



An alternative approach to modeling genetic merit of feed efficiency in dairy cattle

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ABSTRACT

Genetic improvement of feed efficiency (FE) in dairy cattle requires greater attention given increasingly important resource constraint issues. A widely accepted yet occasionally contested measure of FE in dairy cattle is residual feed intake (RFI). The use of RFI is limiting for several reasons, including interpretation, differences in recording frequencies between the various component traits that define RFI, and potential differences in genetic versus nongenetic relationships between dry matter intake (DMI) and FE component traits. Hence, analyses focusing on DMI as the response are often preferred. We propose an alternative multiple-trait (MT) modeling strategy that exploits the Cholesky decomposition to provide a potentially more robust measure of FE. We demonstrate that our proposed FE measure is identical to RFI provided that genetic and nongenetic relationships between DMI and component traits of FE are identical. We assessed both approaches (MT and RFI) by simulation as well as by application to 26,383 weekly records from 50 to 200 d in milk on 2,470 cows from a dairy FE consortium study involving 7 institutions. Although the proposed MT model fared better than the RFI model when simulated genetic and nongenetic associations between DMI and FE component traits were substantially different from each other, no meaningful differences were found in predictive performance between the 2 models when applied to the consortium data.

Key words: Cholesky decomposition, feed efficiency, multiple trait model, residual feed intake

INTRODUCTION

Feed efficiency (FE) based on the efficient conversion of feed nutrients into salable milk directly affects the profitability of dairy production. Thus, increasing FE in cattle is important to maximizing dairy production on limited inputs, especially as constraints on feed production become increasingly relevant. In addition, improving FE is also of environmental importance because more nutrients are directed into milk production with less nutrient loss in manure and methane excreted as FE increases (Richardson and Herd, 2004).

A popular measure of FE is residual feed intake (RFI), which is defined as the difference between actual feed intake and that predicted based on requirements for production and maintenance, collectively referred to as the so-called energy sinks (Koch et al., 1963). However, the use of RFI is fraught with additional challenges from conceptual, statistical, and practical perspectives. First, RFI is not an observable trait and hence is challenging to explain to farmers. Second, any regression analysis used to derive RFI implicitly assumes that all of the covariates (i.e., energy sinks) are recorded or known without (or relatively little) measurement error (Carroll et al., 2006), even though typically at least some of the energy sink covariates during various lactational periods may need to be interpolated using random regression analyses (Tempelman et al., 2015). In such cases, the estimates for partial regression coefficients can be inconsistent and badly biased, even with very large data sets (Bekker, 1986; Chesher, 1991). Furthermore, if any of the energy sink covariates are completely missing for a particular animal, none of the records on that animal can be used to derive its RFI. Missing values are inherently common with FE studies given that different sampling frequencies on different traits might be expected, depending upon recording systems, labor support, and the perceived

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greater importance of a higher frequency of recording on some traits (i.e., DMI) compared with others such as BW. Finally, it is well established that the presence of any genetic and residual correlations between DMI and the various energy sink traits might actually distort heritability estimates for RFI (Kennedy et al., 1993) and hence a clear interpretation of those inferences. For these and other reasons, some FE investigators have gravitated toward analyses focusing on DMI rather than focusing on RFI per se (Berry et al., 2014).

Given these limitations of RFI along with an inherent desire to meaningfully characterize FE beyond a selection index involving DMI (Berry and Pryce, 2014), we propose an alternative parameterization for multiple trait (MT) modeling of DMI jointly with key energy sink traits. Our objective is to demonstrate how this parameterization not only leads to a potentially more elegant characterization of FE compared with RFI, but also reconciles approaches focused on the analyses of RFI versus DMI (Berry and Pryce, 2014).

MATERIALS AND METHODS

RFI Model

The typical statistical modeling strategy for RFI includes 2 stages (Berry and Crowley, 2013). For reasons that will be explained later, we will refer to DMI as trait #3 such that y_{i3} represents the DMI record for animal i . In the first stage, DMI, as the energy source, is typically specified as a linear function of various energy sinks plus other fixed or random (non-animal) effects that potentially influence DMI, i.e.,

$$y_{i3} = \mathbf{x}'_i \boldsymbol{\beta}_3^* + b_1 \text{MILKE}_i + b_2 \text{MBW}_i + b_3 \Delta \text{BW}_i + \text{RFI}_i \quad [1]$$

Here $\boldsymbol{\beta}_3^*$ represents a vector of various fixed effects connected to y_{i3} via known incidence row vector \mathbf{x}'_i . Key energy sinks include milk energy (MILKE), metabolic BW (MBW) being defined as BW raised to the 3/4 power, and BW change (ΔBW) all indexed by animal or record i in Equation [1]. Note then that b_1 , b_2 , and b_3 are partial regression coefficients of DMI on energy sinks MILKE, MBW, and ΔBW , respectively. Now RFI_i is merely the estimated residual from model [1], thereby representing the RFI record for subject i ; this variable is further typically specified as the response variable in a second stage variance components model:

$$\text{RFI}_i = \mu^* + \mathbf{z}'_i \mathbf{u}_{\text{RFI}} + \text{other potential random animal effects} + e_{i,\text{RFI}} \quad [2]$$

In Equation [2], μ^* is the overall mean, whereas \mathbf{u}_{RFI} is the animal genetic merit for RFI and connected to RFI_i via known incidence row vector \mathbf{z}'_i . Furthermore, $\mathbf{u}_{\text{RFI}} = \{\mathbf{u}_{\text{RFI},i}\} \sim \text{MVN}(\mathbf{0}, \mathbf{A}\sigma_{\text{uRFI}}^2)$ for \mathbf{A} being the numerator (Henderson, 1976) or genomic (VanRaden, 2008) relationship matrix or a hybrid of the 2 (Aguilar et al., 2010), whereas other potential random animal effects may include permanent environmental effects if more than one record is present per animal. Finally, $e_{i,\text{RFI}}$ is a corresponding residual such that $e_{i,\text{RFI}} \sim e_{i,\text{RFI}} \sim \text{NIID}(0, \sigma_{e_{\text{RFI}}}^2)$.

Conceptually, Equations [1] and [2] could be combined together as one model as shown in Equation [3], thereby reinforcing that RFI is really just an adjusted measure of DMI; i.e.,

$$y_{i3} = \mathbf{x}'_i \boldsymbol{\beta}_3^* + b_1 \text{MILKE} + b_2 \text{MBW} + b_3 \Delta \text{BW} + \mathbf{z}'_i \mathbf{u}_{\text{RFI}} + \text{other potential random animal effects} + e_{i,\text{RFI}} \quad [3]$$

assuming that μ^* from Equation [2] is subsumed into $\boldsymbol{\beta}_3^*$. As argued by Tempelman et al. (2015), analyses based on a single-stage model [3] may be desirable if effects in Equation [1] are not orthogonal to effects in Equation [2].

Proposed MT Model

Our proposed strategy for characterizing FE is based on the square root free or modified Cholesky decomposition (CD; Pourahmadi et al., 2007), which our group has previously adapted for the joint analysis of milk production and reproduction data, albeit in a nongenetic context (Bello et al., 2010). We apply this decomposition on each variance-covariance matrix (e.g., genetic and residual) partition in a MT model analysis on DMI and 2 key energy sink traits (i.e., MILKE and MBW). As with RFI modeling, we prefer to keep ΔBW as a covariate for DMI even in this proposed approach, in part due to its seemingly very low heritability (<1%) and greater relative variability. Statistically, the order for the 3 traits is rather arbitrary; however, for modeling FE, it is necessary to specify DMI as the last trait in the sequence as noted later.

We write the MT linear mixed model for MILKE, MBW, and DMI in order as traits 1, 2, and 3, respectively; extensions to any other number of FE component traits are relatively straightforward, provided again that DMI is specified last. We momentarily assume one record per animal such that the model can be written in a classical quantitative genetics framework as

$$\mathbf{y}_j = \mathbf{X}_j \boldsymbol{\beta}_j + \mathbf{Z}_j \mathbf{u}_j + \mathbf{e}_j \quad [4]$$

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