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Modeling genetic and nongenetic variation of feed efficiency and its partial relationships between component traits as a function of management and environmental factors

Y. Lu,* M. J. Vandehaar,* D. M. Spurlock,† K. A. Weigel,‡ L. E. Armentano,‡ C. R. Staples,§ E. E. Connor,# Z. Wang,|| M. Coffey,¶ R. F. Veerkamp,** Y. de Haas,** and R. J. Tempelman*¹

*Department of Animal Science, Michigan State University, East Lansing 48824

†Department of Animal Science, Iowa State University, Ames 50011

‡Department of Dairy Science, University of Wisconsin, Madison 53706

§Department of Animal Sciences, University of Florida, Gainesville 32611

#Animal Genomics and Improvement Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705

||Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB, T6G 2P5 Canada

¶Animal and Veterinary Sciences Group, Scottish Agricultural College (SAC), Roslin Institute Building, Easter Bush, Midlothian, EH25 9RG, United Kingdom

**Animal Breeding and Genomics Centre, Wageningen UR Livestock Research, 6700 AH Wageningen, the Netherlands

ABSTRACT

Feed efficiency (FE), characterized as the fraction of feed nutrients converted into salable milk or meat, is of increasing economic importance in the dairy industry. We conjecture that FE is a complex trait whose variation and relationships or partial efficiencies (PE) involving the conversion of dry matter intake to milk energy and metabolic body weight may be highly heterogeneous across environments or management scenarios. In this study, a hierarchical Bayesian multivariate mixed model was proposed to jointly infer upon such heterogeneity at both genetic and nongenetic levels on PE and variance components (VC). The heterogeneity was modeled by embedding mixed effects specifications on PE and VC in addition to those directly specified on the component traits. We validated the model by simulation and applied it to a joint analysis of a dairy FE consortium data set with 5,088 Holstein cows from 13 research stations in Canada, the Netherlands, the United Kingdom, and the United States. Although no differences were detected among research stations for PE at the genetic level, some evidence was found of heterogeneity in residual PE. Furthermore, substantial heterogeneity in VC across stations, parities, and rations was observed with heritability estimates of FE ranging from 0.16 to 0.46 across stations.

Key words: dry matter intake, genetic correlation, heritability, hierarchical Bayesian modeling

INTRODUCTION

Feed efficiency (**FE**) is becoming more important for the economic and environmental sustainability of dairy production and increases as a greater proportion of feed nutrients are directed toward milk production (Connor, 2015). A commonly used measure of FE is residual feed intake (**RFI**), which is defined as the difference between actual and predicted DMI. That is, RFI responses are typically derived as the estimated residuals from a linear model analysis whereby partial regression relationships are specified between DMI and energy sink covariates such as milk energy (**MILKE**) and metabolic BW (**MBW**), for example. Given that there has been some reluctance to directly incorporate RFI in breeding goals for several different reasons (Berry and Pryce, 2014), some investigators have focused their attention on DMI as the key phenotype for FE analyses (Berry et al., 2014; de Haas et al., 2015).

Recently, Lu et al. (2015) proposed a multiple-trait (**MT**) mixed model analysis of DMI with MILKE and MBW that further resolves whether RFI or DMI should be considered as the key response variable for FE. They demonstrated that Cholesky decompositions performed on each of the estimated (e.g., by REML) 3×3 genetic and residual variance-covariance matrices among the 3 key traits (MILKE, MBW, and DMI) lead to a parameterization whereby the estimated partial regression relationships between DMI with MILKE, and between DMI with MBW are essentially partitioned into genetic and residual components. Additionally, the Cholesky decomposition leads to a determination of EBV for FE that is identical to that based on a classical RFI analysis under the special case whereby the partial regression

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¹Corresponding author: tempelma@msu.edu

relationships relating DMI to MILKE and to MBW are specified to be identical at both genetic and residual levels. As a corollary, Lu et al. (2015) demonstrated by simulation that the greater the discrepancy between the partial relationships at genetic and nongenetic levels, the greater the EBV accuracy for their proposed MT approach relative to a classical RFI analysis. Furthermore, the MT approach facilitates the incorporation of data on cows that might be missing, even selectively, on any of the 3 key phenotypes that would otherwise be discarded in a RFI analysis (Pollak et al., 1984).

A hierarchical Bayesian extension of a 2-trait MT model was developed earlier in a nongenetic context by (Bello et al., 2010) who later inferred heterogeneous partial regression relationships between calving intervals and milk yield at both herd and cow levels as a function of environmental and herd management factors for Michigan dairy herds (Bello et al., 2012). We surmise that the genetic and residual partial relationships between DMI with MILKE, or between DMI with MBW, could also be modeled as a linked multifactorial function of various factors including parities, research stations, and rations, for example. Indeed, based on station-specific RFI analyses, Tempelman et al. (2015) determined that estimated partial regression coefficients of DMI on MILKE and on MBW were highly heterogeneous across research stations in several countries. Furthermore, adaptation of the hierarchical Bayesian approach as proposed by Bello et al. (2010) would also infer the degree of heterogeneity in heritabilities of FE across different management conditions.

The 2 primary objectives of this study were (1) to identify potential management or environmental factors that might affect genetic and residual partial regression relationships (i.e., partial efficiencies; **PE**) between DMI with MILKE, and between DMI with MBW, and (2) to determine whether there is evidence of heterogeneity of genetic and residual variances for FE across these same management or environmental factors.

MATERIALS AND METHODS

Multiple Trait Model

Our developments closely combine developments provided in Lu et al. (2015) with those provided in Bello et al. (2010). The 3 key component traits of FE are numbered as follows in the MT model: (1) MILKE, (2) MBW, and (3) DMI. We write this MT model as follows:

$$\mathbf{y}_i = \mathbf{X}_i\boldsymbol{\beta} + \mathbf{Z}_i\mathbf{u} + \mathbf{e}_i. \quad [1]$$

Here, $\mathbf{y}_i = [y_{i1} \ y_{i2} \ y_{i3}]'$ is the vector of responses for the 3 traits on record or animal i , $i = 1, 2, 3, \dots, n$. Furthermore, $\boldsymbol{\beta} = [\boldsymbol{\beta}_1' \ \boldsymbol{\beta}_2' \ \boldsymbol{\beta}_3']'$ is the vector of fixed effects connected to \mathbf{y}_i by known incidence matrix $\mathbf{X}_i = (\mathbf{I}_3 \otimes \mathbf{x}_i')$ such that $\boldsymbol{\beta}_j$ denotes the subvector of fixed effects for trait j ($j = 1, 2, 3$). Note that \otimes denotes the Kronecker product such that we assume the same fixed effects incidence row vector \mathbf{x}_i' for each of the 3 traits for ease of presentation, although further generalization is possible. Similarly, $\mathbf{u} = [\mathbf{u}_1' \ \mathbf{u}_2' \ \mathbf{u}_3']'$ is the vector for animal genetic effects connected to \mathbf{y}_i by known incidence matrix $\mathbf{Z}_i = (\mathbf{I}_3 \otimes \mathbf{z}_i')$ such that $\mathbf{u}_j = \{u_{ij}\}_{i=1}^n$ denotes the subvector of random genetic effects on trait j for all n animals. Hence, we also assume the same random effects incidence row vector \mathbf{z}_i' for each of the 3 traits, although again further generalization is possible. To further simplify presentation, we specifically focus on the situation where there is 1 record per animal, and genetic merit is explicitly modeled only for animals having records, although extensions to the more common situation where genetic evaluations are also desired on animals without any records or multiple records is readily apparent. Finally, $\mathbf{e}_i = [e_{i1} \ e_{i2} \ e_{i3}]'$ denotes the sub-vector of residuals for the 3 traits on animal i . Now \mathbf{e}_i is assumed to be independently multivariate normal across animals; that is, $\mathbf{e}_i \sim MVN(\mathbf{0}, \mathbf{R}_i)$, where \mathbf{R}_i denotes the 3×3 residual (co)variance matrix among 3 traits specific for animal i .

Now \mathbf{u} can be alternatively reordered by traits within animals; i.e., $\mathbf{u} = [\mathbf{u}_1 \ \mathbf{u}_2 \ \dots \ \mathbf{u}_n]$ with $\mathbf{u}_i = \{u_{ij}\}_{j=1}^3$ denoting the vector of random genetic effects for the 3 traits on animal i . Because of potential correlations between animal effects due to, for example, the numerator relationship matrix \mathbf{A} , the breeding values \mathbf{u}_i and $\mathbf{u}_{i'}$ for animals i and i' ($i \neq i'$) are not necessarily independent of each other. To flexibly allow for such correlation as well as for subject-specific genetic trait variances and covariances as developed later, we invoke a Cholesky decomposition on \mathbf{A} , writing $\mathbf{A} = \mathbf{C}\mathbf{C}'$. For clarity of presentation, we specify the dimension of \mathbf{A} as $n \times n$ such that it only pertains to relationships between animals with records; nevertheless, its construction should be suitably based on all available ancestor information. In other words, we define \mathbf{A} as a subset of a larger numerator relationship matrix that involves both animals with records and their ancestors. Nevertheless, if genetic evaluations are also desired on ancestors, the dimensions of both \mathbf{A} and $\mathbf{z}_i' \forall i$ can be augmented accordingly. We define \mathbf{u}_j^* using $\mathbf{u}_j = \mathbf{C}\mathbf{u}_j^*$

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