Options for Incorporating Feed Intake into National Selection Indexes

S. Meyer,[1] P.R. Amer[1], C. Baes[2], F. Miglior[2,3], C. Richardson[2], E. Wall[4] and M. Coffey[4]
[1] *AbacusBio Limited, 442 Moray Place, PO Box 5585, Dunedin 9058, New Zealand*
[2]*University of Guelph, Guelph, Ontario, Canada*
[3]*Canadian Dairy Network, Guelph, Ontario, Canada*
[4]*SRUC, Easter Bush, Penicuik, Midlothian, Scotland*

Abstract

Feed costs are a significant proportion of total costs in most dairy production systems and there is strong evidence for substantial genetic variation in total feed intake. However, a large component of this variation is unfavorably correlated with important maintenance and production functions of the animal. Ideally, selection indexes for improved feed efficiency would consider total feed intake that explicitly accounts for the feed required for valuable energy sinks such as milk production, high fertility and adequate body reserves. Residual feed intake (RFI), which is defined at the phenotypic level as the difference between actual feed intake and predicted feed intake, is a potential selection criterion to improve efficiency of feed utilization. However, there are other potential approaches that might have desirable attributes when considered in the context of well-established genetic evaluation systems with breeding objective definitions that are accepted by industry. In this study, we used simulations to unravel the complex inter-relationships among traits such as milk production, live weight and total feed intake. Feed intake phenotypes were simulated as a composite of simulated component phenotypes, so that the underlying genetic relationships between total feed intake and other traits of interest in dairy production systems could be specified precisely. Genetic variance components were then estimated on animals simulated from a simple pedigree structure and estimated breeding values (EBVs) were populated into several selection indexes with and without feed intake components included. The performance of each index was measured by comparing the index predictions against the true observed merit of simulated sires. Additionally, we examined how feed intake-based selection indexes would perform when only limited feed records are available because feed intake is not routinely recorded in dairy systems. Our results show that selection indexes that explicitly account for feed intake were more strongly correlated with the true observed merit than a selection criterion that is only parameterized with EBVs for milk production. All indexes that included feed intake parameters were more accurate than our base index (i.e. without feed intake) even under poor data conditions with limited feed intake recording (e.g. when only 10% of daughters were phenotyped for feed intake). Including wasted feed by adjusting total feed intake EBVs for other traits that represent known energy sinks while accounting for differences in EBV reliability would be very simple to deploy and we found that such an index was almost as efficient as our selection indexes for feed intake.

Key words: dairy, farm profitability, feed conversion ratio, feed intake, milk production, residual feed intake, sustainability, wasted feed

Introduction

Improving feed efficiency (i.e. the product output per unit feed input) is a key factor for profitable and sustainable dairy farming (Pryce *et al.*, 2014; VandeHar *et al.*, 2015; Hietala & Juga, 2017), such as reducing feed costs and GHG emissions (Connor, 2015). For example, 50 to 60% of dairy farm costs are due to feed (Knoblauch *et al.*, 2012) and between 3 and 12% of consumed energy (in ruminants) is released into the atmosphere (Beauchemin & McGinn, 2008).

Residual feed intake (RFI) is defined as the difference between the actual feed intake and predicted feed intake (Archer *et al.*, 1999) and therefore reflects feed efficiency that is not linked to feed required for milk production. However, whilst RFI is phenotypically independent of production traits, this is not necessarily true at the genetic level (Kennedy *et* *al.,* 1993). Consequently, estimates of genetic relationships between RFI and production traits are needed to acquire an estimate of genotypic RFI (Kennedy *et al.,* 1993).

Implementing feed intake as a selection criterion is desirable but not without challenges because traits already in the index may have some value associated with feed intake that must be removed. Therefore, rebuilding the existing genetic evaluation system and breeding objective, to include feed intake breeding values, could be disruptive to existing industry genetic evaluation structures. In contrast, RFI provides the opportunity to create a novel selection criterion to independently select for RFI (Hietala & Juga, 2017) without the need for adjusting existing indexes (e.g. to avoid double counting of penalties associated with economic values for already implemented traits (Richardson *et al.,* 2017)). However, residual feed intake is not universally accepted as the correct approach to deal with feed intake records and can be difficult to explain to farmers.

The objective of this simulation study was to evaluate alternative approaches to the integration of feed intake records into an overall breeding goal so as to maximize accuracy of prediction for overall profitability. Additionally, we simulated and assessed situations where feed intake recording is inconsistent across relatives of different selection candidates.

Materials and Methods

Feed intake phenotypes were simulated as a composite of simulated component phenotypes, such as milk production and feed intake that is not due to milk production (i.e. for maintenance etc.) which we further refer to as wasted feed (WF). Therefore, the underlying genetic relationships between total feed intake and other traits of interest in dairy production systems could be specified precisely. Genetic variance components and estimated breeding values (EBVs) were then calculated on animals simulated from a simple pedigree structure (note, the results of selection index calculations do not depend on the pedigree structure). The EBVs were populated into alternative multi-trait selection index formulations to predict the aggregate merit for each sire in the pedigree structure. These predictions were compared (by calculating the Pearson correlation coefficient) with simulated true genetic merit or TOM for each sire to evaluate the effectiveness of the different index formulations.

Pedigree and phenotype simulations

We simulated a total of 100 replicate pedigrees and associated phenotypes such as milk production. Each replicate contained 8000 individuals composed of 100 sires and 80 female offspring per sire. True breeding values (TBVs) and phenotypes were simulated using phenotypic means and heritabilities provided in Table 1, and genetic and residual correlations shown in Table 2. Subsequently, phenotypes for heifer total feed intake (HFI) and cow total feed intake (in first and second lactation; CTF1 and CTF2, respectively) were derived from relevant component phenotypes (see Appendix). To test for the influence of completeness of total feed records on selection index performance, we cloned each simulated data set but assumed that only 30% and 10% of all daughters were phenotyped for CTF1 (i.e. 70% and 90% of CTF1 records of daughters were randomly set to be missing).

True observed merit

The TOM was derived from simulated TBVs as:

$$TOM = CTF1 * \$A + HFI * \$A * 0.3 + CME1 * \$B * 0.3 + CME2 * \$B * 0.7 + Other * \$C,$$

where $\$A$ (currency: NZD) is the feed associated with producing an extra unit of milk energy multiplied by the price of feed (assumed for simplicity to be -$1), and $\$B$ is the economic revenue per unit of milk energy ($5.5; see Appendix). The values 0.3 and 0.7 reflect the proportion of cows being in first versus second and later lactations, respectively (i.e. we assume that the genetic traits expressed in second lactation cows are identically expressed in third and later lactation cows). The parameter $\$C$ (see Appendix) accounts for the profit through additional traits that were not explicitly simulated in this analysis.

Selection indexes

Variance components and EBVs were estimated from the simulated data with REML using ASReml 4.1 (Gilmour *et al.,* 2015). The EBVs for CME1, CLW, and various feed intake alternatives (see below) were then used to calculate six selection indexes:

$$I1 = (CME1 * 0.3 + \delta * CME1 * 0.7) * (\$B + \$A) + Other * \$C,$$

$$I2 = (CME1 * 0.3 + \delta * CME1 * 0.7) * \$B + (CTF1 * 0.3 + \varepsilon * CTF1 * 0.7) * \$A + Other * \$C,$$

$$I3 = I1 + RFI1 * \$A,$$

$$I4 = I1 + CLW * \gamma * \$A,$$

$$I5 = I1 + (RFIB1 * 0.3 + \varepsilon * RFI\_B1 * 0.7) * \$A + CLW * \gamma,$$

$$I6 = I1 + (WF * 0.3 + \varepsilon * WF * 0.7) * \$A + CLW * \gamma,$$

where δ and ε denote the linear genetic regression predictor coefficients for CME2 predicted from CME1 and for CTF2 predicted from CTF1, respectively. Both coefficients were estimated with linear regressions of TBVs during first and second lactation and thus were assumed to be known for breeding index calculations. The parameter γ reflects per lactation maintenance feed requirements (158.77 kg) associated with 1 kg heavier live weight multiplied by *$A* (-$1 per kg of feed). RFI1 denotes the residual feed intake during first lactation, which has been estimated from an animal model where total feed intake in first lactation (CTF1) has been adjusted for cow milk energy at first lactation (i.e. CME1 has been used as a covariate for CTF1 variance component estimation). Similarly, RFI_B1 reflects residual feed intake during first lactation but has been additionally adjusted for CLW in addition to CME1.

Indexes I1 and I4 reflect base indexes accounting for feed intake costs (i.e. *$A*) known to be associated with other traits of selection indexes in where there are, as in common practice, no breeding values for feed intake. Index I4 additionally penalizes for the costs of extra cow live weight. In index I2, total feed during first lactation was explicitly included. This places reliance on the feed intake estimated breeding values to account for feed intake in the breeding objective. Selection indexes I3 and I5 penalize for RFI that is adjusted for milk only (RFI1) and RFI that is adjusted for milk and cow live weight (RFI_B1), respectively. As an alternative to adjusting EBVs of CME for CLW (i.e. I2 and I5), we created Index I6 that explicitly includes a parameter for WF efficiency that is a prediction of genetic merit for feed intake that is not due to milk production and live weight (see Appendix), similar to a trait criterion previously described by Richardson *et al.* (2017).

The results reported here are based on EBVs estimated from univariate animal models, because a preliminary analysis showed negligible differences between EBVs (and selection indexes) for the simulated sires derived from univariate models and multivariate BLUPs.

Results & Discussion

Performance among selection indexes

The correlation between selection indexes and TOM were all positive but lowest for our base index I1 (here the correlation coefficient was 0.588; Fig. 1). As per definition, index I1 places strong emphasis on increased CME1 (see methods and Figs. 2C). Note, CLW was not explicitly included in index I1 but genetically correlated (genetic correlation was assumed to be 0.2; Table 2) with CME1, which resulted in a positive correlation between index I1 and CLW (Fig. 2A). Thus, selection towards high CME1 was accompanied by increased CLW (Fig. 2A) and thus index I1 was also positively correlated with CTF1 (Fig. 2D). Therefore, selection for index 1 increases both live weight and milk yield, without any ability to target the wasted feed component of the total variation in feed intake. This shows as an absence of correlation for index I1 with CWF1 (Fig. 2B) and explains why index I1 had the lowest correlation with TOM among all indexes (Fig. 1).

The correlation with TOM significantly increased to 0.638 when cow live weight was included (index I4; Fig. 1). Here, the correlation between the selection index and CLW was negative because index I4 explicitly penalizes for the costs of live weight maintenance (Fig. 2A). However, index I4 was uncorrelated with CWF1 and CTF1 (Figs. 2B and 2D).

The highest correlations with TOM were achieved for indexes that explicitly included total feed intake (index I2), total feed adjusted for milk production (indexes I3 and I5), and wasted feed (index I6). These indexes performed equally well (correlation coefficients ranged between 0.658 and 0.662) when all daughters were phenotyped for CTF1 (Fig. 1). The improved index performance was due to their negative correlation with wasted feed (i.e. higher ranked sires required less wasted feed) (Fig. 2B); their correlations with CTF1 were small (Fig. 2D). As for index I3, these indexes were positively correlated with CME1 (though lower than the TOM correlation with index I1) and negatively correlated with CLW1 (Figs. 2C and 2A, respectively). That means, indexes that include feed information provide good predictors for high milk producing cows that, however, require less feed, hence resulting in lower live weights.

Index performance with incomplete records

Our results show that the performance of (total and residual) feed intake-based selection indexes (indexes I2, I3, I4, and I6) could be compromised by incomplete feed intake information. For example, the original correlation of 0.662 (when all CTF1 records were available) between TOM and index I2 (i.e. explicitly including total feed at first lactation) decreased to 0.644 and 0.628 (absolute change was -0.018 and -0.016, respectively) when only 30% and 10% of daughters were phenotyped for CTF1, respectively (Fig. 3). The correlations between TOM and index I3 changed similarly when CTF1 records were reduced (absolute change was -0.013 and -0.015 when CTF1 records were reduced to 30% and 10%, respectively). For these indexes (I2 and I3) the correlation with CME1 increased when less feed intake records were available and the negative correlation with CLW (note that a positive genetic correlation between CLW and CME1 exists) eroded correspondingly (Figs. 2C and 2A, respectively). In other words, greater emphasis was shifted towards milk production (i.e. both indexes performed similarly to that of index I1) (Fig. 2C) when less feed intake information was populated into the selection index (Fig. 2B and 2D).

In contrast, indexes I5 (i.e. residual feed intake adjusted for milk production and cow live weight) and I6 (i.e. wasted feed included) additionally included information on CLW that has been penalized for its maintenance. In this case, limited CTF1 records reduced the index correlation with CWF1 (Figs. 2D) but the negative correlation with CLW was unaffected and close to the CLW correlation with index I4 (Fig. 2A). Thus, the correlations for the indexes I5 and I6 with CME1 were unaffected by the amount of available feed intake records (Fig. 2C). Correspondingly, indexes I5 and I6 were also affected by incomplete CTF1 data, but were the best performing indexes under poor data conditions (correlations with TOM decreased from 0.660 to 0.651, and from 0.658 to 0.643, respectively; Fig. 3). In this case, the absolute change of correlations was -0.004 and -0.005, and -0.011 and -0.005 for indexes I5 and I6, respectively.

Conclusions

The selection indexes assessed in this study performed differently depending on the extent of recording of feed intake records. In order to avoid rebuilding the existing genetic evaluation system and breeding objective, we advocate to deploy a selection index that adjusts total feed intake estimated breeding values for other traits that represent known energy sinks while accounting for differences in estimated breeding value reliability. We found that such an approach is almost as efficient as the alternative approaches, including for situations where reliability of total feed intake estimated breeding values is highly variable within selection candidates.

Acknowledgements

C. Baes gratefully acknowledges funding from Alberta Innovates Technology Futures, Alberta Milk, the Canadian Dairy Network, and the Ontario Government through the Ontario Centres of Excellence (Ontario Network of Entrepreneurs ONE). We acknowledge partial funding by the Efficient Dairy Genome Project, funded by Genome Canada (Ottawa, Canada), Genome Alberta (Calgary, Canada), Ontario Genomics (Toronto, Canada), Alberta Ministry of Agriculture (Edmonton, Canada), Ontario Ministry of Research and Innovation (Toronto, Canada), Ontario Ministry of Agriculture, Food and Rural Affairs (Guelph, Canada), Canadian Dairy Network (Guelph, Canada), GrowSafe Systems (Airdrie, Canada), Alberta Milk (Edmonton, Canada), Victoria Agriculture (Australia), Scotland's Rural College (Edinburgh, UK), USDA Agricultural Research Service (United States), Qualitas AG (Switzerland), Aarhus University (Denmark).

References

Archer, J., Richardson, E., Herd, R. & Arthur, P. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Australian Journal of Agricultural Research 50*, 147-161.

Beauchemin, K.A. & McGinn, S.M. 2008. Reducing Methane in Dairy and Beef Cattle Operations: What is Feasible? *Prairie Soil Crop 1*, 17-21.

Connor, E. 2015. Invited review: Improving feed efficiency in dairy production: challenges and possibilities. *Animal 9*, 395-408.

DairyNZ. 2015. “Can we select for feed conversion efficiency.” https://www.dairynz.co.nz/news/latest-news/can-we-select-for-feed-conversion-efficiency/. Accessed Sep 08 2017.

Garrick, D., Taylor, J. & Fernando, R. 2009. Deregressing estimated breeding values and weighting information for genomic regression analyses. *Genetics Selection Evolution 41:55*.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Welham, S.J. & Thompson, R. 2015. ASReml User Guide Release 4.1 Structural Specification, VSN International Ltd, Hemel Hempstead, UK.

Hietala, P. & Juga, J. 2017. Impact of inlcudingincluding growth, carcass and feed efficiency traits in the breeding goal for combined milk and beef production systems. *Animal 11*, 564-573.

Kennedy, B.W., Van der Werf, J.H. & Meuwissen, T.H. 1993. Genetic and statistical properties of residual feed intake. *Journal of Animal Science 71*, 3239-3250.

Knoblauch, W.A., Putnam, L.D., Karszes, J., Overton, R. & Dymond, C. 2012. Dairy Farm Management Business Summary, New York State, 2011 *Research Bulletin 2012–01.* Cornell Univ., Ithaca, NY

Pryce, J., Wales, W., de Haas, Y., Veerkamp, R. & Hayes, B. 2014. Genomic selection for feed efficiency in dairy cattle. *Animal 8*, 1-10.

Richardson, C.M., Baes, C.F., Amer, P., Martin, C.P., Osborne, V., Pryce, J.E. & Miglior, F. 2017. (submitted). Determining the economic value of daily dry matter intake and associated methane emissions.

VandeHar, M., Armentano, L., Weigel, K., Spurlock, D., Tempelman, R. & Veerkamp, R. 2015. Harnessing the genetics of the modern dairy cow to continue improvements in feeding efficiency. *Journal of Dairy Science 99*, 4941-4954.

Table 1. Description of values used in phenotype simulation.

Phenotype[1]	h^2	Mean	CV (%)	SD	Unit
HLW	0.3	400	10	40	kg
HWF	0.3	65253.9	5	3262.69	MJME
CLW	0.35	600	8	48	kg
CME1	0.3	47768	10	4776.77	MJME
CME2	0.3	53075	10	5307.52	MJME
CBE1	0.2	8000	10	800	MJME
CBE2	0.2	5000	10	500	MJME
CWF1	0.3	90501.2	5	4525.06	MJME
CWF2	0.3	95264.4	5	4763.22	MJME
Other	0.1	10	10	1	-

[1] Acronyms (in given order) denote heifer live weight, heifer wasted feed, cow live weight, cow milk energy at 1st and 2nd lactation, cow energy released through mobilization at 1st and 2nd lactation, cow wasted feed at 1st and 2nd lactation, and other traits.

Table 2. Genetic (sub-diagonal) and phenotypic (upper triangular) correlations among simulated phenotypes (see Table 1 for phenotype description).

	HLW	HWF	CLW	CME1	CME2	CBE1	CBE2	CWF1	CWF2	Other
HLW	-	0	0.2	0	0	0	0	0	0	0
HWF	0	-	0	0	0	0	0	0.3	0.3	0
CLW	0.8	0	-	0	0	0	0	0	0	0
CME1	0.15	0	0.2	-	0.4	0	0	0	0	0
CME2	0.15	0	0.2	0.85	-	0	0	0	0	0
CBE1	0	0	0	0.3	0.2	-	0.4	0	0	0
CBE2	0	0	0	0.2	0.3	0.85	-	0	0	0
CWF1	0	0.8	0	0	0	0	0	-	0.3	0
CWF2	0	0.8	0	0	0	0	0	0.8	-	0
Other	0	0	0	-0.2	-0.2	-0.2	-0.2	0	0	-

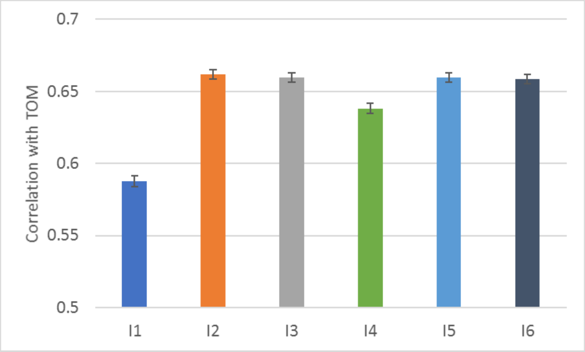

Fig. 1 Average correlation of selection indexes with TOM, the true observed merit (standard errors are shown).

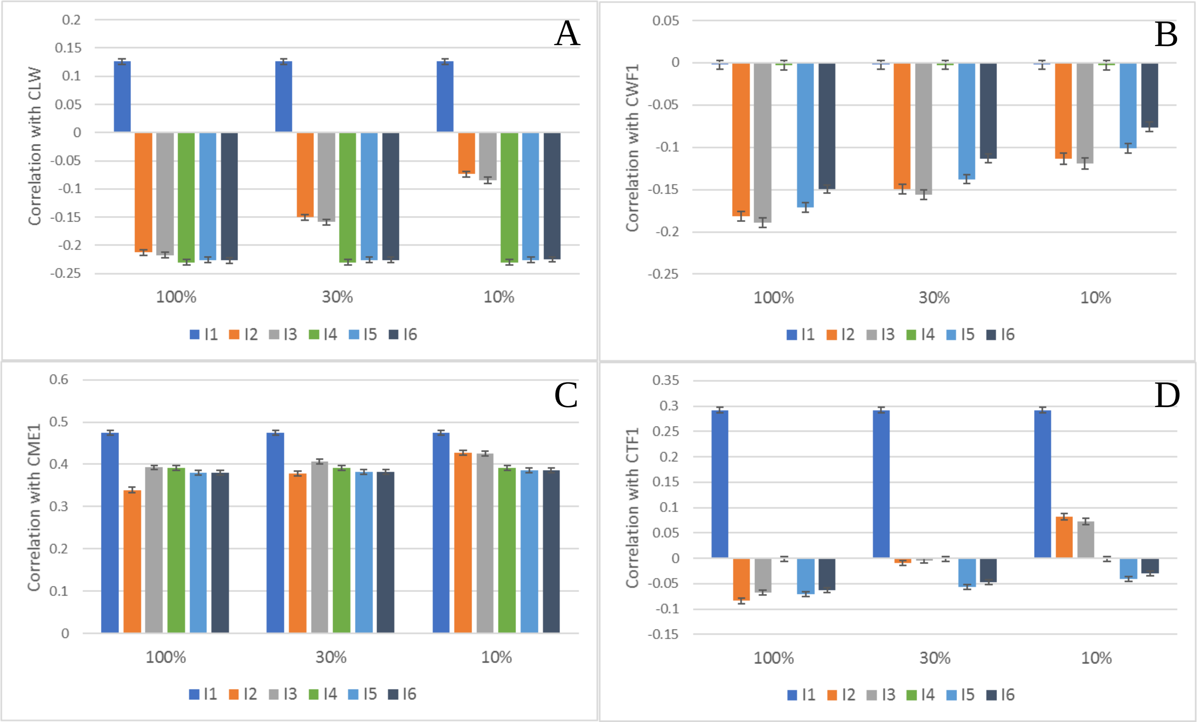

Fig. 2 Average correlation of selection indexes with CLW (panel A), CME1 (panel B), CWF1 (panel C), and CTF1 (panel D); shown are indexes based on EBVs that were estimated from data with 100%, 30%, and 10% of daughters with CTF1 records (standard errors are shown).

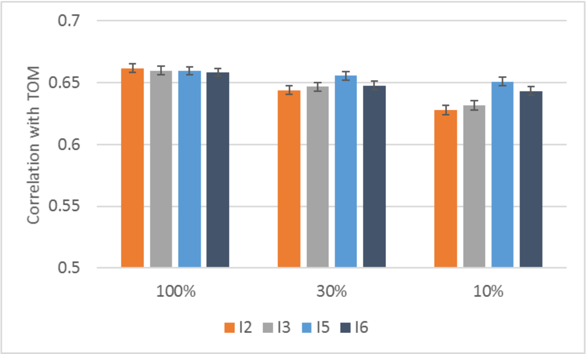

Fig. 3 Average correlation of selection indexes (that include feed intake) with true observed merit (TOM) for different percentages of daughters that were phenotyped for feed intake (standard errors are shown).

Appendix

Derivation of feed intake phenotypes

For heifers, the phenotype for feed intake (HFI) was specified as:

HFI = u_HFI + (TBV_HLW + R_HLW) * k_HLW + TBV_HWF + R_HWF,

where u_HFI denotes the phenotypic mean for heifer feed intake (Table 1); TBV_HLW and TBV_HWF are true breeding values for heifer live weight and heifer wasted feed, respectively. R_HLW and R_HWF denote the residual or environmental effects on heifer live weight and heifer wasted feed, respectively. k_HLW is a scale conversion parameter to convert heifer live weight into feed units (see Table A1).

Individual phenotypes for cow total feed intake (CTF1) at lactation 1 were modelled as:

CTF1 = u_CTF1 + (TBV_CLW + R_CLW) * k_CLW + (TBV_CME1 + R_CME1) * k_CME1 + (TBV_CBE1 + R_CBE1) * k_CBE1 + TBV_CWF1 + R_CWF1,

where u_CTF1 is the phenotypic mean of total feed intake at first lactation (Table 1), and TBV_CLW, TBV_CME1, TBV_CBE1, and TBV_CWF1 are true breeding values for cow live weight, cow milk energy at first lactation, cow energy released through mobilization at first lactation, and cow live weight at first lactation, respectively. R_CLW, R_CME1, R_CBE1, and R_CWF1 denote residual environmental deviates added to each TBV. Phenotypes for cow live weight, milk energy and energy released through mobilization were converted into feed units through the parameters k_CLW, k_CME1, and k_CBE1 (Table A1), respectively. Similarly, we defined phenotypes for cow total feed intake (CTF2) at lactation 2:

CTF2= u_CTF2 + (TBV_CLW + R_CLW) * k_CLW + (TBV_CME2 + R_CME2) * k_CME2 + (TBV_CBE2 + R_CBE2) * k_CBE2 + TBV_CWF2 + R_CWF2 .

Table A1. Scale conversion parameters to derive the feed intake components HFI, CTF1, and CTF2 from simulated component phenotypes.

Description	**Variable**	**Value**
Cow body energy already defined in feed intake units	k_CBE1	1
Cow body energy already defined in feed intake units	k_CBE2	1
Extra kg of total feed energy for a cow for extra 1kg of live weight at maturity	k_CLW	158.77
Cow milk energy already defined in feed intake units	k_CME1	1
Cow milk energy already defined in feed intake units	k_CME2	1
Extra kg of total feed energy for a replacement for extra 1kg at the time when the herd average is 400kg	k_HLW	163.13
Ave total cow feeding intake in L1	u_CTF1	90501.18
Ave total cow feeding intake in L2	u_CTF2	95264.4
Ave Total mean heifer feed intake	u_HFI	65253.87
Cow body energy already defined in feed intake units	k_CBE2	1
Extra kg of total feed energy for a cow for extra 1kg of live weight at maturity	k_CLW	158.774
Cow milk energy already defined in feed intake units	k_CME1	1
Cow milk energy already defined in feed intake units	k_CME2	1
Extra kg of total feed energy for a replacement for extra 1kg at the time when the herd average is 400kg	k_HLW	163.1347
Ave total cow feeding intake in L1	u_CTF1	90501.18
Ave total cow feeding intake in L2	u_CTF2	95264.4
Ave Total mean heifer feed intake	u_HFI	65253.87
Cow body energy already defined in feed intake units	k_CBE2	1

Parametrization of milk (and other traits) profit and feed costs

The economic revenue per unit milk energy (*$B*) has been derived so that the ratio of the milk and feed components would equate to an arbitrary constant of -0.4, implying that the total system cost of feed is roughly 40% of milk income, as follows:

*(CTF1 * $A + HFI * $A * 0.3) / (CME1 * $B * 0.3 + CME2 * $B * 0.7) = -0.4,*

which when solved for *$B* gives

$$\$B = (\$A * (CTF1 + HFI * 0.3)) / (-0.4 * (CME1 * 0.3 + CME2 * 0.7)) \quad .$$

Similarly, the marginal per unit change in profit based on other traits is specified under the assumption that the genetic variance in true merit expressed in dollars due to other traits is about 2/3 of the genetic variance in true merit expressed in dollars for first lactation milk yield as follows:

$$(\$C^2 * h^2\_Other * \sigma^2\_Other) / (\$B^2 * h^2\_CME1 * \sigma^2\_CME1) = 0.66,$$

where h^2_Other and h^2_CME1 are the heritabilities of other phenotypic traits and cow milk energy at first lactation, respectively. Similarly, σ^2_Other and σ^2_CME1 denote genetic variances of both traits. This relationship has been solved for *$C* to give:

$$\$C = \$B * ((0.66 * h^2\_CME1 * \sigma^2\_CME1) / (h^2\_Other * \sigma^2\_Other))^{0.5} \quad .$$

Wasted feed derivation

WF efficiency can be defined as:

$$WF = CTF1 - CME1 * k\_CME1 - CLW * k\_CLW,$$

where we assume the constants k_CME1 and k_CLW known to be 1 and 158.774 (Table A1), reflecting the expected change in total feed intake per unit change in milk production and cow live weight, respectively. Our aim was to obtain EBVs for WF with minimum prediction error variance and being unbiased (i.e. E(EBV_WF) = E(TBV_WF)). For that purpose, we assume that the predictions for CTF1, CME1, and CLW1 are independent (i.e. milk is measured on different animals to what feed intake is measured on, which mean there are no correlated errors of predictions). To predict EBVs for WF based on other phenotypes' EBVs, we first de-regressed the predictors (i.e. CTF1, CME1, and CLW) by dividing each predictor by its reliability (Garrick, Taylor, & Fernando, 2009), the latter derived as:

$$r^2 = 1 - (\sigma\_ebv / n^{0.5}) / \sigma^2\_G,$$

where *σ_ebv* is the standard deviation of EBVs, *n* is the sample size, and σ^2_G denotes the estimated genetic variance. After de-regression we obtain:

$$dEBV\_WF = dEBV\_CTF1 - dEBV\_CME1 * k\_CME1 - dEBV\_CLW * k\_CLW \; .$$

dEBV_WF was converted back on EBV scale as:

$$EBV\_WF = dEBV\_WF * B\_TBV\_WF.dEBV\_WF,$$

where B_TBV_WF.dEBV_WF denotes the regression of the TBV for wasted feed on dEBV_WF which we derived as:

$$B\_TBV\_WF.dEBV\_WF = K`VK/S`VS * r^2\_CTF1$$

where K is a vector with the constants k_CME1 and k_CLW; V denotes a variance covariance matrix for true breeding values for CTF1, CME1, and CLW; and S is given as:

S= [SQRT(((1/R_TF): k1* SQRT(((1/R_1) : k2* SQRT(((1/R_2): …kn* SQRT(((1/R_n)],

with n+1 rows and R_TF is the reliability of total feed, R_1 is the reliability of energy sink trait 1 etc.