assumed to be normal having the form

62   $$\boldsymbol{y} \mid \boldsymbol{b}, \boldsymbol{h}, \boldsymbol{u_0}, \boldsymbol{u_h}\, \boldsymbol{a_0}, \boldsymbol{a_h}, \boldsymbol{R} \ \sim \ \mathrm{N}\,(\boldsymbol{Xb} + \boldsymbol{Eh} + \boldsymbol{Z_u u_0} + \boldsymbol{H_u u_h} + \boldsymbol{Z_a a_0} + \boldsymbol{H_a a_h}, \boldsymbol{R}),$$

63   where **R** is the matrix (order n) of random residual covariances. Without loss of generality, it is

64   assumed that residuals are homoscedastic and independent of each other so that $\mathbf{R} = \mathbf{I}\sigma_e^2$, where **I** is

65   the identity matrix and σ_e^2 is the residual variance.

66

Prior distribution of location parameters

68   The prior distribution of vector **b** is assumed to be improper uniform with density

69   p(**b**) ∝ constant.   (2)

70   The random vectors **h**, (**u**$_0$, **u**$_h$) and (**a**$_0$, **a**$_h$) are assumed to have normal, mutually independent

71   prior distributions. The prior density function of **h** given σ_h^2 is

72   $$p(\boldsymbol{h} \mid \sigma_{\boldsymbol{h}}^2) = (2\pi\sigma_{\boldsymbol{h}}^2)^{-n_h/2} \exp\!\left[\frac{-\boldsymbol{h'h}}{2\sigma_{\boldsymbol{h}}^2}\right]$$ (3)

73   where σ_h^2 is the variance of h$_i$, and it is assumed that Var(**h**)=**I**σ_h^2.

74

75   Let $\boldsymbol{u} = \begin{bmatrix} \boldsymbol{u_0} \\ \boldsymbol{u_h} \end{bmatrix}$, and let $\boldsymbol{U}_0 = \begin{bmatrix} \sigma_{u_0}^2 & \sigma_{u_0,u_h} \\ \sigma_{u_0,u_h} & \sigma_{u_h}^2 \end{bmatrix}$ be the covariance matrix of u_{0_i} and u_{h_i}. Then, with

76    $Var\begin{bmatrix} \boldsymbol{u_0} \\ \boldsymbol{u_h} \end{bmatrix} = \boldsymbol{U}_0 \otimes \boldsymbol{I}$, the prior joint density function of $\boldsymbol{u_0}$ and $\boldsymbol{u_h}$ given $\mathbf{U}_0$ is

77    $p(\boldsymbol{u} | \boldsymbol{U_0}) = (2\pi)^{-n_u} | \boldsymbol{U}_0 |^{-n_u/2} \exp\left[\dfrac{-\boldsymbol{u}'(\boldsymbol{U_0^{-1}} \otimes \boldsymbol{I})\boldsymbol{u}}{2} \right]$.   (4)

78   Similarly, let $\boldsymbol{g} = \begin{bmatrix} \boldsymbol{a_0} \\ \boldsymbol{a_h} \end{bmatrix}$, $\boldsymbol{G}_0 = \begin{bmatrix} \sigma_{a_0}^2 & \sigma_{a_0,a_h} \\ \sigma_{a_0,a_h} & \sigma_{a_h}^2 \end{bmatrix}$, and $Var\begin{bmatrix} \boldsymbol{a_0} \\ \boldsymbol{a_h} \end{bmatrix} = \boldsymbol{G}_0 \otimes \boldsymbol{A}$, where $\mathbf{A}$ is the numerator

79   relationship matrix among n_g individuals. Then the prior density function of $\mathbf{g}$, given $\mathbf{G_0}$ and $\mathbf{A}$ is

80    $p(\boldsymbol{g} | \boldsymbol{G_0}) = (2\pi)^{-n_g} | \boldsymbol{G}_0 |^{-n_g/2} | \boldsymbol{A} |^{-k_g/2} \exp\left[\dfrac{-\boldsymbol{g}'(\boldsymbol{G_0^{-1}} \otimes \boldsymbol{A^{-1}})\boldsymbol{g}}{2} \right]$ (5)

81   where $k_g = 2$ is the dimension of $\mathbf{G}_0$.

82

Prior distribution of dispersion parameters

84   The prior distributions of σ_h^2 and σ_e^2 are assumed to be scaled inverse Chi-square distributions

85   with density

86    $p(\sigma_h^2) \propto (\sigma_h^2)^{-(\frac{v_h}{2}+1)} \exp\left[\dfrac{-v_h s_h^2}{2\sigma_h^2} \right]$,   (6)

87   and

88    $p(\sigma_e^2) \propto (\sigma_e^2)^{-(\frac{v_e}{2}+1)} \exp\left[\dfrac{-v_e s_e^2}{2\sigma_e^2} \right]$,   (7)

89   where v_I is the degree of freedom, and s_i^2 is a scale parameter, $i = h, e$. These reduce to improper

90   uniform distributions if $v_i = -2$ and $s_i^2 = 0$.

91   The prior distributions of $\mathbf{G}_0$ and $\mathbf{U}_0$ are assumed to be inverse Wishart distributions, with

92   density

93    $p(\boldsymbol{G_0} | \boldsymbol{V_g}, v_g) = | \boldsymbol{G}_0 |^{-(v_g+k_g+1)/2} \exp(-\dfrac{1}{2} tr(\boldsymbol{G_0}^{-1} \boldsymbol{V_g^{-1}}))$ (8)

94   and

95    $$p(\boldsymbol{U}_0 \mid \boldsymbol{V}_u, \nu_u) = \mid \boldsymbol{U}_0 \mid^{-(\nu_u + k_u + 1)/2} \exp(-\frac{1}{2} tr(\boldsymbol{U}_0^{-1} \boldsymbol{V}_u^{-1})) \qquad (9)$$

96   where k_i is the dimension of $\mathbf{G}_0$ or $\mathbf{U}_0$, $\mathbf{V}_i$ is the scale matrix and ν_i is the degree of freedom, $i = u$,

97   g. Setting $\mathbf{V}_i = \mathbf{0}$ and $\nu_i = -(k_i + 1)$, retrieves an improper uniform distribution.

98

99   ***Joint posterior distribution of all the parameters***

100   Let θ be the vector of all location parameters except $\mathbf{h}$, i.e., $\theta = (\mathbf{b'}, \mathbf{u}_0', \mathbf{u}_h', \mathbf{a}_0', \mathbf{a}_h')$. The joint

101   posterior distribution of all the parameters is

102    $$\begin{aligned} &p(\boldsymbol{\theta}, \boldsymbol{h}, \sigma_h^2, \boldsymbol{U_0}, \boldsymbol{G_0}, \sigma_e^2 \mid \boldsymbol{y}) \\ &\propto p(\boldsymbol{y} \mid \boldsymbol{\theta}, \boldsymbol{h}, \sigma_e^2) p(\sigma_h^2) p(\boldsymbol{h} \mid \sigma_h^2) p(\boldsymbol{U_0}) p(\boldsymbol{u_0}, \boldsymbol{u_h} \mid \boldsymbol{U_0}) p(\boldsymbol{G_0}) p(\boldsymbol{a_0}, \boldsymbol{a_h} \mid \boldsymbol{G_0}) p(\sigma_e^2) \end{aligned} \qquad (10)$$

103

104   ***Fully conditional posterior distribution of the location parameters θ***

105   The fully conditional posterior distribution of θ can be directly derived from (10) by extracting

106   terms involving θ. This results in

107    $$\begin{aligned} &p(\boldsymbol{\theta} \mid \boldsymbol{y}, \boldsymbol{h}, \sigma_h^2, \boldsymbol{U_0}, \boldsymbol{G_0}, \sigma_e^2) \\ &\propto p(\boldsymbol{y} \mid \boldsymbol{\theta}, \boldsymbol{h}, \sigma_e^2) p(\boldsymbol{u_0}, \boldsymbol{u_h} \mid \boldsymbol{U_0}) p(\boldsymbol{a_0}, \boldsymbol{a_h} \mid \boldsymbol{G_0}) \end{aligned} \qquad (11)$$

108

109   Further, assuming $\mathbf{h}$ known, define

110    $$\boldsymbol{y}_\theta = \boldsymbol{y} - \boldsymbol{E}\boldsymbol{h} = \boldsymbol{X}\boldsymbol{b} + \boldsymbol{Z}_u \boldsymbol{u_0} + \boldsymbol{H}_u \boldsymbol{u_h} + \boldsymbol{Z}_a \boldsymbol{a_0} + \boldsymbol{H}_a \boldsymbol{a_h} + \boldsymbol{e} \qquad (12)$$

111   Correspondingly, let $\boldsymbol{W}_\theta = (\boldsymbol{X} : \boldsymbol{Z}_u : \boldsymbol{H}_u : \boldsymbol{Z}_a : \boldsymbol{H}_a)$, $\boldsymbol{r}_\theta = \boldsymbol{W}_\theta' \boldsymbol{y}_\theta / \sigma_e^2$, and

112    $$\boldsymbol{\Omega}_\theta = \begin{bmatrix} \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & (\boldsymbol{U_0} \otimes \boldsymbol{I})^{-1} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & (\boldsymbol{G_0} \otimes \boldsymbol{A})^{-1} \end{bmatrix}, \quad \boldsymbol{C}_\theta = \boldsymbol{W}_\theta' \boldsymbol{W}_\theta / \sigma_e^2 + \boldsymbol{\Omega}_\theta.$$

113   Then the mixed model equations associated with (12) can be written as

114    $$\boldsymbol{C}_\theta \hat{\boldsymbol{\theta}} = \boldsymbol{r}_\theta. \qquad (13)$$

115   Since $p(\mathbf{y} \mid \boldsymbol{\theta}, \mathbf{h}, \sigma_e^2) = p(\mathbf{y}_\theta \mid \boldsymbol{\theta}, \sigma_e^2)$, the fully conditional posterior distribution of $\boldsymbol{\theta}$ is

116    $$p(\boldsymbol{\theta} \mid \mathbf{y}, \mathbf{h}, \sigma_h^2, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2) = p(\boldsymbol{\theta} \mid \mathbf{y}_\theta, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2)$$
$$\propto p(\mathbf{y}_\theta \mid \boldsymbol{\theta}, \sigma_e^2) p(\mathbf{u}_0, \mathbf{u}_h \mid \mathbf{U}_0) p(\mathbf{a}_0, \mathbf{a}_h \mid \mathbf{G}_0)$$

117    $$= \exp\left[-\frac{1}{2\sigma_e^2} \left(\begin{array}{l} (\mathbf{y}_\theta - \mathbf{W}_\theta \boldsymbol{\theta})' \ (\mathbf{y}_\theta - \mathbf{W}_\theta \boldsymbol{\theta}) + (\mathbf{u}_0', \mathbf{u}_h')(\mathbf{U}_0 \otimes \mathbf{I})^{-1} \begin{pmatrix} \mathbf{u}_0 \\ \mathbf{u}_h \end{pmatrix} \sigma_e^2 \\ + (\mathbf{a}_0', \mathbf{a}_h')(\mathbf{G}_0 \otimes \mathbf{A})^{-1} \begin{pmatrix} \mathbf{a}_0 \\ \mathbf{a}_h \end{pmatrix} \sigma_e^2 \end{array} \right) \right] \qquad (14)$$

118

119   Using results in Lindley and Smith (1972) and Gianola and Fernando (1986), it is easy to show that

120   the posterior distribution of location parameters, given dispersion parameters, is multivariate

121   normal. That is,

122         $\boldsymbol{\theta} \mid \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta \ \sim N(\hat{\boldsymbol{\theta}}, \mathbf{C}_\theta^{-1})$.

123

124   Let $\boldsymbol{\theta}_i$ denote an arbitrary element (or set of elements) of $\boldsymbol{\theta}$, and let $\boldsymbol{\theta}_{-i}$ denote the vector $\boldsymbol{\theta}$ with

125    $\boldsymbol{\theta}_i$ excluded, and partition the vector $\mathbf{r}_\theta$ and the matrix $\mathbf{C}_\theta$ appropriately, such that

126         $\boldsymbol{\theta}' = (\boldsymbol{\theta}_i', \ \boldsymbol{\theta}_{-i}')$, $\qquad \mathbf{r}_\theta' = (\mathbf{r}'_{\theta_i}, \ \mathbf{r}'_{\theta_{-i}})$, $\quad \mathbf{C}_\theta = \begin{bmatrix} \mathbf{C}_{\theta(i,i)} & \mathbf{C}_{\theta(i,-i)} \\ \mathbf{C}_{\theta(-i,i)} & \mathbf{C}_{\theta(-i,-i)} \end{bmatrix}$.

127   From standard multivariate normal theory, it can readily be established that if the distribution of

128    $\boldsymbol{\theta} \mid \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta$ is normal, then that of $\boldsymbol{\theta}_i \mid \boldsymbol{\theta}_{-i}, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta$ is also normal, with conditional

129   mean and variance given by (Sorensen and Gianola, 2002)

130    $E(\boldsymbol{\theta}_i \mid \boldsymbol{\theta}_{-i}, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta) = \mathbf{C}_{\theta(i,i)}^{-1}(\mathbf{r}_{\theta_i} - \mathbf{C}_{\theta(i,-i)}\boldsymbol{\theta}_{-i})$,

131    $Var(\boldsymbol{\theta}_i \mid \boldsymbol{\theta}_{-i}, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta) = \mathbf{C}_{\theta(i,i)}^{-1}$.

132   Consequently the fully conditional posterior distribution of $\boldsymbol{\theta}_i$ is

133    $\boldsymbol{\theta}_i \mid \boldsymbol{\theta}_{-i}, \mathbf{U}_0, \mathbf{G}_0, \sigma_e^2, \mathbf{y}_\theta \sim N(\mathbf{C}_{\theta(i,i)}^{-1}(\mathbf{r}_{\theta_i} - \mathbf{C}_{\theta(i,-i)}\boldsymbol{\theta}_{-i}), \mathbf{C}_{\theta(i,i)}^{-1})$.

134

135   ***Fully conditional posterior distribution of h***

136   From (10), the density of the fully conditional posterior distribution of **h** is

137    $p(\boldsymbol{h} \mid \boldsymbol{y}, \boldsymbol{\theta}, \sigma_h^2, \boldsymbol{U_0}, \boldsymbol{G_0}, \sigma_e^2) \propto p(\boldsymbol{y} \mid \boldsymbol{\theta}, \boldsymbol{h}, \sigma_e^2) p(\boldsymbol{h} \mid \sigma_h^2)$ (15)

138   Based on (1), an observation y can be described as

139
$$y = \boldsymbol{x'b} + h + u_0 + u_h h + a_0 + a_h h + e$$
$$= \boldsymbol{x'b} + u_0 + a_0 + (1 + u_h + a_h)h + e$$

140   Therefore, an alternative formulation of the reaction-norm model (1) is

141    $\boldsymbol{y} = \boldsymbol{Xb} + + \boldsymbol{E}^* \boldsymbol{h} + \boldsymbol{Z_u u_0} + \boldsymbol{Z_a a_0} + \boldsymbol{e}$ (16)

142   where $\mathbf{E}^*$ is the coefficient matrix obtained by replacing the non-zero element in the i$^{\text{th}}$ row of

143   matrix $\mathbf{E}$ with $(1 + \mathbf{z}_{ui}'\mathbf{u}_h + \mathbf{z}_{ai}'\mathbf{a}_h)$.

144   Assuming $\boldsymbol{\theta}$ known, define

145    $\mathbf{y}_h = \mathbf{y} - \mathbf{Xb} - \mathbf{Z_u u_0} - \mathbf{Z_a a_0} = \mathbf{E}^*\mathbf{h} + \mathbf{e}$ (17)

146   Further, let $\boldsymbol{C}_h = \boldsymbol{E}^{*\prime}\boldsymbol{E}^* / \sigma_e^2 + (\boldsymbol{I}\sigma_h^2)^{-1}$, and write the mixed model equations associated with (17)

147   as

148    $\boldsymbol{C}_h \hat{\boldsymbol{h}} = \boldsymbol{E}^{*\prime} \boldsymbol{y}_h / \sigma_e^2 = \boldsymbol{r}_h$,   (18)

149   Then, with $p(\boldsymbol{y} \mid \boldsymbol{\theta}, \boldsymbol{h}, \sigma_e^2) = p(\boldsymbol{y}_h \mid \boldsymbol{h}, \sigma_e^2)$, the fully conditional posterior distribution of **h** is

150
$$p(\boldsymbol{h} \mid \boldsymbol{y}, \boldsymbol{\theta}, \sigma_h^2, \boldsymbol{U_0}, \boldsymbol{G_0}, \sigma_e^2) = p(\boldsymbol{h} \mid \boldsymbol{y}_h, \sigma_h^2, \sigma_e^2)$$
$$\propto p(\boldsymbol{y}_h \mid \boldsymbol{h}, \sigma_e^2) p(\boldsymbol{h} \mid \sigma_h^2)$$
$$\propto \exp\left[-\frac{1}{2\sigma_e^2}((\boldsymbol{y}_h - \boldsymbol{E}^*\boldsymbol{h})'(\boldsymbol{y}_h - \boldsymbol{E}^*\boldsymbol{h}) + \boldsymbol{h}'\boldsymbol{h}\frac{\sigma_e^2}{\sigma_h^2}) \right]$$
(19)

151   Therefore,

152    $\boldsymbol{h} \mid \sigma_h^2, \sigma_e^2, \boldsymbol{y}_h \sim N(\hat{\boldsymbol{h}}, \boldsymbol{C}_h^{-1})$

153   and for the i$^{\text{th}}$ element,

154

155    $\boldsymbol{h}_i \mid \boldsymbol{h}_{-i}, \sigma_h^2, \sigma_e^2, \boldsymbol{y}_h \sim N(\boldsymbol{C}_{h(i,i)}^{-1}(\boldsymbol{r}_{h_i} - \boldsymbol{C}_{h(i,-i)}\boldsymbol{h}_{-i}), \boldsymbol{C}_{h(i,i)}^{-1}\sigma_e^2)$.

156

157   ***Fully conditional posterior distribution of dispersion parameters***

158　　　　The fully conditional posterior distribution of dispersion parameters is deduced from (10). Let

159　　Θ be the vector of all the location parameters, and $\mathbf{W} = (\mathbf{X}: \mathbf{E}_,: \mathbf{Z}_u: \mathbf{H}_u: \mathbf{Z}_a,:\mathbf{H}_a)$. For the residual

160　　variance one obtains

$$
\begin{aligned}
p(\sigma_e^2 \mid \boldsymbol{\Theta}, \sigma_h^2, \boldsymbol{U}_0, \boldsymbol{G}_0, \boldsymbol{y}) &\propto p(\boldsymbol{y} \mid \boldsymbol{\Theta}, \sigma_e^2) p(\sigma_e^2) \\
&\propto (\sigma_e^2)^{-\left(\frac{\nu_e+n}{2}+1\right)} exp\left[\frac{-\left[(\boldsymbol{y}-\boldsymbol{W}\boldsymbol{\Theta})'(\boldsymbol{y}-\boldsymbol{W}\boldsymbol{\Theta})+\nu_e s_e^2\right]}{2\sigma_e^2}\right]
\end{aligned}
\tag{20}
$$

161

162　　which is recognized as a scaled inverse Chi-square distribution with degrees of freedom $\nu_e + n$ and

163　　scale parameter $\left[(\boldsymbol{y}-\boldsymbol{W}\Theta)'(\boldsymbol{y}-\boldsymbol{W}\Theta)+\nu_e s_e^2\right]/(\nu_e + n)$.

164　　　　The fully conditional posterior distribution of the variance of environmental values is

$$
\begin{aligned}
p(\sigma_h^2 \mid \boldsymbol{\Theta}, \boldsymbol{U}_0, \boldsymbol{G}_0, \sigma_e^2 \boldsymbol{y}) &\propto p(\sigma_h^2) p(\boldsymbol{h} \mid \sigma_h^2) \\
&\propto (\sigma_h^2)^{-(\frac{\nu_h+n_h}{2}+1)} exp\left[\frac{-(\boldsymbol{h}'\boldsymbol{h}+\nu_h s_h^2)}{2\sigma_h^2}\right]
\end{aligned}
\tag{21}
$$

165

166　　which is a scaled inverse Chi-square distribution with degrees of freedom ν_h+n_h and scale parameter

167　　$(\mathbf{h'h}+\nu_h s_h^2)/(\nu_h+n_h)$.

168　　　　The fully conditional posterior distribution of the covariance matrix of the reaction norm of the

169　　non-genetic random effect is

$$
\begin{aligned}
p(\boldsymbol{U}_0 \mid \boldsymbol{\Theta}, \sigma_h^2, \boldsymbol{G}_0, \sigma_e^2, \boldsymbol{y}) &\propto P(\boldsymbol{U}_0) p(\boldsymbol{u}_0, \boldsymbol{u}_h \mid \boldsymbol{U}_0) \\
&\propto |\boldsymbol{U}_0|^{-(\nu_u+k_u+1+n_u)/2} \exp(-\frac{1}{2} tr(\boldsymbol{U}_0^{-1}\boldsymbol{V}_u^{-1})) \exp\left[\frac{-\boldsymbol{u}'(\boldsymbol{U}_0^{-1}\otimes\boldsymbol{I})\boldsymbol{u}}{2}\right]
\end{aligned}
\tag{22}
$$

170

171　　　　Let $\boldsymbol{S}_u^2 = \begin{bmatrix} \boldsymbol{u}_0'\boldsymbol{u}_0 & \boldsymbol{u}_h'\boldsymbol{u}_0 \\ \boldsymbol{u}_0'\boldsymbol{u}_h & \boldsymbol{u}_h'\boldsymbol{u}_h \end{bmatrix}$, and note that $\boldsymbol{u}'(\boldsymbol{U}_0^{-1}\otimes\boldsymbol{I})\boldsymbol{u} = tr(\boldsymbol{U}_0^{-1}\boldsymbol{S}_u^2)$. Consequently,

$$
\begin{aligned}
p(\boldsymbol{U}_0 \mid \boldsymbol{\Theta}, \sigma_h^2, \boldsymbol{G}_0, \sigma_e^2, \boldsymbol{y}) &\\
\propto |\boldsymbol{U}_0|^{-(\nu_u+k_u+1+n_u)/2} &\exp\left(-\frac{1}{2} tr(\boldsymbol{U}_0^{-1}(\boldsymbol{V}_u^{-1}+\boldsymbol{S}_u^2))\right)
\end{aligned}
\tag{23}
$$

172

173　　This is an inverse Wishart distribution of dimension $k_u=2$, with degrees of freedom ν_u+n_u and scale

174　　matrix $(\mathbf{S}_u^2+\mathbf{V_u}^{-1})^{-1}$.

175　　　　The fully conditional posterior distribution of the covariance matrix of the additive genetic

176　　reaction norm is

177
$$p(\boldsymbol{G_0} \mid \boldsymbol{\Theta}, \sigma_h^2, \boldsymbol{U_0}, \sigma_e^2, \boldsymbol{y}) \propto P(\boldsymbol{G_0})\, p(\boldsymbol{a_0}, \boldsymbol{a_h} \mid \boldsymbol{G_0})$$

$$\propto \mid \boldsymbol{G_0} \mid^{-(v_g + k_g + 1 + n_g)/2} \exp\left(-\frac{1}{2} tr(\boldsymbol{G_0}^{-1} \boldsymbol{V_g}^{-1})\right) \exp\left[\frac{-\boldsymbol{g'}(\boldsymbol{G_0^{-1}} \otimes \boldsymbol{A^{-1}})\boldsymbol{g}}{2}\right] \quad (24)$$

178   Let $\boldsymbol{S_g^2} = \begin{bmatrix} \boldsymbol{a_0'A^{-1}a_0} & \boldsymbol{a_h'A^{-1}a_0} \\ \boldsymbol{a_0'A^{-1}a_h} & \boldsymbol{a_h'A^{-1}a_h} \end{bmatrix}$, and again note that

179

180    $\boldsymbol{g'}(\boldsymbol{G_0^{-1}} \otimes \boldsymbol{A^{-1}})\boldsymbol{g} = tr(\boldsymbol{G_0^{-1}}\boldsymbol{S_g^2})$.

181

182   Therefore, the fully conditional posterior distribution has density

183
$$p(\boldsymbol{G_0} \mid \boldsymbol{\Theta}, \sigma_h^2, \boldsymbol{U_0}, \sigma_e^2, \boldsymbol{y})$$

$$\propto \mid \boldsymbol{G_0} \mid^{-(v_g + k_u + 1 + n_u)/2} \exp\left(-\frac{1}{2} tr(\boldsymbol{G_0}^{-1}(\boldsymbol{V_g}^{-1} + \boldsymbol{S_g^2}))\right) \quad (25)$$

184   which is an inverse Wishart distribution of dimension $k_g = 2$ with degrees of freedom $v_g + n_g$ and scale

185   matrix $(\boldsymbol{S_g}^2 + \boldsymbol{V_g}^{-1})^{-1}$.

186

187   ***Implementation of the Gibbs sampler***

188   The Gibbs sampler is a Monte Carlo method for obtaining samples from joint or marginal

189   posterior distributions of all parameters in the model, by repeated sampling from fully conditional

190   posterior distributions. The algorithm for the proposed model is as follows:

191   1. Construct the mixed model equations (14 and 19).

192   2. Set initial values for all the parameters.

193   3. Sample a new $\mathbf{h}_i$ and replace the old $\mathbf{h}_i$: a) calculate $\mathbf{y}_h$, $\mathbf{E}^*$, $\mathbf{C_h}$ and $\mathbf{r_h}$ based on the current

194   samples of $\boldsymbol{\theta}$ and variances; b) draw $\mathbf{h}_i$ from $N(\boldsymbol{C}_{h(i,i)}^{-1}(\boldsymbol{r_{hi}} - \boldsymbol{C_{h(i,-i)}}\boldsymbol{h_{-i}}), \boldsymbol{C}_{h(i,i)}^{-1})$; c) use the new $\mathbf{h}_i$ to

195   replace the old $\mathbf{h}_i$.

196   4. Sample the new θ_i and replace the old θ_i: a) calculate $\mathbf{y_\theta}$, $\mathbf{C_\theta}$ and $\mathbf{r_\theta}$ using the current samples of

197       $\mathbf{h}$ and variances; b) draw θ_i from $N(C_{\theta(i,i)}^{-1}(\mathbf{r}_{\theta i} - C_{\theta(i,-i)}\boldsymbol{\theta}_{-i}), C_{\theta(i,i)}^{-1})$; c) replace the old θ_i with the

198   new θ_i.

199   5. Sample a new σ_h^2 from $Inv - X^2\left(v_h + n_h, (\mathbf{h'h} + v_h s_h^2)/(v_h + n_h)\right)$.

200   6. Sample a new $\mathbf{G}_0$ from $Inv - W_2\left((S_g^2 + V_g^{-1})^{-1}, v_g + n_g\right)$. V_g can be determined by using the

201   expectation of the prior inverse Wishart distribution of $\mathbf{G}_0$.

202   7. Sample a new $\mathbf{U}_0$ from $Inv - W_2\left((S_u^2 + V_u^{-1})^{-1}, v_u + n_u\right)$.

203   8. Sample a new σ_e^2 from $Inv - X^2\left[v_e + n, \left((\mathbf{y} - \mathbf{W\Theta})'(\mathbf{y} - \mathbf{W\Theta}) + v_e s_e^2\right)/(v_e + n)\right]$.

204   9. Replace the old variances with the new variances.

205   10. Repeat (3) – (9) until enough samples are available to meet the accuracy of various Monte

206   Carlo computations.

207   A Gibbs sampling algorithm has been implemented in the DMU-package (Madsen and Jensen,

208   2004). In the actual implementation, the "iteration on data" technique is applied in order to avoid

209   storing $\mathbf{C_\theta}$ and $\mathbf{C_h}$.

210

211   ***Simulation studies***

212   *Data generation*

213   The proposed method was evaluated using a simulation study. Observations were generated

214   using the model

215    $\mathbf{y} = \mathbf{1}\mu + \mathbf{Eh} + \mathbf{Za}_0 + \mathbf{Ha}_h + \mathbf{e}$,

216   where $\mathbf{h}$ was the vector of environment values (herd-year effects), $\mathbf{a}_0$ was the vector of levels and

217    $\mathbf{a}_h$ was the vector of slopes of additive genetic reaction norms, $\mathbf{e}$ was the vector of random residuals.

218   Vectors $\mathbf{h}$, $(\mathbf{a}_0, \mathbf{a}_h)$ and $\mathbf{e}$ were assumed to be mutually independent and were sampled from

219    $\mathbf{h} \sim N(\mathbf{0}, \mathbf{I}\sigma_h^2)$, $\begin{pmatrix} \mathbf{a_0} \\ \mathbf{a_h} \end{pmatrix} \sim N(\mathbf{0}, \begin{bmatrix} \sigma_{a_0}^2 & \sigma_{a_0 a_h} \\ \sigma_{a_0 a_h} & \sigma_{a_h}^2 \end{bmatrix} \otimes A)$, and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$.

220   Five generations (five years) of data were simulated and distributed over 50 herds. In each

221   generation, 50 sires were mated to 1000 dams and each dam produced 5 offspring with records.

222   Both sires and dams were chosen randomly. Sires were used across herds and each sire was mated

223   to 20 dams from 5 herds. Dams were used within herds. Consequently there were 100 individuals

224   from 5 sires and 20 dams in each herd each generation.

225   The parameters used in the simulation were: $\sigma_h^2 = 80, \sigma_{a0}^2 = 100, \sigma_{ah}^2 = 1, r_{a0,ah} = 0.5,$ and

226    $\sigma_e^2 = 300$. This corresponds to a G x E variance $Var(a_h h) = \sigma_{ah}^2 . \sigma_h^2 = 80$ and a marginal variance

227   of a datum (phenotypic variance across herd-years) $\sigma_P^2 = \sigma_h^2 + \sigma_{ao}^2 + \sigma_{ah}^2 \sigma_h^2 + \sigma_e^2 = 560$.

228

229   *Statistical analysis*

230   The simulated data were analyzed using the following models:

231   1) M1: The model with unknown covariate of the reaction norm, treating herd-years as random

232   effects (the proposed approach),

233    $\boldsymbol{y = 1\mu + Eh + Za_0 + Ha_h + e}$ (M1)

234   2) M2: The model using true herd-year effects as covariate ($\boldsymbol{H}^t$) of the reaction norm and including

235   herd-years as fixed effects,

236    $\boldsymbol{y = 1\mu + Xh + Za_0 + H^t a_h + e}$ (M2)

237   3) M3: The model using phenotypic means of herd-years as proxies for the unknown covariates

238   ($\boldsymbol{H}^m$) of the reaction norm and including herd-years as fixed effects,

239    $\boldsymbol{y = 1\mu + Xh + Za_0 + H^m a_h + e}$ (M3)

240   Note that in models M2 and M3, the covariates of the reaction norm ($\mathbf{H}^t$, $\mathbf{H}^m$) are not necessarily

241   equivalent to the corresponding elements of $\mathbf{h}$, while in M1, the non-zero elements of $\mathbf{H}$ are

242   equivalent with those of $\mathbf{h}$.

243   The additive genetic variance (σ_a^2) and heritability (h_a^2) in a particular herd-year were calculated

244   as $\sigma_a^2 = \sigma_{a_0}^2 + \sigma_{a_h}^2 h^2 + 2\sigma_{a0ah} h$ and $h_a^2 = \dfrac{\sigma_a^2}{(\sigma_a^2 + \sigma_e^2)}$. Since the covariate features in the additive

245   genetic and phenotypic variances, for ease of comparison of heritabilities among models, the

246   covariate was expressed in units of the appropriate standard deviation ($h^* = h/\sigma_h$). Thus

247    $\sigma_a^2 = \sigma_{a_0}^2 + \sigma_{a_h}^2 h^2 + 2\sigma_{a_0 a_h} h = \sigma_{a_0}^2 + \sigma_{a_h}^2 h^{*2} \sigma_h^2 + 2\sigma_{a_0 a_h} h^* \sigma_h$, where σ_h^2 was the empirical variance of

248   the estimated herd-year effect using M1, the variance of true herd-year effect using M2, and the

249   variance of herd-year average using M3.

250

251   **Results**

252   Shown in Table 1 are correlations between the true and herd-year effects estimated with the

253   proposed method and estimated using phenotypic means. The correlation between true value of

254   herd-year effects and herd-year averages was significantly lower than 1 (0.901 averaged over 20

255   replicates). On the other hand, the proposed method resulted in a correlation between estimated

256   herd-year effects and the true values of 0.970, averaged over the 20 replicates. Thus the phenotypic

257   mean was a poorer estimator of herd-year effects than the estimates derived from the proposed

258   method. In the simulation study the variation of herd-year averages included variation of breeding

259   values across herd-years. Therefore the variance of herd-year averages was larger than the variance

260   of true herd-year effects (by 35%).

261   As shown in Table 2, the proposed method (M1) yields estimates of variance components with

262   no detectable bias, while using herd-year averages as proxies for herd-year effects (M3) resulted in

263   biased estimates. Averaged over the 20 replicates, the variance components estimated from the

264   proposed method and from the model using true herd-year effects as covariates in the reaction norm

265   (M2) resulted in similar inferences. These estimates agreed well with the true values. On the other

266   hand using herd-year averages as covariates in the reaction norm resulted in an overestimation of

267   the variance component associated with "level" ($\sigma_{a_0}^2$) and an underestimation of the variance

268   component associated with the "slope" ($\sigma_{a_h}^2$). These biases were significant. The sampling standard

269   deviation of the estimates of $\sigma_{a_h}^2$ is largest using M1, lowest using M2, and intermediate using M3,

270   while the standard deviation of the estimates of $\sigma_{a_0}^2$ was largest using M3. Mean squared errors

271   favored M1 to M3 in all cases.

272   Estimates of within herd-year heritabilities over different herd-year levels were unbiased for M1

273   and M2, but biased for M3 (Figure 1). Averaged over the 20 replicates, the estimates from the

274   proposed approach (M1) or from a model using true herd-year effects as covariates of reaction norm

275   (M2) agreed well with the true heritabilities in all levels of herd-years. When herd-year averages

276   were used as covariates (M3), the estimate of total additive genetic variance was biased but the bias

277   was less serious than that for $\sigma_{a_h}^2$. The effect of underestimation of σ_h^2 on the total additive genetic

278   variance was partly compensated by the larger variation of herd-year averages (relative to the

279   variance of true herd-year effects). Despite this, the bias was still considerable. As can be seen from

280   Figure 1, estimates of heritabilities derived from M3 were different from the true heritabilities in

281   both quantity and pattern.

282

283   **Discussion**

284   In the present work we describe a method to infer unknown environmental values

285   simultaneously with other parameters in a reaction norm model. Using computer simulation, this

286   method is compared with an approximation traditionally implemented in the literature, whereby the

287   unknown environmental value is replaced by the average of the observations in the appropriate

288   environment. It is shown that the proposed method leads to better inferences than those derived

289   from the approximate method.

290   The variance between herd-year phenotypic means includes a genetic component. As a result,

291   this variance was 35% larger than that of true herd-year effects, and the correlation between the

292   herd-year means and true herd-year effects was 0.901. Taking the herd-year average as a covariate

293   in the reaction norm model resulted also in biased estimation of variance components. The variance

294   component associated with the "slope" (σ_{ah}^2) was underestimated by 42% and that associated with

295   "level" (σ_{a0}^2) was overestimated by 11%.

296　　　The amount and sign of the bias depend on the data and the statistical model. An additional

297　　study was carried out with data simulated from the same sampling model as reported above, but

298　　with the difference that from generation 1 onwards individuals were selected on the basis of their

299　　predicted additive genetic values for "level". The results showed that the correlation between herd-

300　　year averages and true herd-year effects was approximately 0.80 and the variance of herd-year

301　　averages was approximately 5 times larger than the variance of the true herd-year effects. Using the

302　　herd-year average as a covariate of the reaction norm, $\sigma^2_{a_0}$ was overestimated by 50%, while $\sigma^2_{a_h}$

303　　was underestimated by 88%.

304　　　Many approximations and ad-hoc procedures have been reported in previous studies to account

305　　for unknown covariates in reaction norm models. In a study of production and fertility traits in dairy

306　　cattle, Kolmodin et al. (2002) estimated herd-year values using herd-year means computed from

307　　data that had been pre-adjusted for fixed effects other than herd-years. In addition, herd-year values

308　　were estimated using herd-year means that were computed from data including animals with

309　　records in the appropriate herd-year, while dispersion parameters and breeding values were inferred

310　　from data that only included individuals whose sires were to be evaluated. The adequacy of this

311　　approximation could not be tested because it was applied using real (as opposed to simulated) data,

312　　but Kolmodin et al. (2002) made a plea in their conclusion for the development of alternative

313　　procedures that avoid using functions of the data in the sampling model. Calus et al. (2004)

314　　proposed to estimate environment values via an iterative procedure whereby the estimated

315　　environmental effect in a given iteration replaces the value of the covariate in the next. Using

316　　computer simulation, the authors observed a negligible reduction in bias of estimates of variance

317　　components using this approach when compared with the standard use of replacing covariates by

318　　phenotypic averages. They suggested replacing environment values by estimates of herd effects

319　　obtained from a large number of animals per herd, instead of from herd-years, at the cost of losing

320　　information on G x E interaction.

321   The overall picture that emerges is that the conventional approximations do not always produce

322 reliable results, and it is difficult to decide a priori how they behave in any given dataset/modeling

323 scenario. In contrast, the method that we propose here avoids ad-hoc constructs, it is theoretically

324 coherent, easy to implement, and leads to adequate inferences. An important caveat associated with

325 the reaction norm model with unknown covariates is that of identifiability of parameters in the

326 likelihood. This is a technically elaborate problem which is presently under investigation and

327 hopefully will be reported elsewhere.

328

329   **Implications**

330   The reaction norm model is becoming a popular approach for the analysis of G x E interactions

331 because it can deal with a very large number of environmental levels with few parameters. The

332 unknown effects of environments (environmental values) are commonly used as an environmental

333 gradient in reaction norm models. They are typically estimated using the phenotypic means of the

334 environments and subsequently used in lieu of the true, unknown covariates when fitting the model.

335 This approach leads to biased inferences. The present study provides a method to infer parameters

336 in a reaction norm model with unknown environmental values. The proposed method estimates

337 environmental values simultaneously with the other parameters in the reaction norm model. The

338 method was tested using simulated data and it is shown to lead to estimates of parameters with no

339 detectable bias and with smaller mean squared errors than those obtained using the conventional

340 approximations.

341

342

343

343

344 **Literatures Cited**

345 Calus, M. P. L., A. F. Groen, and G. de Jong. 2002. Genotype × environment interaction for protein

346   yield in Dutch dairy cattle as quantified by different models. J. Dairy Sci. 85:3115-3123.

347 Calus, M. P. L., and R. F. Veerkamp. 2003. Estimation of environmental sensitivity of genetic merit

348   for milk production traits using a random regression model. J. Dairy Sci. 86:3756-3764.

349 Calus M. P. L., P. Bijma, and R. F. Veerkamp. 2004. Effects of data structure on the estimation of

350   covariance functions to describe genotype by environment interaction in a reaction norm

351   model. Genet. Sel. Evol. 36:489-507.

352 Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics, 4th ed. Longman

353   Group, Essex.

354 Gianola, D., and R. F. Fernando. 1986. Bayesian methods in animal breeding. J. Anim. Sci. 63:217-

355   244.

356 Karan,D, B. Moreteau, and J. R. David. 1999. Growth temperature and reaction norms of

357   morphometrical traits in a tropical drosophilid: Zaprionus indianus. Heredity, 83: 398-407

358 Kingsolver, J. R., G. J. Ragland, and J. G. Shlichta. 2004. Quantitative genetics of continuous

359   reaction norms: thermal sensitivity of caterpillar growth rates. Evolution. 58:1521-1529.

360 Kolmodin, R., E. Strandberg, P. Madsen, J. Jensen, and H. Jorjani. 2002. Genotype by environment

361   interaction in Nordic dairy cattle studied using reaction norms. Acta Agric. Scand., Sect. A

362   Animal Sci. 52:11-24.

363 Lindley, D., V. and A. F., M. Smith. 1972. Bayes estimates for the linear model. J. R. Stat. Soc.

364   Sect. B 34:1-41.

365 Madsen, P., and J. Jensen. 2004. A user's Guide to DMU, version 6, release 4.5, Danish Institute of

366   Agricultural Sciences, Denmark.

367 Ravagnolo O., and I. Misztal. 2000. Genetic components of heat stress in dairy cattle, parameter

368   estimation. J. Dairy Sci. 83:2126-2130.

369   Sorensen, D. and D. Gianola. 2002. Likelihood, Bayesian, and MCMC Methods in Quantitative

370   Genetics. Springer-Verlag, New York, NY.

Table 1. Correlations between true herd-year effects and herd-year phenotypic means, $r(h, h_m)$, and between true herd-year effects and herd-year effects estimated from the proposed method $r(h, h_E)$, averaged over 20 replicate simulations.

Correlation	mean	Range
$r(h, h_m)$	0.901	0.861 – 0.940
$r(h, h_E)$	0.970	0.955 – 0.980

Table 2.Mean and standard error of estimates of variance components (over 20 replicate

simulations) ($\sigma^2_{a_0}$ =variance of the level and $\sigma^2_{a_h}$ = variance of the slope of additive genetic reaction

norm, σ_{a_0,a_h} = covariance between the level and the slope, and σ^2_e =residual variance).

Model	$\sigma^2_{a_0}$	$\sigma^2_{a_h}$	σ_{a_0,a_h}	σ^2_e
Realized[*]	100.4±0.04	1.01±0.00	5.11±0.06	298.3±0.00
M1	101.7±1.10	1.02±0.03	5.04±0.11	297.1±0.87
M2	99.3±1.05	1.01±0.00	5.00±0.08	298.5±0.87
M3	111.5±1.44	0.58±0.00	3.68±0.11	305.5±0.70

[*]Realized: the variance components were calculated from the realized values of the simulation.

M1: model with unknown covariate of reaction norm (the proposed approach).

M2: model using true herd-year effect as covariate of reaction norm.

M3: model using phenotypic mean of herd-year as covariate of reaction norm.
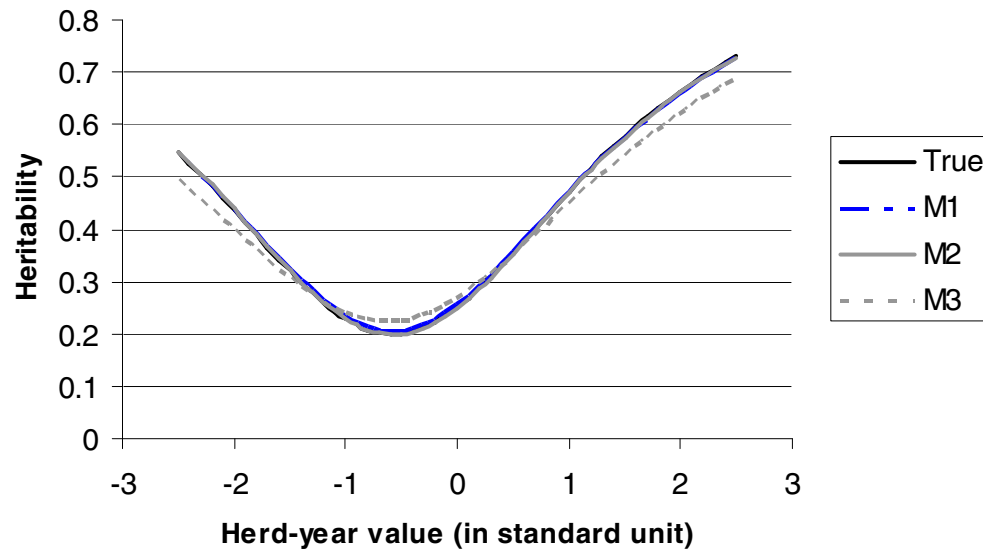
Figure 1. Heritability as a function of herd-year value (covariate of the reaction norm) in unit of standard deviation, based on the true variances (True) and the variances estimated from the model with unknown covariate of reaction norm (M1, the proposed approach), the model using true herd-year effect as covariate of reaction norm (M2), and the model using phenotypic mean of herd-year as covariate of reaction norm (M3).