Genomic evaluation for feed efficiency in Canadian Holsteins

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Abstract

Genomic evaluation was developed for feed efficiency for Canadian Holsteins, with the first official release in April 2021. The model defines all traits in two periods of first lactation: 5-60 and 61-305 days in milk. Traits are: a) Metabolic Body Weight (MBW), calculated as (body weight)$^{0.75}$; b) Energy Corrected Milk (ECM), calculated as 0.25*Milk + 12.2*Fat + 7.7*Protein; and c) Dry Matter Intake (DMI). All traits are weekly averages expressed in kg/day (ECM and DMI) or kg$^{0.75}$ (MBW). Single-step method is used to fit the multiple-trait linear animal model for 6 traits (ECM, MBW, and DMI, in two DIM intervals) with genotypic information, using the MiX99 software. GEBV of DMI are re-parameterized using linear regressions of DMI on ECM and MBW, giving a measure of feed efficiency (RFI) genetically independent of ECM and MBW. Genetic parameters were estimated using 99,713 weekly records on 4,952 cows. Heritability of RFI was 0.10 and 0.05 for early and later periods in first lactation, respectively, and were smaller than estimates for DMI (0.29 and 0.27). By definition, RFI and the energy sink traits were genetically uncorrelated. Correlations between DMI and RFI were 0.50 and 0.37 for first and second DIM intervals, respectively. Finally, RFI in 5-60 DIM was genetically less correlated with RFI in 61-305 DIM compared to DMI between these two DIM intervals (0.63 vs. 0.88). Estimated breeding values (GEBV) for RFI are reversed in sign and proofs are expressed as RBV (mean = 100 and SD = 5, for base bulls). Proofs for RFI in 61 – 305 DIM, labeled as Feed Efficiency (FE), are considered a principal selection criterion for feed efficiency in Canadian Holsteins. Average reliability of FE for young genomic bulls was 0.41.

Key words: Feed efficiency, single-step genomic evaluation, individual feed intake

Introduction

Feed represents a large proportion of dairy cattle production expenses. Generally, feed efficiency describes units of product output per unit of feed input, with the units generally being mass, energy, protein, or economic value (VandeHaar et al., 2016). Koch et al. (1963) described a measure of feed efficiency, residual feed intake (**RFI**), that is independent of an animal's body size and production level and is considered to represent the inherent variation in basic metabolic processes that determine efficiency. As reviewed by Connor (2015), heritability estimates for RFI in lactating cows range from 0.01 to 0.40. For some time, feed intake was estimated based on body weight (**BW**) and production. However, Gibson (1986)

presented a correlation between true feed efficiency and predicted feed efficiency (derived from BW and production) of 0.84, indicating that there could be value to actually measuring feed intake. In the 1990s, there was great interest from the industry in including feed efficiency in dairy breeding objectives, which motivated various organizations to collect individual feed intake records for research and genetic evaluations, as described in various studies (Van Arendonk et al., 1991; Veerkamp, 1998). Williams et al. (2011) reported that significant variation in RFI exists in growing heifers and that this could be an alternative to indirectly select dairy cows for improved feed efficiency because it is easier to record feed intake in growing heifers. Spurlock et al. (2012)

estimated genetic parameters of various traits associated with energy balance and related traits, including feed intake, production, and gross feed efficiency, and suggested that these traits will likely respond to genetic selection in Holstein cows. A negative genetic correlation was found between gross feed efficiency (defined as the ratio of total ECM yield to total DMI over the first 150 d of lactation) and energy balance (from -0.73 to -0.99), indicating that selection for more efficient cows might increase the likelihood of negative Energy Balance (EB) in early lactation, if it is not properly managed.

In order to optimize selection for feed efficiency, the use of both dry matter intake and predictor traits have been suggested (Veerkamp and Brotherstone, 1997, Berry and Crowley, 2013). Some dry matter intake predictor traits are fat-and-protein corrected milk and live weight (**LW**). As reported by Manzanilla-Pech et al. (2018), using genomics combined with these predictor traits, could be an alternative to optimize selection for feed efficiency.

In Australia, genomic selection for feed efficiency has been implemented since 2015 and has been termed as "Feed Saved" (Pryce et al., 2018). It includes a genomic component for RFI combined with EBV for LW derived from type traits. Feed saved is defined as the amount of feed that is saved through improved metabolic efficiency and reduced maintenance requirements. Feed Efficiency evaluations have also been implemented in 2016 in The Netherlands (CRV, 2018), and in December 2020 in US (CDCB, 2020).

The focus of this paper is to present the implementation of a routine genomic evaluation system for feed efficiency, launched officially in Canada in April 2021 for the Holstein breed.

Materials and Methods

Traits

The Canadian model for feed efficiency defines all traits in two periods of first lactation: 5-60 and 61-305 days in milk. Traits are:

- Metabolic Body Weight (**MBW**), calculated as (body weight)$^{0.75}$;
- Energy Corrected Milk (**ECM**), calculated as 0.25*Milk + 12.2*Fat + 7.7*Protein, and
- Dry Matter Intake (**DMI**).

All traits are weekly averages expressed in kg/day (ECM and DMI) or kg$^{0.75}$ (MBW). A measure of feed efficiency, RFI, is subsequently derived using linear regressions of DMI on ECM and MBW.

Data

The feed efficiency data available at Lactanet includes data from seven herds in five countries within the EDGP project. These herds are: **BELTSVILLE** (USA), **DCRCFOUL** (Denmark), **DRTC** (Alberta, Canada), **ELLINBANK** (Australia), **ELORA** (Ontario, Canada), **POSIEUX** (Switzerland), and **SUNALTA** (Alberta, Canada). Data from an additional seven US herds were recently added to the database. The new herds are: University of Florida (**FL**), Iowa State University (**ISU**), Dairy Research Facility at the Miner Institute (**MINER**), Michigan State University (**MSU**), Purina Animal Nutrition Centre (**PANC**), University of Wisconsin (**UW**), and Virginia Polytechnic Institute and State University (**VT**).

The data are organized in several files including: **Pedigree**, **Calving**, **Production** (milk, fat, protein), and **Event** (body weight, DMI). After merging the Pedigree file with the official Lactanet counterparts, the April 2021 Holstein extract included 22,861,185 Pedigree records; 15,575 Calving records; 821,751 Production records, and 1,123,751 event records. The traits MBW and DMI are standardised within herds to the mean and SD of the ELORA herd.

The final data (after edits) for the co-variance component estimation using June 2020 extract consisted of 99,713 weekly records on 4,952 first lactation cows from 1,101 sires. Distributions of cows, all records, and records with data on a particular trait, by herd, are in Table 1. The data description of the phenotypes

Table 1: June 2020 data (after edits), by herd

Herd[1]	# Cows	# Records	#Records ECM[2]	#Records MBW	#Records DMI	# Cows DMI
BELTSVILLE	691	13,611	12,040	6,719	13,513	683
DCRCFOUL	958	26,592	24,411	25,848	26,391	757
DRTC	427	12,558	4,893	887	11,243	331
ELLINBANK	115	723	621	695	697	115
ELORA	511	14,965	13,319	8,214	8,802	366
FL	202	2,406	2,217	2,039	2,350	202
ISU	722	10,002	7,547	9,131	9,647	721
MINER	21	146	116	84	146	21
MSU	138	1,611	1,501	1,554	1,601	138
PANC	65	1,092	968	1,003	1,091	65
POSIEUX	45	686	486	290	300	28
SUNALTA	300	5,953	5,947	390	387	99
UW	713	8,878	7,318	6,802	8,716	709
VT	45	490	443	476	471	45

[1]See the 'Data' paragraph for the description of the herd codes
[2]ECM = Energy Corrected Milk, MBW = Metabolic Body Weight, DMI = Dry Matter Intake

Table 2: June 2020 data (after edits), by DIM class

Trait[1]/DIM interval	5 – 60 DIM			61 – 305 DIM		
	# Records	Mean	SD	# Records	Mean	SD
ECM	18,923	31.9	6.6	62,934	32.3	6.2
MBW	14,100	115.0	8.7	50,032	122.3	10.2
DMI	20,893	17.4	3.3	64,462	21.3	3.1

[1]ECM = Energy Corrected Milk, MBW = Metabolic Body Weight, DMI = Dry Matter Intake

within two DIM classes (5 – 60 DIM and 61 – 305 DIM) are in Table 2.

The pedigree file for genetic evaluation was created by tracing the ancestry of cows with phenotypes 4 generations back. It resulted in 18,085 animals to be included in the estimation.

Model

The linear animal model for genomic prediction is the same for each of the 6 feed efficiency traits (ECM, MBW and DMI, in 2 DIM intervals), as in Chud et al. (2019). Factors in the model are:

$AGEC$ = Age at calving (6 classes),
$weeklact$ = Lactation week,
YS = Year-Season of calving (4 seasons),
HY = Herd-Year of calving,
a = Additive genetic effect,

pe = Permanent Environmental (**PE**) effect
e = Residual.

All effects except a, pe and e are treated as fixed in the model. In matrix notation, the model can be written as:

$$\mathbf{y} = \mathbf{X\,b} + \mathbf{Z}_1\,\mathbf{a} + \mathbf{Z}_2\,\mathbf{p} + \mathbf{e},$$

where **y** is a vector of observations (traits within DIM intervals within cows), **b** is a vector of all fixed effects, **a** is a vector of animal additive genetic effects, **p** is a vector of PE effects, **e** is a vector of residuals, **X** and $\mathbf{Z}_i$ (i = 1, 2) are respective incidence matrices.

Assumptions are that:

v(**a**) = **H** ⊗ **G**, **H** is a combined pedigree-genotype relationship matrix, **G** is the additive genetic covariance (6x6) matrix;

$v(\mathbf{p}) = \mathbf{I} \otimes \mathbf{P}$, $\mathbf{P}$ is the covariance (6x6) matrix for the PE effect;

$v(\mathbf{e}) = \sum_{i=1}^{N} {}^{+}\mathbf{E}_i$, $\mathbf{E}_i$ is a residual covariance matrix (3x3) for either first or second DIM interval, N is the total number of weekly records. Residuals for traits collected in the same week of lactation were assumed correlated, and uncorrelated otherwise.

Co-variance components of the model for ECM, MBW and DMI were estimated with the Monte Carlo-Expectation Maximization-Restricted Maximum Likelihood- (**MC-EM-REML**) algorithm (Matilainen et al., 2012) implemented in the Mix99 software package (MiX99 Development Team, 2017). The same model as above was used, with the **H** relationship matrix replaced by the additive relationships matrix (**A**).

RFI Derivation

For each DIM interval, let $\mathbf{a} = [a_1, a_2, a_3]'$ represent the EBV for ECM, MBW and DMI, respectively. A linear re-parameterization of these EBV is defined as:

$$\mathbf{a}^* = \mathbf{\Lambda} \, \mathbf{a},$$

with

$$\mathbf{\Lambda} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -L_{31} & -L_{32} & 1 \end{bmatrix},$$

such that $v(\mathbf{a}^*) = \mathbf{G}^* = \mathbf{\Lambda G \Lambda}'$, with a_3^* being uncorrelated with a_1^* and a_2^*. Non-zero elements of $\mathbf{\Lambda}$, L_{31} and L_{32} can be expressed as functions of elements of genetic covariance matrix **G** as:

$L_{31} = (g_{12}*g_{23} - g_{13}*g_{22})/(g_{12}*g_{12} - g_{11}*g_{22})$
$L_{32} = (g_{12}*g_{13} - g_{11}*g_{23})/(g_{12}*g_{12} - g_{11}*g_{22})$,

and they are partial (genetic) regression coefficients of DMI on ECM and MBW. These 2 traits (i.e. ECM and MBW) are often called 'energy sinks'.

The EBV of ECM and MBW remain unchanged, and EBV for DMI is transformed into

$$a_3^* = a_3 - L_{31} \, a_1 - L_{32} \, a_2,$$

which is uncorrelated with EBV for ECM and MBW.

The re-parameterized EBV of DMI are equivalent to genetic RFI, as discussed in Kennedy et al. (1993).

Co-variance components involving RFI can be obtained as:

$$\mathbf{G}^* = \mathbf{\Lambda G \Lambda}',$$
$$\mathbf{P}^* = \mathbf{\Lambda P \Lambda}',$$
$$\mathbf{R}^* = \mathbf{\Lambda R \Lambda}'.$$

The re-parameterization described above can be derived using a recursive model approach (Jamrozik et al., 2017). Let Y_1, Y_2, and Y_3 refer to phenotypes for ECM, MBW and DMI, respectively, and recursive equations (within DIM interval) for the DMI model be:

$Y_1 = \text{fixed}_1 + \text{random}_1 + e_1$
$Y_2 = \text{fixed}_2 + \text{random}_2 + e_2$
$Y_3 = L_{31}* Y_1 + L_{32}* Y_2 + \text{fixed}_3 + \text{random}_3 + e_3$,

with L_{ij} denoting a recursive coefficient parameter (effect of change in trait i caused by the phenotype of trait j). Imposing restrictions on genetic co-variances, i.e. setting $g_{13}^* = g_{12}^* = 0$ of the genetic co-variance matrix $\mathbf{G}^*$ of the recursive model, will lead to exactly the same form of $\mathbf{\Lambda}$ and expressions of co-variance components and EBVs on a recursive scale (RFI), as presented earlier using a simple re-parametrization of EBVs.

The derivations of proxies for RFI were presented in a 'within DIM interval' framework. This can be easy generalized for the current feed efficiency model (involving multiple traits for 2 DIM intervals) by defining $\mathbf{\Lambda}$ as $\sum^{+}\mathbf{\Lambda}_i$. where $\mathbf{\Lambda}_i$ refers to the i-th DIM interval. See Jamrozik et al. (2020) for more details on the RFI derivation.

Genomic Evaluation

As mentioned previously, the single-step method is used to fit the multiple-trait linear animal model for 6 traits (ECM, MBW and DMI, in 2 DIM intervals) with genotypic information via MiX99 software (MiX99

Development Team, 2017). Specifics of the methods can be summarized as below:

1. The reference population is defined as genotyped animals included in the pedigree for the data,
2. The genomic relationship matrix ($\mathbf{G_V}$) is constructed by Van Raden (2008) Method I.,
3. $\mathbf{G_V}$ is blended with the additive relationship matrix ($\mathbf{A}$) assuming that 80% of the total genetic variance was explained by the SNP effects,
4. Scaling of $\mathbf{G_V}$ and $\mathbf{A}$ is performed using the O.F. Christensen method,
5. Groups for unknown parents are not included in the model,
6. SNP effects, to be used for calculating Genomic Estimated Breeding Values (**GEBV**) for genotyped animals not included in the single-step core analysis, are estimated from the GEBV of reference animals (as in Lourenco et al, 2015),
7. Reliability of GEBV is approximated by a weighted (80:20) average of Direct Genomic Value (**DGV**) and animal model reliabilities (Sullivan et al., 2005). DGV reliabilities are calculated using SNP prediction error co-variances with the SNP-BLUP-REL software (Luke, Finland). Animal model reliabilities are calculated based on Effective Daughter Contributions (**EDC**). The EDC software of Sullivan (2010) is used.

GEBV of DMI are re-parameterized, giving a measure of feed efficiency (RFI) that is genetically independent of ECM and MBW, using formulae as below:

$RFI_{5-60} = DMI_{5-60} - 0.203 * ECM_{5-60} - 0.193 * MBW_{5-60}$

$RFI_{61-305} = DMI_{61-305} - 0.484 * ECM_{61-305} - 0.136 * MBW_{61-305}$.

The re-parameterized GEBV of DMI are GEBV of RFI. Reliabilities of GEBV for RFI, being a linear function of three traits, are approximated by a selection index method (Sullivan et al., 2005).

Relative Breeding Values

The sign of evaluations for DMI and RFI is reversed, thus the higher values indicate a better (more desirable) feed efficiency of an animal. All evaluations (six individual traits and two RFI indices) are expressed as Relative Breeding Values (**RBV**) with a mean of 100 and SD = 5 for base bulls (born 2005 – 2014, with an official LPI (Lifetime Performance Index) and the equivalent of an official GEBV for FE). Sire evaluation for all traits is defined as 'Official' when the bull has at least 5 daughters with DMI data and a minimum reliability for GEBV for RFI_{61-305} of 50%.

The overall aim is to select for cows that use less feed at the same level of production and body size after peak of lactation, i.e. to increase cow efficiency of turning feed into energy. It is not aimed at reducing maintenance requirements by lowering body weight. Additionally, a secondary objective is to not target a reduction in feed intake in early lactation when animals usually have a negative energy balance. Consequently, published proofs are for RFI in 61 – 305 DIM, further labeled as Feed Efficiency (**FE**) and are considered as a principal selection criterion for feed efficiency in Canadian Holsteins. Jamrozik and Kistemaker (2020) provide more details on genomic evaluation of Canadian Holsteins for feed efficiency.

Results and Discussion

Genetic Parameters

Estimates of the co-variance components were obtained with 552 iterations of the MC-EC-REML algorithm, assuming the convergence criterion of 1.e-7.

There was a positive relationship among DMI and both energy sink traits across the 1st lactation. The effects of ECM on DMI were stronger in the second part of lactation, with larger absolute values of regression coefficients for ECM. Phenotypic variance of RFI was slightly smaller than the variance of DMI (Table 3). Genetic and PE components of RFI

contributed less to the total variance of RFI than corresponding variance components of DMI, as expected.

Heritability of RFI was 0.10 and 0.05 for early and later lactation, respectively, smaller than estimates for DMI (0.29 and 0.27) (Table 4). This means that a significant portion of genetic variability caused by ECM and MBW was removed by the adjustment of DMI. By definition, RFI and the energy sink traits were genetically uncorrelated. Genetic correlations between DMI and energy sink traits were strong, up to 0.79 for ECM in 61 – 305 DIM. Phenotypically, RFI was also less correlated with energy sinks compared to DMI. Overall, DMI and RFI were not the same traits genetically. Correlations were 0.50 and 0.37 for first and second DIM intervals, respectively. Finally, RFI in 5 - 60 DIM was genetically less correlated with RFI in 61 – 305 DIM compared to DMI in these 2 DIM intervals (0.63 vs. 0.88).

Repeatability of RFI was also reduced compared to repeatability of DMI (Table 5), but to a lesser degree than corresponding heritabilities. Permanent environmental correlations between RFI and energy sinks were weaker than those between DMI and energy sinks. The 2 measures of feed efficiency (DMI and RFI) were environmentally less correlated at 61 – 305 DIM compared to the 5 – 60 DIM interval. Residual correlations between DMI and RFI were strong, 0.87 and 0.75 in 1st and the 2nd DIM interval, respectively. Residuals for traits at 5 – 60 DIM were independent of residuals of traits at 61 – 305 DIM.

Heritability of RFI was comparable to the whole lactation estimates of Lu et al. (2015) (0.16); our estimates of repeatability, however, were slightly lower than those reported in Lu et al. (2015) (0.65). Note that the US estimates for RFI refer to DMI recorded between 50 and 200 DIM and included data from all lactations.

Table 3: Estimates (posterior means) of phenotypic variance and ratios (%) with respect to phenotypic variance for genetic (h^2), permanent environment (pe^2), and residual (e^2) variances

DIM Interval	Trait[1]	Total variance	h^2	pe^2	e^2
	ECM	33.6	33.9	29.8	36.3
	MBW	55.0	56.7	32.7	10.5
5 - 60	DMI	7.9	29.1	31.6	38.0
	RFI	5.9	10.1	35.6	54.2
	ECM	28.0	29.3	37.1	33.6
	MBW	64.1	58.5	32.2	9.2
61 - 305	DMI	10.8	26.9	30.6	42.6
	RFI	8.0	5.0	33.8	61.3

[1]ECM = Energy Corrected Milk, MBW = Metabolic Body Weight, DMI = Dry Matter Intake, RFI = Residual Feed Intake

Table 4: Heritability (diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations (all values x100)

DIM Interval/	Trait[1]	5 - 60				61 – 305			
		ECM	MBW	DMI	RFI	ECM	MBW	DMI	RFI
	ECM	**34**	7	50	0	95	-10	77	11
5 – 60	MBW	11	**57**	74	0	10	96	54	-5
	DMI	36	43	**29**	50	54	65	88	33
	RFI	-14	-14	73	**10**	8	3	31	63
	ECM	54	8	27	0	**29**	-7	79	0
61 – 305	MBW	-5	82	35	-5	1	**59**	44	0
	DMI	31	28	43	19	50	31	**27**	37
	RFI	-11	-7	12	24	-33	-4	59	**5**

[1]ECM = Energy Corrected Milk, MBW = Metabolic Body Weight, DMI = Dry Matter Intake, RFI = Residual Feed Intake

Table 5: Repeatability (diagonal), PE (above diagonal) and residual (below diagonal) correlations (all values x100)

DIM Interval/	Trait[1]	5 - 60				61 – 305			
		ECM	MBW	DMI	RFI	ECM	MBW	DMI	RFI
	ECM	**64**	17	44	-6	73	-2	26	-40
5 – 60	MBW	11	**89**	31	-30	12	81	21	-19
	DMI	17	16	**62**	73	32	24	58	25
	RFI	26	-15	87	**46**	-5	-18	40	56
	ECM	0	0	0	0	**67**	6	51	-41
61 – 305	MBW	0	0	0	0	11	**91**	32	-9
	DMI	0	0	0	0	29	19	**57**	37
	RFI	0	0	0	0	-41	-3	75	**38**

[1]ECM = Energy Corrected Milk, MBW = Metabolic Body Weight, DMI = Dry Matter Intake, RFI = Residual Feed Intake

All genetic correlations among RFI and energy sink traits were, by the definition of the recursive model (and/or the re-parameterization), equal to 0. That means that genetic effects for RFI and energy sink traits were uncorrelated.

Genomic Evaluations

The April 2021 run included 5,325 cows with data (4,585 cows with DMI; 4,313 genotyped cows with data). There were 1,160 sires of those cows with data (934 genotyped sires). In total, there were 19,137 animals in pedigree, and the reference population included 8,375 genotyped animals. There were 298 Holstein sires with official status in the April 2021 run. Few bulls have daughters with feed intake data and reliabilities of FE were lower compared to other traits. Top 100 young GPA (Genomic Parent Average) LPI bulls had an average reliability of 41% (ranging from 36% to 46%). Top 100 Domestic LPI bulls had an average reliability of 51%. Overall, FE had low correlations (less then 0.20) with all other traits evaluated and under selection, in particular 0.09 with both national indexes LPI and Pro$.

Relationships Between sire RBV
and Daughter Phenotypes

Daughter averages for DMI were regressed on sire RBV for FE, to translate RBV expressions to an equivalent expected reduction in DMI of daughters. A 5-point increase in FE (1 SD) has the expected effect of decreasing DMI in daughters by 53 kg between 61-305 DIM, which is approximately a 1% reduction in DMI.

Conclusions

Routine genomic evaluation for feed efficiency was officially implemented in Canada in August 2021 for the Holstein breed. The definition of RFI (and FE), based on partial genetic regressions of DMI on energy sink traits is simple and easy to interpret, it does not require phenotypes for RFI to generate EBVs for this trait, and it is very similar to the classical RFI model based on phenotypes, but with better statistical properties. It can also be easily generalized for any number of energy sink traits.

Acknowledgements

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