



Heterogeneity in genetic and nongenetic variation and energy sink relationships for residual feed intake across research stations and countries

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ABSTRACT

Our long-term objective is to develop breeding strategies for improving feed efficiency in dairy cattle. In this study, phenotypic data were pooled across multiple research stations to facilitate investigation of the genetic and nongenetic components of feed efficiency in Holstein cattle. Specifically, the heritability of residual feed intake (RFI) was estimated and heterogeneous relationships between RFI and traits relating to energy utilization were characterized across research stations. Milk, fat, protein, and lactose production converted to megacalories (milk energy; MilkE), dry matter intakes (DMI), and body weights (BW) were collected on 6,824 lactations from 4,893 Holstein cows from research stations in Scotland, the Netherlands, and the United States. Weekly DMI, recorded between 50 to 200 d in milk, was fitted as a linear function of MilkE, $BW^{0.75}$, and change in BW (ΔBW), along with parity, a fifth-order polynomial on days in milk (DIM), and the interaction between this polynomial and parity in a first-stage model. The residuals from this analysis were considered to be a phenotypic measure of RFI. Estimated partial regression coefficients of DMI on MilkE and on $BW^{0.75}$ ranged from 0.29 to 0.47 kg/Mcal for MilkE across research stations, whereas estimated partial regression coefficients on $BW^{0.75}$ ranged from 0.06 to 0.16 kg/kg^{0.75}. Estimated partial regression coefficients on ΔBW ranged from 0.06 to 0.39 across stations. Heritabilities for country-specific RFI were based on fitting second-stage random regression models and ranged from 0.06 to 0.24 depending on DIM. The overall heritability estimate across all research stations and all DIM was 0.15 ± 0.02 , whereas an alternative

analysis based on combining the first- and second-stage model as 1 model led to an overall heritability estimate of 0.18 ± 0.02 . Hence future genomic selection programs on feed efficiency appear to be promising; nevertheless, care should be taken to allow for potentially heterogeneous variance components and partial relationships between DMI and other energy sink traits across environments when determining RFI.

Key words: heritability, international study, random regression model, residual feed intake

INTRODUCTION

Lifetime feed efficiency of dairy cows has increased over the past 60 yr, as cows have produced more milk and thus decreased the portion of feed needed for maintenance. Elite Holsteins currently produce at more than 4 times their maintenance requirement, so the advantage of higher production at the population level to improve biological efficiency in dairy cattle genetics due to the dilution of maintenance costs has been mostly exploited (VandeHaar and St-Pierre, 2006). Further increases in feed efficiency must focus on selecting cows directly for their ability to convert feed to milk production. Feed intake is expensive to collect relative to other economically important traits (e.g., milk yield or reproduction variables); hence, extensive collaboration among researchers is required (Banos et al., 2012). Estimates of genetic parameters (i.e., heritabilities) require large enough sample sizes to facilitate reliable inferences (Klein, 1974), and probably much larger than the few hundred cows that have characterized many previous studies on feed efficiency. Finally, a robust scope of inference necessitates the contribution of data from a broad range of management systems and environments. Understanding the relationships among feed intake and energy outputs in cows across environments is critical to the possible development of successful selection strategies for feed efficiency.

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Residual feed intake (**RFI**) has been proposed as a measure of dairy feed efficiency as an alternative to ratio-based (i.e., input/output) measures, partly because of its ability to take into account changes in energy dynamics over the course of a lactation due to BW changes, for example (Berry and Crowley, 2013). The determination of RFI is typically a 2-step modeling process. The first stage model is an energy sink model (Berry and Crowley, 2013) whereby feed intake, whether recorded as DMI (kg) or energy intake (Mcal), is typically specified as partial linear regression functions of key energy sinks such as milk energy (**MilkE**), metabolic BW (**MBW**) defined as $BW^{0.75}$, BW changes (**ΔBW**), and cohort effects. The resulting estimated residuals from this first stage model are deemed to be RFI phenotypes. These RFI phenotypes are then used as the response variables in a second stage quantitative genetics model to estimate heritabilities and, subsequently, breeding values for feed efficiency.

Heritability estimates for RFI in lactating dairy cattle range widely, from 0.0 to 0.38 in Holsteins, as reported in a review by Berry and Crowley (2013); these estimates are typically smaller than heritability estimates for RFI in growing heifers (Williams et al., 2011; Pryce et al., 2012; Gonzalez-Recio et al., 2014), as further noted by Berry and Crowley (2013). Each lactating RFI study cited in that review was based on limited cow numbers, ranging from 204 (Veerkamp et al., 1995) to 970 (Vallimont et al., 2011). Furthermore, some studies were limited by infrequent (i.e., monthly) recording of DMI (Vallimont et al., 2011). A recent study (Berry et al., 2014) involving nearly 7,000 lactating cows determined an average estimated heritability of 0.34 for DMI; however, heritability estimates for DMI tend to be larger than that for RFI (Berry and Crowley, 2013; Gonzalez-Recio et al., 2014), likely because DMI is strongly genetically correlated with MilkE and BW. Finally, in contrast to some recent work involving DMI (Manzanilla Pech et al., 2014), most quantitative genetic analyses of dairy feed efficiency have not modeled potential DIM-specific genetic effects nor the gradually changing temporal effects that can be inferred upon using random regression model analyses, now considered to be the global standard for genetic evaluation of milk production traits (Schaeffer, 2004).

Berry and Crowley (2013) further cautioned that in some cases RFI may not represent true feed efficiency but can be due, in part, to biases in estimated regression coefficients in the first-stage model resulting from measurement or prediction errors in the covariates. This can consist of several different scenarios, including feed intake not being recorded daily, and different recording frequencies or different types of recording equipment for various traits. Furthermore, the partial regression

relationships between DMI and MilkE, MBW, and ΔBW can be highly heterogeneous across different trials (Davis et al., 2014). Finally, heterogeneous variances might exist across regions or herds such that, without accounting for it, the estimated genetic merit of RFI could be inflated in high-variance regions but be unduly muted in low-variance herds (Hill, 1984).

Our long-term goal is to develop breeding strategies for dairy feed efficiency. As a step toward that goal, we pooled data from several research stations across 3 countries to address several key research questions pertinent to a quantitative genetic analysis of RFI. Because of its implications for deriving RFI phenotypes, our first objective was to characterize any potential heterogeneity in the partial regression coefficients of DMI on various energy sinks (i.e., MilkE, MBW, ΔBW) across research stations or studies. Our second objective was to determine how genetic and permanent environmental variability in RFI might vary across stage of lactation, separately by country, and jointly together.

MATERIALS AND METHODS

Data

Milk yields (**MY**), DMI, BW, fat (**FAT%**), protein (**PROT%**), and lactose (**LACT%**) components, were collected from Holstein cows on research stations within 3 countries: the United States (**US**), the Netherlands (**NL**), and the United Kingdom (**UK**). Data from US were derived from 6 research stations: Iowa State University (**ISU**; Ames), Michigan State University (**MSU**; East Lansing), the University of Florida (**UF**; Gainesville), the University of Wisconsin-Madison (**UW**), the United States Dairy Forages Research Center (**FRC**; Madison, WI), and the USDA Animal Genomics and Improvement Laboratory (**AGIL**; Beltsville, MD). Some of the data provided by ISU has been analyzed previously and described in more detail by Spurlock et al. (2012) and Yao et al. (2013), whereas some of the UW data has been analyzed previously as well (Ferraretto et al., 2011; Ferraretto et al., 2012; He et al., 2012). Data from AGIL were previously analyzed by Connor et al. (2013).

Data from NL were derived from 4 primary experimental herds and studies: (1) an experimental herd 't Gen (**TGEN**) in Lelystad previously described by Veerkamp et al. (2000) and Banos et al. (2012), (2) the Nij Bosma Zathe (**NBZ**) herd located near Leeuwarden and also previously described by Banos et al. (2012), (3) a third study (**ZOM**) based on the work by Zom et al. (2012), and (4) a compilation of studies labeled **NLN** based on data collected from various nutritional experiments. Data on all variables (i.e., DMI, MY, BW,

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