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Genetic and phenotypic correlations among feed efficiency, production and selected conformation traits in dairy cows

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The difficulties and costs of measuring individual feed intake in dairy cattle are the primary factors limiting the genetic study of feed intake and utilisation, and hence the potential of their subsequent industry-wide applications. However, indirect selection based on heritable, easily measurable, and genetically correlated traits, such as conformation traits, may be an alternative approach to improve feed efficiency. The aim of this study was to estimate genetic and phenotypic correlations among feed intake, production, and feed efficiency traits (particularly residual feed intake; RFI) with routinely recorded conformation traits. A total of 496 repeated records from 260 Holstein dairy cows in different lactations (260, 159 and 77 from first, second and third lactation, respectively) were considered in this study. Individual daily feed intake and monthly BW and body condition scores of these animals were recorded from 5 to 305 days in milk within each lactation from June 2007 to July 2013. Milk yield and composition data of all animals within each lactation were retrieved, and the first lactation conformation traits for primiparous animals were extracted from databases. Individual RFI over 301 days was estimated using linear regression of total 301 days actual energy intake on a total of 301 days estimated traits of metabolic BW, milk production energy requirement, and empty BW change. Pair-wise bivariate animal models were used to estimate genetic and phenotypic parameters among the studied traits. Estimated heritabilities of total intake and production traits ranged from 0.27 ± 0.07 for lactation actual energy intake to 0.45 ± 0.08 for average body condition score over 301 days of the lactation period. RFI showed a moderate heritability estimate (0.20 ± 0.03) and non-significant phenotypic and genetic correlations with lactation 3.5 % fat-corrected milk and average BW over lactation. Among the conformation traits, dairy strength, stature, rear attachment width, chest width and pin width had significant ($P < 0.05$) moderate to strong genetic correlations with RFI. Combinations of these conformation traits could be used as RFI indicators in the dairy genetic improvement programmes to increase the accuracy of the genetic evaluation of feed intake and utilisation included in the index.

Keywords: conformation traits, correlations, dairy cows, feed efficiency, indirect selection

Implications

Measuring individual feed intake for dairy cows is expensive and difficult because it requires special equipment and has a high cost. Indirect selection based on moderate to strongly correlated indicators, such as conformation traits, could provide an alternative approach to improve individual animal feed utilisation. The results of this research indicated that residual feed intake, an efficiency trait, was moderately genetically correlated with five conformation traits. Combinations of these traits could be considered as indicators of residual feed intake for the genetic improvement of feed intake and utilisation in the dairy genetic evaluation programme.

Introduction

The relatively high cost of measuring individual feed intake is a primary limiting factor for genetic studies on feed efficiency and for implementing effective genetic improvement programmes for dairy feed utilisation (Hüttmann *et al.*, 2008; Tetens *et al.*, 2014; Connor, 2014; Manzanilla Pech *et al.*, 2014). Selection based on indicator traits is an alternative approach to improve individual feed intake and utilisation. Indicator traits can be implemented in the selection index to improve the goal traits when data on primary breeding objectives, such as feed utilisation, are limited. Ideally, indicator trait(s) should be moderately to highly heritable, moderately to strongly genetically correlated with the traits of interest, relatively inexpensive and easy to record (Berry and Crowley, 2013; Manzanilla Pech *et al.*, 2014), as well

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as measurable early in life, specifically before selection decisions are made.

Conformation traits (first classification linear type traits) are heritable (Schaeffer, 1983; Miglior *et al.,* 2008), are routinely recorded in a dairy recording programme mostly during the animal's first lactation, and are easily measurable at a low cost (Canadian Dairy Network, 2006). Researchers (Parke *et al.,* 1999; Vallimont *et al.,* 2010; Berry and Crowley, 2013) are interested in using conformation traits as indicators, especially if these traits are correlated to feed intake and BW, and can therefore be used to improve feed efficiency. For example, genetic and phenotypic parameters among conformation traits with production and common measures of feed efficiency, including feed conversion ratio (FCR) and gross energy efficiency (GEE) in dairy cattle, have been estimated by Van Arendonk *et al.* (1991), Parke *et al.* (1999) and Vallimont *et al.* (2010). These studies showed that combinations of several conformation traits, such as chest width and pin width, may be useful indicators of GEE, FCR and production traits. However, several researchers (Gunsett, 1984; Kennedy *et al.*, 1993; Van der Werf *et al.*, 2004) reviewed the challenges of selection on ratio traits such as FCR and GEE. In addition, Vallimont *et al.* (2011) concluded that estimated genetic parameters for FCR and GEE may be inflated during the lactation period because the contribution of energy from body tissue changes in early lactation is not taken into consideration. To address the problems associated with FCR and GEE, alternative efficiency measures have been proposed (Crews, 2005). The proposed measures could effectively distinguish contributions from different energy sinks to increase the accuracy of evaluating feed intake (Crews, 2005; Vallimont *et al.*, 2011; Connor, 2014).

Residual feed intake (RFI) is an alternative measure for characterising feed efficiency (Koch *et al.*, 1963) and is equivalent to a restricted selection index for decreased feed intake, holding other energy deposition constant (Kennedy *et al.*,1993; Van der Werf *et al.*, 2004). However, RFI prediction still requires the records of individual feed intake, thereby limiting its application in the breeding programme of the dairy industry (Connor, 2014). Identifying indicator traits, such as conformation traits, may increase the chances of adoption of feed utilisation improvement using RFI in multiple trait selection tools for industry-wide application (Berry and Crowley, 2013; Connor, 2014). Recently published reports of parameters between RFI and conformation traits in dairy cattle are generally lacking. Moreover, RFI *per se* is phenotypically independent of production level, but (co)variances involving feed intake are needed to address the potential issues of long term correlated responses on other related economically important traits due to selection for RFI. The objective of this study was to estimate genetic and phenotypic parameters among intake, production, efficiency, and the selected conformation traits.

Material and methods

Data acquisition

A total of 496 repeated records from 260 individual Holstein dairy cows were used in this study from which 260, 159 and 77 of them were first, second and third lactation records, respectively. Individual daily feed intake was recorded from 5 (the first 4 days of colostrum milk were excluded) to 305 days in milk within each parity. BWs and body condition scores (BCS) of all animals were recorded at 5 day after calving and monthly from 5 to 305 days in milk when DHI milk sampled. Methodologies for collecting feed intake, BW and BCS are described in detail by Manafiazar *et al.* (2013). On average, number of observations per cow for feed intake, BW, and BCS were 289, 8 and 8, respectively, over a 301 days lactation period. Data of each animal's milk, fat and protein yield were retrieved from the official Dairy Herd Improvement (DHI) programme. The DHI programme collects individual milk yield and composition every 26 to 35 days in the morning and evening of the test day starting from 5 days after calving. Each animal has up to 10 daily milk yield and composition observations within a standard lactation period (305 days in milk). Daily observations and test day intervals are used to calculate the lactation yield to date. Then, the to-date yield and last test day yield are used to predict 305 days projected milk yield and composition. The last test day closest to 305 days provides the more accurate projected milk yield (Western Canadian Dairy Herd Improvement Services, 2015). In our study, the retrieved 301 days projected milk yield and composition data from DHI database had a minimum accuracy of 0.98 because a minimum of 250 days in milk was considered as the last test day.

Conformation traits (first lactation type classification) records for primiparous animals ($n = 260$) were extracted from the Canadian Dairy Network database. Conformation traits are evaluated at a 7-month interval or 'round' and in most cases each animal is classified one time during its first lactation period (Canadian Dairy Network, 2006). A total of 29 conformation traits are available in the Canadian Dairy Network database from which 24 descriptive traits are recorded on a linear scale ranging from 1 to 9. Then, combinations of different recorded traits are used to derive an extra four composite traits, and these composite traits are used to calculate the overall conformation score (Canadian Dairy Network, 2006). This analysis included 10 descriptive traits out of 24 plus 5 composite traits that were potentially correlated with the RFI component traits (feed intake, BW, and milk production). The 10 selected linear classification traits were stature, height at front, chest width, angularity, body depth, udder depth, udder texture, rear attachment height, rear attachment width and pin width. The five composite (derived) traits were overall conformation, dairy strength, mammary system, rump, and feet and legs.

All procedures involving animals were reviewed and approved by the University of Alberta Animal Care & Use Committee, and all cows were cared for in accordance with the guideline of the Canadian Council on Animal Care (Olfert *et al.*, 1993).

Data preparation

Intake traits. The individual daily dry matter intake was calculated by multiplying daily feed intake (offered minus refused) for each animal by the dry matter content (kg DM/kg as fed) of the diet, while daily actual energy intake was calculated multiplying individual daily dry matter intake by energy density of the diet. In the current study, it was proposed to calculate efficiency traits over the lactation period, with the objective to calculate dry matter intake and energy intake over 301 days of lactation for each animal. All animals had a minimum of 250 intake observations over 301 days. The daily missing values of dry matter intake and actual energy intake for each animal with >250 and <301 observations were predicted using the Legendre polynomial random regression model described by Manafiazar *et al.* (2013). The daily dry matter intake and actual energy intake values over 301 days were summed to give the lactation dry matter intake (LDMI) and lactation actual energy intake (LAEI) for each animal, respectively.

Production traits. Milk yield and composition data obtained from the DHI database were used to derive 301 days total lactation 3.5% fat corrected milk (LFCM) (NRC, 2001) and lactation energy corrected milk (LECM) for 3.5% fat and 3.2% protein (Tyrrell, and Reid, 1965) over 301 days as:

$$\begin{aligned}\text{LFCM (kg)} = {} & [301\,\text{days Milk yield (kg)}] \\ & \times \left[0.423 + \frac{(16.216 \times \text{Fat}(\,\%\,))}{100}\right], \\ \text{LECM (kg)} = {} & [301\,\text{days Milk yield (kg)}] \\ & \times \left[\left(\frac{(12.82 \times \text{Fat}(\,\%\,))}{100}\right)\right. \\ & \left. + \left(\frac{(7.13 \times \text{Protein}(\,\%\,))}{100}\right) + 0.323\right].\end{aligned}$$

Furthermore, average BW (ABW) and BCS (ABCS) within each parity were calculated for each animal over 301 days of lactation.

Feed efficiency traits. Lactation feed conversion ratio (LFCR), gross energy efficiency (LGEE), and RFI over 301 days were considered as lactation feed efficiency traits. Lactation feed conversion ratio was calculated as the ratio of LDMI to LFCM (Crews, 2005), and LGEE was defined as the ratio of LECM to LAEI (Veerkamp and Emmans, 1995). Based on the LFCR and LGEE definitions, efficient animals had lower LFCR but greater LGEE values. The individual lactation RFI within each lactation was calculated based on the methods described by Manafiazar *et al.* (2013). In summary, individual daily actual dry matter intake and monthly BW of animals were recorded from 5 to 305 days in milk, and individual monthly milk yield and composition data were extracted from the DHI Programme. Individual daily dry matter intake and monthly milk yield and composition data were used to derive daily actual energy intake and monthly milk production energy requirement, respectively. Milk production energy requirement was considered as sum of the heat combustion of milk fat, protein and lactose. Moreover, individual monthly BW measurements were used to derive empty BW and metabolic BW. Empty BW was adjusted BW for gut fill using individual dry matter intake in test day and metabolisable energy density of the diet, and metabolic BW was calculated as BW to power of 0.75. In order to account for non-linear profile of the traits, one out of 25 fitted models using Legendre polynomial random regression consisted of fixed (F) and random (R) parts was selected based on log likelihood ratio test and Bayesian information criteria as the best model for each of the traits. The F_5R_3, F_5R_3 and F_5R_2 (subscripts indicate in the order fitted) models were selected for metabolic BW, milk production energy requirement and empty BW traits, respectively, and they were used to predict daily values for the traits. The predicted daily empty BWs were used to calculate daily empty BW change as the differences of two consecutive days over 301 days. Predicted daily values for each trait were summed to calculate the total for that traits over 301 days. Finally, the individual total of 301 days actual energy intake was linearly regressed on a total of 301 days estimated traits of metabolic BW, milk production energy requirement, and empty BW change to obtain the individual RFI over 301 days. The daily average lactation RFI was obtained by dividing the total lactation RFI by days in record for each animal (Manafiazar *et al.*, 2013). In this study, individual RFI over 301 days was calculated, but RFI also could be calculated across a relatively short period, such as weekly; however, Manafiazar *et al.* (2013) described and noted that predicted weekly RFI and then summed weekly RFIs over 301 days had almost identical results with correlation of 0.97 and same animal ranking.

Parameter estimation

A mixed model was implemented using ASREML-W software (Gilmour *et al.*, 2006) to determine significant fixed effects on each of the derived intake, production, efficiency and selected conformation traits. The significant ($P < 0.10$) fixed factors that remained in the model were as follows: overall mean for each trait; year × month, parity and calving age for LDMI and LAEI; total days in milk, year × month, parity and calving age for LFCM, LECM, LFCR and LGEE; days in record and parity for RFI; number of observations and parity for ABW and ABCS; and round and stage of lactation for conformation traits. The stage of lactation was coded in ~30 days intervals starting from calving (Canadian Dairy Network, 2006). Serial pair-wise bivariate animal models were used to estimate heritabilities and phenotypic and genetic correlations for all traits considered in this analysis. The heritability estimate and its associated standard error of estimation for each trait were the average of pair-wised estimates for the same traits in all bivariate models involved in the analyses. Fixed effects were specified for each trait as described above, and random effects were animal additive genetic effect and residual error in the pair-wise models, as well as permanent environment effect specified for traits with repeated records. The additive genetic relationship matrix was constructed based on the pedigree file containing 20 397 animals in which their ancestry was traced back to as many as 47 generations. Initial variance components for the pair-wise bivariate models were obtained from univariate analyses.

Results and discussion

Descriptive statistics

Descriptive statistics for intake, production, and efficiency traits are shown in Table 1. Daily average of LFCM, LDMI, LAEI and ABW were 32.2 (kg), 21.08 (kg), 37.8 (Mcal) and 603.28 (kg), respectively. The greater average LFCM and LDMI in this study compared to other Canadian studies (Moore *et al*., 1990; Parke *et al*., 1999) could be attributed to infrequent measurement (once per month) in this study and genetic and management improvements in the last 23 years. This discrepancy at least partially supported by the 104 kg/cow per day increase in milk production from 1991 to 2013 in Holsteins by Dairy Herd Improvement Program (2013). It may also be inferred that Canadian dairy cattle are under intense selection for milk, fat, and protein production (Parke *et al*., 1999), similar to genetic trends reported in the United States and other countries outside North America.

In addition, primiparous animals consumed less feed, produced less milk, and had lower ABW than multiparous cows, but they had better average feed efficiency (lesser LFCR and greater LGEE) results which were comparable to results reported by Spurlock *et al.* (2012). However, the average of LGEE across parities was greater (0.90 *v.* 0.75) than that reported by Parke *et al*. (1999). This increase could be attributed to the relatively greater milk yield in the current study compared with previous studies. Greater milk yield dilutes the maintenance requirements, and generates positive auto-correlation between milk production and feed efficiency measures (LGEE and LFCR).

All of the linear conformation traits had a scale of 1 to 9, while all the composite traits had a different range. The overall conformation ranged from 640 to 840, and mammary system ranged from 40 to 85; the dairy strength and rump ranged from 46 to 90 and from 50 to 88, respectively. All the ranges were similar to the previously reported ranges on conformation traits in dairy cows (Canadian Dairy Network, 2006; Miglior *et al*., 2008).

Heritabilities

Average estimated heritabilities and their associated standard errors generated from bivariate analyses for intake, production, and efficiency traits are reported on the diagonal of Table 2. Heritability for LAEI (0.27 ± 0.07) was >0.21 reported by Parke *et al*. (1999) and 0.18 reported by Vallimont *et al*. (2010). The relatively greater heritability estimates for intake traits in the current study may reflect the accuracy of individual feed intake measurements, or it may be due to the sampling variance attributable to the present population size and numbers of records.

Estimated heritability for LFCM was similar (0.37 ± 0.05) to that reported in previous studies (0.33) by Lee *et al*. (1992) and Parke *et al*. (1999), but lower than 0.46 reported by Manzanilla Pech *et al*. (2014). In the literature, wide ranges of heritability estimates have been reported for BW (0.23 to 0.60) and BCS (0.08 to 0.60), which varied with stage of lactation (Moore *et al*., 1990; Bewley and Schutz, 2008; Vallimont *et al*., 2010), and our estimates were within the range of previous estimates. Difference between our results and those available in the literature may be due to the average of BW and BCS over the 301 days lactation period being used in our study, rather than within a specific time period used in previous studies. It has also been reported that the heritability estimates of averaged over monthly intervals were greater than daily estimates (Spurlock *et al*., 2012).

Estimated heritability for LFCR (0.25 ± 0.03) in this study was similar to that reported by Parke *et al*. (1999) who also calculated LFCR over 305 days of lactation. However, the estimate of LGEE was lower (0.29 *v.* 0.38) than that reported by Van Arendonk *et al*. (1991), whose study was restricted to the first 15 weeks of lactation rather than over 301 days. This difference could be due to the length of the study period (105 *v.* 301 days), since a range of 0.12 to 0.63 was reported in the literature for feed efficiency traits (FCR and GEE) depending on the stage of lactation (Parke *et al*., 1999). Estimated heritability for RFI over 301 days (0.20 ± 0.03) was similar (0.21) to that reported by Van Arendonk *et al*. (1991) for the first 105 days of lactation, but it was different from the result of Connor *et al*. (2013) at 0.36 during 90 days of early lactation, Vallimont *et al*. (2011) at 0.07 over 305 days of lactation, and pooled estimates of 0.04 reported by Berry and Crowley (2013). The discrepancies between our results with those of Vallimont *et al*. (2011) may be due to frequency of feed intake data where our study measured daily feed intake data on each animal over 301 days and

Table 1 *Descriptive statistics for intake, production, and efficiency traits of dairy cows during lactation (301 days)*

Parity	N	LDMI	LAEI	ABW	ABCS	LFCM	LECM	LFCR	LGEE	RFI
Mean										
1	260	5857.61	10 485.40	566.92	3.05	8893.60	8880.70	0.63	0.90	−0.02
2	159	6773.72	12 125.03	622.90	2.97	10 188.61	10 171.74	0.66	0.89	+0.01
3	77	7170.15	12 834.51	667.32	3.01	10 713.94	10 669.82	0.67	0.87	+0.01
overall	496	6345.72	11 379.92	603.61	3.00	9703.22	9416.58	0.65	0.90	−0.05
Min		4233.26	7168.50	454.00	2.25	4857.53	4840.32	0.47	0.65	−7.06
Max		8758.23	14 116.01	803.30	3.75	13 448.34	13 209.79	1.15	1.17	9.93
SD		838.41	1595.23	62.51	0.22	1882.52	1782.48	0.09	0.09	2.73

LDMI = lactation dry matter intake over 301 days (kg); LAEI = lactation actual energy intake over 301 days (Mcal /kg); ABW = average BW over 301 days (kg); ABCS = average body condition score over 301 days; LFCM = lactation fat corrected milk over 301 days (kg); LECM = lactation energy corrected milk over 301 days (kg): LFCR = lactation feed conversion ratio over 301 days: LDMI/LFCM; LGEE = lactation gross energy efficiency over 301 days: LECM/LAEI; RFI = average residual feed intake over 301 days (Mcal/day); SD = standard deviation.

Table 2 *Heritabilities (diagonal), phenotypic (upper diagonal) and genetic correlations (below diagonal) among intake, production and efficiency traits (± SE) in dairy cattle*

	LDMI	LAEI	ABW	ABCS	LFCM	LECM	LFCR	LGEE	RFI
LDMI	0.28 ± 0.06	0.91 ± 0.05**	0.51 ± 0.05**	−0.04 ± 0.03	0.54 ± 0.05**	0.57 ± 0.05**	0.13 ± 0.05*	−0.17 ± 0.07*	0.49 ± 0.05**
LAEI	0.96 ± 0.03**	0.27 ± 0.07	0.50 ± 0.05**	−0.07 ± 0.06	0.56 ± 0.05**	0.59 ± 0.06**	0.01 ± 0.07	−0.16 ± 0.06**	0.61 ± 0.08**
ABW	0.46 ± 0.22*	0.47 ± 0.13*	0.42 ± 0.05	0.50 ± 0.06**	0.17 ± 0.07*	0.20 ± 0.07**	0.15 ± 0.09	−0.15 ± 0.08	0.06 ± 0.08
ABCS	−0.57 ± 0.21*	−0.57 ± 0.26	0.35 ± 0.22	0.45 ± 0.08	−0.12 ± 0.09	−0.10 ± 0.08	0.15 ± 0.07	−0.11 ± 0.08	−0.12 ± 0.05*
LFCM	0.69 ± 0.10**	0.67 ± 0.15**	−0.21 ± 0.15	−0.07 ± 0.12	0.37 ± 0.05	0.97 ± 0.01**	−0.75 ± 0.03**	0.67 ± 0.04**	0.03 ± 0.05
LECM	0.71 ± 0.15**	0.70 ± 0.14**	−0.28 ± 0.24	−0.06 ± 0.23	0.97 ± 0.03**	0.39 ± 0.05	−0.73 ± 0.04**	0.66 ± 0.04**	0.04 ± 0.06
LFCR	−0.11 ± 0.12	−0.06 ± 0.17	0.18 ± 0.17	0.34 ± 0.14*	−0.78 ± 0.14**	−0.77 ± 0.11**	0.25 ± 0.03	−0.94 ± 0.01**	0.51 ± 0.07**
LGEE	0.13 ± 0.23	−0.18 ± 0.24	0.07 ± 0.15	−0.29 ± 0.13	0.61 ± 0.19**	0.59 ± 0.11**	−0.90 ± 0.07**	0.29 ± 0.02	−0.35 ± 0.06**
RFI	0.51 ± 0.13**	0.64 ± 0.26*	−0.23 ± 0.24	−0.09 ± 0.19	−0.10 ± 0.13	−0.08 ± 0.13	0.33 ± 0.23	−0.57 ± 0.22*	0.20 ± 0.03

LDMI = lactation dry matter intake over 301 days (kg); LAEI = lactation actual energy intake over 301 days (Mcal); ABW = average BW over 301 days (kg); ABCS = average body condition score over 301 days; LFCM = lactation fat corrected milk over 301 days (kg); LECM = lactation energy corrected milk over 301 days (kg); LFCR = lactation feed conversion ratio over 301 days: LDMI/LFCM; LGEE = lactation gross energy efficiency over 301 days: LECM/LAEI; RFI = average residual feed intake over 301 days (Mcal/day).

Diagonal elements are average of heritability estimations from bivariate analysis, and all were significant at $P < 0.01$.

**Statistically significant at $P < 0.01$; *statistically significant at $P < 0.05$.

Vallimont *et al.* (2011) measured feed intake six times over 305 days during lactation. Vallimont *et al.* (2011) have concluded that their method of feed intake measurement was not sensitive enough to capture the difference among the animals in their study. Moreover, the difference between our result with Connor *et al.* (2013) could be due to differences in test length (90 *v.* 301), feed intake data collection methods (automated *v.* manual), BW and BCS data collection intervals (almost 2 weeks *v.* 4 weeks), and other management procedures. However, these results altogether suggest that feed efficiency and of particular interest RFI in dairy cattle could be improved through genetic selection.

Estimated heritabilities for conformation traits are presented in Table 3 and ranged from 0.07 for udder texture to 0.47 for stature. Overall, most of the heritability estimates for the conformation traits considered in this study were greater than those reported by Schaeffer (1983), but comparatively lower than those reported by the Canadian Dairy Network (2007) although the ranking of the estimates by magnitude was similar.

Correlations among intake, production, and efficiency traits

Phenotypic (upper diagonal) and genetic (below diagonal) correlations of production and efficiency traits along with their standard errors are shown in Table 2. It is noteworthy that in some cases standard errors associated with genetic correlation estimates in this study were comparable in magnitude to the correlation estimates themselves, reflecting relatively small numbers of animals used in this study due to limited individual feed intake records available. Greater standard error of estimation, due to limited sample size, causes the genetic correlation not to differ significantly from zero, although their magnitude was greater than zero (Hüttmann *et al.*, 2008; Spurlock *et al.*, 2012). Falconer and Mackay (1996) proposed an equation to calculate the standard error of genetic correlations when the sample size is limited, which is a function of the traits heritabilities, estimates' standard error, and the additive genetic covariance between the traits. We also computed and compared the standard errors of genetic correlations by using Falconer and Mackay (1996) equation, and in all cases the equation yielded slightly lower standard errors compared to the ASREML estimates. However, in order to avoid any possible type I error due to the reduced standard error, we present the resulting estimates from ASREML software. Although we presented all phenotypic and genetic correlation estimates in Tables 3 and 4 for completeness, only the significant ($P < 0.05$) correlation coefficients are discussed here, except for RFI with production traits. In addition, as expected, LDMI with LAEI, LFCM with LECM, and LFCR with LGEE had genetic and phenotypic correlations that were greater than 0.90 or lower than −0.90. Traits with strong phenotypic and genetic correlations, generally 0.90 or −0.9, could be considered genetically equivalent, such that the two traits could share nearly equivalent genetic control and/or an extensive part-whole relationship (Crews *et al.*, 2003). Therefore, among the strongly correlated traits, LDMI, LFCM and LFCR were considered phenotypically and genetically similar to LAEI, LECM and LGEE, respectively, and their association with production, efficiency and conformation traits were discussed hereafter.

There were strong ($P < 0.05$) positive phenotypic (0.54) and genetic (0.69) correlations between LDMI and LFCM, and they were comparable to estimates reported by Van Arendonk *et al.* (1991) and Vallimont *et al.* (2010), implying that strong additive genetic correlation exits between dry matter intake and milk yield (Hüttmann *et al.*, 2008; Spurlock *et al.*, 2012). Lactation dry matter intake and ABW were phenotypically (0.51) and genetically (0.46) correlated ($P < 0.05$), and the correlation estimates were similar to those reported in other studies (Van Arendonk *et al.*, 1991; Vallimont *et al.*, 2010), indicating that animals with greater BW consume more feed. In the present study, LFCM had a positive phenotypic correlation (0.17) with ABW. However, a wide range of genetic correlations (−0.42 to 0.48) between LFCM and BW were reported in the literature (Veerkamp and Emmans, 1995; Parke *et al.*, 1999; Vallimont *et al.*, 2010; Manafiazar *et al.*, 2012). These results all together indicate that large cows may not necessarily produce more milk, and this conclusion is supported by VandeHaar (1998), whose results suggested an optimum point of relationship exists between milk production and BW.

Table 3 *Genetic correlations between conformation traits and intake, production, and efficiency in dairy cattle*

	OC	MS	DS	RU	FL	AN	UD	UT	RAH	RAW	ST	HF	CW	BD	PW
LDMI	0.25**	0.09	0.50**	−0.12	−0.20	0.44**	−0.26**	0.08	0.11	0.51**	0.45**	0.47**	0.68**	0.44**	0.24**
SE	0.09	0.09	0.07	0. 09	0.11	0.09	0.09	0.06	0.09	0.07	0.09	0.09	0.08	0.09	0.09
LAEI	0.23*	0.11	0.45**	0.09	−0.06	0.37**	−0.29**	−0.10	0.08	0.52**	0.47**	0.12	0.55**	0.34**	0.33**
SE	0.09	0.09	0.07	0.09	0.11	0.09	0.09	0.08	0.06	0.07	0.09	0.09	0.08	0.09	0.09
ABW	0.12	0.09	0.39**	−0.05	0.39**	−0.34	−0.08	−0.09	−0.15	0.25	0.54**	0.42**	0.61**	0.22**	0.20**
SE	0.08	0.07	0.07	0.08	0.13	0.18	0.07	0.07	0.08	0.13	0.08	0.07	0.06	0.07	0.07
ABCS	0.07	0.14	−0.03	−0.15	−0.03	−0.41**	0.04	−0.27*	−0.10	0.15	0.07	−0.06	0.35**	−0.06	−0.03
SE	0.08	0.08	0.08	0.09	0.07	0.11	0.08	0.11	0.09	0.08	0.07	0.08	0.08	0.08	0.08
LFCM	−0.15	−0.16	−0.27	0.16	−0.08	0.09	−0.36*	−0.11	0.27	0.29	0.11	−0.19	0.09	−0.22	−0.39*
SE	0.17	0.16	0.15	0.18	0.19	0.18	0.14	0.17	0.19	0.22	0.17	0.16	0.04	0.18	0.16
LECM	−0.05	0.16	−0.04	0.12	0.05	0.11	−0.34*	−0.10	0.23	0.33	0.12	−0.14	0.08	−0.25	−0.36*
SE	0.17	0.15	0.13	0.16	0.11	0.17	0.15	0.18	0.14	0.18	0.17	0.16	0.15	0.18	0.15
LFCR	0.19	0.18	0.37	−0.37	0.37	−0.26	0.32	0.03	−0.39	−0.35	0.33	0.34	0.27	0.37	0.33
SE	0.27	0.21	0.23	0.26	0.23	0.14	0.19	0.11	0.16	0.21	0.19	0.24	0.18	0.20	0.20
LGEE	−0.13	−0.19	−0.19	0.08	−0.27	0.11	−0.32	0.09	0.40	0.41	−0.32	−0.43	−0.18	−0.09	−0.38
SE	0.21	0.26	0.29	0.27	0.18	0.21	0.17	0.22	0.21	0.20	0.20	0.33	0.24	0.26	0.21
RFI	0.15	0.12	0.36**	−0.40	−0.34	0.41	0.14	0.03	0.11	0.45**	0.35**	0.11	0.39**	0.11	0.46**
SE	0.17	0.17	0.14	0.21	0.24	0.20	0.17	0.17	0.17	0.16	0.13	0.17	0.15	0.26	0.17
h^2	0.13	0.21	0.19	0.29	0.11	0.14	0.46	0.07	0.14	0.18	0.47	0.14	0.19	0.30	0.41
SE	0.09	0.08	0.08	0.03	0.03	0.02	0.04	0.03	0.03	0.03	0.10	0.04	0.09	0.08	0.07

LDMI = lactation dry matter intake over 301 days (kg); LAEI = lactation actual energy intake over 301 days (Mcal); ABW = average BW over 301 days (kg); ABCS = average body condition score over 301 days; LFCM = lactation fat corrected milk over 301 days (kg); LECM = lactation energy corrected milk over 301 days (kg); LFCR = lactation feed conversion ratio over 301 days: LDMI/LFCM; LGEE = lactation gross energy efficiency over 301 days: LECM/LAEI; RFI = average residual feed intake over 301 days (Mcal/day); OC = overall conformation; MS = mammary system; DS = dairy strength; RU = rump; FL = feet and LEGS; AN = angularity; UD = udder depth; UT = udder texture; RAH = rear attachment height; RAW = rear attachment width; ST = stature; HF = high at front; CW = chest width; BD = body depth; PW = pin width; SE = Standard error.

**Statistically significant at $P<0.01$; *statistically significant at $P<0.05$.

Table 4 *Phenotypic correlations between conformation traits and intake, production, and efficiency in dairy cattle*

	OC	MS	DS	RU	FL	AN	UD	UT	RAH	RAW	ST	HF	CW	BD	PW
LDMI	0.24**	0.15*	0.39**	0.21**	−0.03	0.23**	−0.13	−0.06	0.07	0.43**	0.32**	0.04	0.35**	0.24**	0.17**
SE	0.06	0.07	0.06	0.07	0.06	0.07	0.07	0.07	0.07	0.05	0.06	0.07	0.06	0.07	0.06
LAEI	0.22**	0.15*	0.41**	0.17**	0.05	0.24**	−0.15*	−0.09	−0.06	0.39**	0.29**	0.05	0.33**	0.21**	0.21**
SE	0.06	0.07	0.06	0.06	0.04	0.06	0.06	0.06	0.06	0.05	0.06	0.07	0.06	0.06	0.06
ABW	0.11	0.08	0.31**	−0.07	0.11	−0.03	−0.05	−0.09	−0.13	0.21	0.45**	0.11	0.42**	0.23**	0.21**
SE	0.06	0.06	0.05	0.06	0.07	0.07	0.06	0.06	0.07	0.10	0.05	0.06	0.05	0.06	0.06
ABCS	0.03	0.09	−0.07	−0.14*	0.05	−0.31**	0.08	−0.21**	−0.07	0.11	−0.03	0.05	0.24**	−0.11	−0.04
SE	0.06	0.06	0.06	0.06	0.07	0.06	0.07	0.06	0.06	0.07	0.07	0.07	0.06	0.06	0.04
LFCM	0.14**	0.18**	0.21**	0.09	0.07	0.25**	−0.24**	−0.02	0.08	0.18**	0.08*	−0.05	0.02	0.15*	0.03
SE M	0.04	0.07	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
LECM	0.15**	0.21**	0.22**	0.10*	0.05	0.24**	−0.23**	−0.03	0.08	0.20**	0.09*	−0.01	0.04	0.09*	0.06
SE	0.04	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.09
LFCR	−0.11	−0.12	−0.14*	−0.08	0.10	−0.26**	0.12	−0.10	−0.11	−0.12	−0.02	0.07	0.11	−0.05	0.07
SE	0.07	0.07	0.07	0.07	0.07	0.07	0.08	0.07	0.07	0.07	0.08	0.07	0.07	0.08	0.07
LGEE	0.08	0.08	0.11	0.03	−0.08	0.20**	−0.11	0.07	0.11	0.14	0.01	−0.08	−0.10	0.02	−0.09
SE	0.07	0.08	0.06	0.07	0.08	0.07	0.08	0.07	0.07	0.08	0.08	0.08	0.07	0.08	0.07
RFI	0.12	0.11	0.14*	0.11	−0.11	0.12	0.04	−0.05	0.11	0.17**	0.12*	0.06	0.17**	0.14**	0.15**
SE	0.07	0.07	0.07	0.07	0.06	0.08	0.06	0.06	0.07	0.06	0.06	0.08	0.06	0.06	0.06

LDMI = lactation dry matter intake over 301 days (kg); LAEI = lactation actual energy intake over 301 days (Mcal); ABW = average BW over 301 days (kg); ABCS = average body condition score over 301 days; LFCM = lactation fat corrected milk over 301 days (kg); LECM = lactation energy corrected milk over 301 days (kg); LFCR = lactation feed conversion ratio over 301 days: LDMI/LFCM; LGEE = lactation gross energy efficiency over 301 days: LECM/LAEI; RFI = average residual feed intake over 301 days (Mcal/day); OC = overall conformation; MS = mammary system; DS = dairy strength; RU = rump; FL = feet and legs; AN = angularity; UD = udder depth; UT = udder texture; RAH = rear attachment height; RAW = rear attachment width; ST = stature; HF = height at front; CW = chest width; BD = body depth; PW = pin width; SE = standard error.

**Statistically significant at $P<0.01$; *statistically significant at $P<0.05$.

Average body condition score had negative (−0.57) and positive (0.34) genetic correlations ($P<0.05$) with LDMI and LFCR, respectively, and it had positive (0.50) phenotypic correlation ($P<0.05$) with ABW. These results were not in agreement with Vallimont *et al.* (2010), who reported genetic correlations of 0.29 and −0.33 between standardised 305 days BCS with dry matter intake and FCM, respectively. The inconsistency of our results with those of Vallimont *et al.* (2010) may be because we used an average BCS over 301 days, rather than analysing standardised 305 days BCS and having different data collection frequency. The positive correlation between ABCS and LFCR in our study suggests that on average, losing BCS may be accompanied with an improvement (decrease) in LFCR. This improvement is supported in a review by Bewley and Schutz (2008) who summarised that losing one unit of BCS would increase milk production by around 2000 kg over a 305 days lactation period, and increase LGEE by 1.5 % (Manafiazar *et al.,* 2012). However, improved LFCR could also be a drawback due to animal losing BCS to support milk production, possibly causing health and reproductive related issues in the animals (Vallimont *et al.*, 2010; Spurlock *et al.,* 2012). Therefore, an alternative measure of efficiency, RFI, has been proposed to minimise the correlated response of selection for efficiency on BCS and energy balance (Spurlock *et al.*, 2012; Connor, 2014). However, ABCS had a favourable significant ($P < 0.05$) phenotypic correlation (−0.12) with RFI, which implies efficient animals may increase their BCS, and this could be considered as an advantage of selection for RFI to overcome any concerns related to efficiency, health, and reproduction. More research in this regard focussed on different stages of lactation is encouraged.

Although LFCR did not have significant correlations with LDMI and ABW, it had significant phenotypic (−0.75) and genetic (−0.78) correlations with LFCM (Table 2). Our results suggested that LFCR was most likely influenced by production (LFCM) rather than by intake (LDMI), which is also supported by the results reported by Parke *et al.* (1999) and Spurlock *et al.* (2012). The above mentioned results indicated that phenotypically and genetically, LFCR would favour the animals with reduced BW to support her milk production, and selection for FCR would not necessarily improve feed efficiency and utilisation (Manafiazar *et al.,* 2012).

RFI, however, had strong ($P < 0.05$) positive genetic (0.51) and phenotypic (0.49) correlations with LDMI, which is supported by reports from other dairy researchers (Van Arendonk *et al.*, 1991; Vallimont *et al.*, 2011). Phenotypic and genetic correlations of RFI with LFCM and ABW were near zero or were not different from zero. Van Arendonk *et al.* (1991) also reported near zero genetic and phenotypic correlations of RFI with both BW and FCM over 105 test day. Phenotypic correlations were expected from the nature of the RFI calculation. However, the genetic correlations results of RFI with ABW and LFCM should be interpreted with caution and warrant further investigations since their magnitudes were large but were not differed from zero due to a large standard error of estimations. The reasons for possible genetic correlations between RFI and production traits have been explained elsewhere by Kennedy *et al.* (1993) and Crews (2005). Kennedy *et al.* (1993) showed that RFI is by definition phenotypically independent of its component traits, but can have a non-zero genetic correlation with production. Subsequently, they proposed an alternative RFI prediction method that utilise genetic information with the resulting metric termed genetic RFI (RFI_g). RFI_g, *per se,* is genetically independent of the production traits, an attribute which has been further discussed by others (Crews, 2005). Therefore, RFI_g may provide breeders with a tool to selection for efficient animals without compromising their production level (Kennedy *et al.*, 1993). Further investigations are encouraged to calculate RFI_g and its potential correlations with other traits.

Correlations of intake, production and efficiency with conformation traits

Genetic and phenotypic correlations between the 15 selected conformation traits and intake, production and efficiency traits are presented in Tables 3 and 4, respectively. Lactation dry matter intake had significant ($P < 0.05$) moderate to strong genetic correlations with pin width, overall conformation, udder depth, body depth, angularity, stature, height at front, dairy strength, rear attachment width and chest width, and ranged from 0.24 to 0.68 (Table 3). A similar trend was observed for phenotypic correlations (Table 4). Berry and Crowley (2013) included chest width and stature in a selection index to predict mature cow feed intake, and they showed that proportion of feed intake genetic variance increased from 0.45 to 0.89 compared to the index containing milk yield and BW. These correlations imply that combinations of most conformation traits could potentially be used as indicator traits for LDMI.

Average BW had significant ($P < 0.05$) moderate to high positive genetic (Table 3) and phenotypic (Table 4) correlations with dairy strength and its component (stature, chest width and body depth) traits. These results were comparable with those reported for similar traits in previous studies (Parke *et al.*, 1999; Berry *et al.*, 2004; Vallimont *et al.*, 2010), and these results suggest the potential for using dairy strength and its component traits to predict phenotypic and genetic variability of BW in dairy cattle

There were significant ($P < 0.05$) moderate negative genetic and phenotypic correlations between ABCS with angularity, udder texture, and positive genetic and phenotypic correlations with chest width (Tables 3 and 4). Angularity and udder texture are traits related to the mammary system and ultimate capacity of milk production, while chest width is a trait related to body size and BW (Canadian Dairy Network, 2006). These correlations showed that animals with greater score of mammary systems tend to lose ABCS, and animals with greater score of chest width tend to have greater ABCS. This correlation confirms our earlier conclusion on relationships between LFCM, ABW and ABCS.

The LFCM was significantly ($P < 0.05$) genetically correlated only with udder depth and pin width (Table 3), but significant ($P < 0.05$) phenotypic correlations existed with several conformation traits ranging from −0.24 to 0.25 (Table 4), including mammary system and its component traits. Short and Lawlor (1992) reported similar phenotypic and genetic correlations between milk yield and the conformation traits of stature, body depth, udder depth and overall conformation.

The LFCR was only significantly phenotypically correlated with angularity (−0.26) and dairy strength (−0.14) (Table 4). LFCR (and LGEE) did not show significant genetic correlations with LDMI and most of the conformation traits. Therefore, we are not in a position to suggest any indicator traits for LFCR and similarly for LGEE from the studied conformation traits.

The RFI was significantly ($P < 0.05$) phenotypically correlated with dairy strength, stature, chest width, rear attachment width, body depth, and pin width ranging from 0.12 to 0.17 (Table 4). Further, RFI had significant ($P < 0.05$) moderate to strong positive genetic correlations ranging from 0.35 to 0.46 with stature, dairy strength, chest width, rear attachment width, and pin width (Table 3). Combinations of these traits may be considered as a useful indicator trait to improve RFI through indirect selection. These traits except rear attachment width are related to body size, and their correlation with RFI implies that animals with high RFI (inefficient) tend to have greater body size. This finding is, partially, counter to our earlier results on the non-significant correlation between RFI with ABW, which implies RFI is independent of BW. This contradiction may results because RFI was directly adjusted for BW but not for body size or conformation traits. However, this contradictory aspect requires further investigation as we discussed earlier. This study attempted to determine the correlation between RFI and various conformation and production traits in dairy cattle where published data are currently unavailable. Thus, we cannot yet offer an extensive direct comparison of the results of this study with other work. Some of the genetic correlations in the current research were associated with a large standard error of estimations, which were caused by relatively smaller sample size ($n = 496$) and family size ($n = 2.16$) limited by individual feed intake data available. A smaller family size means lower genetic connectedness between the animals which reduces additive genetic variance and yields larger standard error of estimations. However, further investigations are encouraged by sharing the data to create a larger sample size to reduce the standard error of estimations, which would consequently validate the results of this study.

Conclusion

Results indicated that RFI was moderately heritable and, as expected, largely reflects the (co)variance structure among component traits. Therefore, there is potential to develop selection tools to improve feed utilisation in dairy cattle using feed intake. Five conformation traits (stature, dairy strength, chest width, rear attachment width, and pin width) had significant moderate to strong genetic correlations with RFI. Their combination may provide useful indicators of RFI in the genetic improvement of feed efficiency in dairy breeding programmes to overcome difficulties and costs associated with recording individual feed intake. It should be noted that RFI had near zero phenotypic correlations with production traits as expected, while having potentially non-zero genetic correlations with production traits. Therefore, animal selection based on phenotypic RFI may raise concerns in a long term response to direct selection, especially with regard to production traits. Future research should focus on using directly economic important dairy traits or their indicators to develop breeding objectives to improve overall profitability with increased selection accuracy.

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