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Research Article

# Genetic Parameters of Residual Energy Intake and Its Correlations with Other Traits in Holstein Dairy Cattle

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**Abstract:** Residual energy intake (REI) or residual feed intake (RFI), defined as the difference between actual energy intake, is predicted on the basis of requirements for maintenance, milk production, and body weight change of an animal. Genetic variation of REI and its relationships with dry matter intake, milk yield, fat corrected milk yield and milk fat, and protein yields was investigated using 3503 monthly records collected from 906 Holstein lactating cows. Variance components were estimated using univariate and multivariate animal models with the derivative-free approach of restricted maximum likelihood algorithm, fitting animal models with fixed effects of herd-year-season, parity number and stage of lactation, and random effects of animal additive genetic and permanent environment. The estimated heritability and repeatability for REI were 0.15 and 0.53 from univariate, and 0.21 and 0.60 from multivariate models, respectively. REI had a genetically weak and negative correlation with yield traits (from -0.05 to -0.08) and a positive correlation with dry matter intake (0.61). Moderate heritability estimate for REI, along with negligible genetic correlations with yield traits and high genetic correlation with dry matter intake, might reveal that selection against REI improves feed efficiency by reducing feed intake and increasing yield traits a little.

Key Words: Residual energy intake, residual feed intake, genetic parameters, dairy cattle

## Introduction

Feed costs represent approximately one-half of the total costs in most livestock operations and 80% of the variable cost of milk production (1). Therefore, improving a cow's biological efficiency for converting feed to milk should be an important goal for the dairy industry and in animal breeding programs.

Energetic efficiency is a common measure of biological efficiency, because energy is the most limiting nutrient for dairy cow, and the intake of which is most closely related to the level of milk production; furthermore, protein is a form of feed energy and accounted for in calculations of energetic efficiency as well (2).

Researchers have proposed several criteria for the measurement of energetic efficiency, including gross energy efficiency and net energy efficiency. Gross efficiency is the percentage of a given category of feed energy recovered in milk (3) and net efficiency is the ratio of energy contained in the milk over the available portion of energy intake used to produce it above maintenance requirements (3,4).

When some traits, such as gross efficiency, net efficiency, or feed conversion ratio, are expressed as a ratio of 2 quantities or characters, we are concerned with 2 possible disadvantages: an increase in the error variance as a proportion of total variance in the statistical analysis, and strong positive phenotypic and genetic correlations between those traits and their components, for example feed efficiency and milk yield (5). Moreover, gross efficiency does not consider the importance of body reserves in energetic efficiency of a lactating cow. To overcome the problems arising from the use of gross or net energy efficiency, an alternative measure of energetic efficiency can be expressed as residual energy intake (REI) or residual feed intake. Residual energy intake seems to have been first proposed by Koch et al. (6).

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Residual energy intake can be defined as the difference between actual energy intake and the one predicted on the basis of requirements for maintenance, lactation, and body weight change of an animal (7-9). Thus, the REI is a measure of efficiency, because animal efficiency increases as the used proportion of energy intake increases or REI decreases.

Several studies have shown the genetic variation of residual energy intake in dairy cattle. Van Arendonk et al. (8) and Kennedy et al. (7) have reported heritability estimates of 0.19 and 0.14, respectively. Veerkamp et al. (9) reported a heritability of 0.30 to 0.38 for residual feed intake, depending on the way of calculating the energy requirements from phenotypic regressions. However, when they estimated the energy requirements, using coefficients based on partial genetic regressions of energy intake on milk energy yield, metabolic live weight, and live weight change, the heritability of residual feed intake was only 0.05. The difference between the estimates of heritability for genetic residual feed intake and phenotypic residual feed intake was a consequence of (i) the antagonistic genetic and environmental correlations between live weight change and energy intake and (ii) a strong bias downwards in the estimation of $h^2$ for genetic residual feed intake (9). On the other hand, Ngwerume and Mao (10) and Svendsen et al. (11) found no evidence for any additive genetic variation in REI, where they have reported heritability estimates of 0.016 and 0.00 – 0.11 for REI, respectively.

Most of the previous studies estimated REI using intrapopulation models. In intrapopulation models, energy or feed requirement and RFI are estimated from the regression of dry matter intake on yield, metabolic body weight, and live weight change, using the same population data. In this procedure, residual feed intakes are equated to the residual errors from the model, so the mean of RFI in such studies is zero and no coefficient of variation is defined (Figure).

The objective of this study was to estimate the degree of genetic variation in REI estimated using an extra-population model and its association with other production traits, and to determine its importance for genetic improvement of feed efficiency in dairy cattle. In extra-population models, different energy requirements and residual energy (feed) intake are estimated using some extra-population models, such as National Research Council (13) and Agricultural and Food Research Council (14) models, so the mean of RFI in such populations may differ from zero.

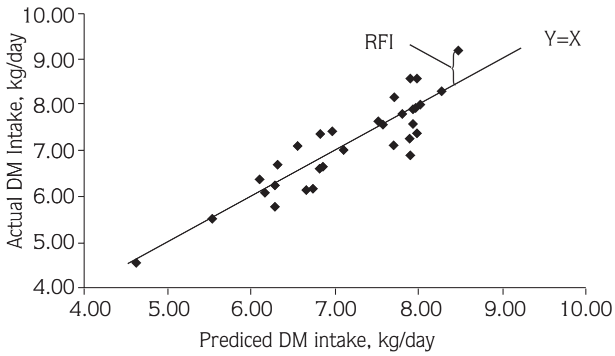


Figure. Actual and predicted dry matter (DM) intakes. Residual feed intake (RFI) is the difference between actual and predicted DM intakes (12)

## Materials and Methods

### Data

The data used in this study were collected from some available lactating Holstein cows of 3 herds. All cows involved in this study were kept in a tie-stall housing system and milked 3 times per day. During the test, animals had ad libitum access to total mixed rations.

Milk production was measured once a week and its composition was determined monthly. Feed intake, as the difference between feed offered and orts, was measured once per week. Cows were weighed and their body conditions were scored once per month. Body condition scores were based on the scoring system of Edmonson et al. (15). The average monthly milk yield and feed intake comprised a record. Because all traits were needed for estimation of energy requirements, records with at least one missed trait were deleted. Thus, 3503 individual monthly records from 906 animals for each trait were used for analysis.

The pedigree of the study included 3238 animals and traced back at least 3 generations. In the pedigree, number of total sires and dams were 549 and 1909, and the numbers of sires and dams with progeny records were 254 and 750, respectively.

### Derivation of traits

The estimation of net energy requirements ($NE_L$) was based on models from National Research Council (13):

Maintenance requirement:

$NE_m$ (Mcal/kg) = $0.079 \times BW^{0.75}$ (kg) where BW = body weight and $BW^{0.75}$ is metabolic body weight. This maintenance requirement includes a 10 percent allowance for activity, which should provide sufficient energy for the usual activity of lactating cows that are fed in individual stalls or dry-lot systems.

Net energy requirement for lactation was defined as the energy contained in the milk produced:

$NE_L$ (Mcal/kg) = (0.0929 × Fat %) + (0.0563 × Crude Protein %) + (0.0395 × Lactose %)

The energy required for gestation was assumed to be 0 when the day of gestation was less than 190. For the days between 190 and 279, $NE_L$ requirement for pregnancy is:

$NE_{preg}$ (Mcal/d) = [(0.00318 × D − 0.0352) × (CBW/45)]/0.218

where D = day of gestation between 190 and 279, and CBW is calf birth weight in kilograms.

Tissue mobilization and repletion during lactation:

The energy value of a kilogram of true body tissue that is lost or gained is dependent on the relative proportions of fat and protein in the tissue and their respective heat of combustion. The proportions of empty body fat and protein were estimated as:

Proportion of empty body fat = 0.037683 × $BCS_{(9)}$

Proportion of empty body protein = 0.200886 − 0.0066762 × $BCS_{(9)}$

where, $BCS_{(9)}$ is body condition score on a 1 to 9 scale.

To determine the total energy contained in 1 kg of reserves, the heats of combustion were multiplied by the estimated proportions of fat and protein:

Total reserves energy (Mcal/kg) = Proportion of empty body fat × 9.4 + Proportion of empty body protein × 5.55

The residual energy intake was estimated as:

$REI = NEI - (NE_m + NE_l + NE_{preg} + BWCE)$

where, NEI is net energy intake, and $NE_m$, $NE_l$, $NE_{preg}$, and BWCE are estimations of energy requirements for maintenance (including activity), lactation, pregnancy and body weight change, all in Kcal/day, respectively.

In addition to REI, other considered traits were dry matter intake (DMI) of feed, milk yield (MY), 4% fat corrected milk yield (FCM), and yields of milk fat (FY) and protein (PY).

Milk yield corrected for 4% fat according to National Research Council (13):

$FCM_{(4\%)}$ = [0.4 × Milk yield (Kg)] + [15 × Fat yield (Kg)]

Analysis

Preliminary analyses using PROC MIXED in SAS (16) were applied to test all potential effects on different traits. The tested potential effects were the fixed effects of herd-year-season, age, parity, lactation stage, pregnancy stage, and random additive genetic effect.

General linear model analysis (16) was employed to determine which effects might best describe the data. The model that best fitted the data, based on the significance of the effects, contained the fixed effects of herd-year-season, parity number, and lactation stage (months after parturition). For the estimation of genetic parameters, random effects of additive genetic and permanent environment for each animal were added. The following animal model was used for all traits:

$Y_{ijklmn} = \mu + HYS_j + P_k + M_l + a_m + PE_m + e_{ijklmn}$

where $Y_{ijklmn}$ is observation jklmn for the trait i; μ is the population mean; $HYS_j$ is the fixed effect of herd-year-season j (1 to 15; years: 2002 – 2003; 3 months per season); $P_k$ is the fixed effect of parity k (1 to 7); $M_l$ is fixed effect of lactation stage l (months 1 to 12 after parturition); $a_m$ and $PE_m$ are random additive genetic effects and permanent environment of $m^{th}$ animal and $e_{ijklmn}$ is random residual effects.

Variance components and genetic parameters of the studied traits were estimated using multivariate and univariate analysis with derivative free approach of restricted maximum likelihood algorithm (17). The DFREML program (18) was run in this respect.

## Results

Over all means and estimates of variance components, heritability and repeatability for different traits, estimated from multivariate and univariate analysis, are shown in Table 1 and Table 2, respectively. In multivariate analysis, REI was moderately heritable ($h^2$ = 0.21). Heritability estimates of other traits including MY, FCM, and PY (0.26, 0.29, and 0.34, respectively) were higher than REI, but DMI and FY had lower heritabilities (0.12 and 0.15, respectively) compared with REI. REI had the highest coefficient of additive genetic variation (45% in multivariate and 36% in univariate analysis) in comparison to other studied traits (Tables 1 and 2).

Estimates for both phenotypic and genetic correlations for different traits are shown in Table 3. Estimates of genetic and phenotypic correlation of REI with yield traits were negative but small. Residual energy intake had genetic correlations from -0.08 to -0.05, and phenotypic correlations from -0.09 to -0.05 with yield traits (Table 3).

## Discussion

Before the estimated parameters are discussed, it should be noted that in most studies on genetic aspects of feed efficiency, because of the difficulties in measuring feed intake, low number of records are used. For example, Buttazzoni and Mao (4), Van Arendonk et al. (8), Ngwerume and Mao (10), and Svendsen et al. (11) used 79, 360, 247, and 353 records from lactating cows, respectively. So estimates of genetic parameters for RFI in such studies, including our study, could not be very accurate, and more studies are needed for more accurate estimates.

The overall mean of REI (4.64 Mcal/d) does not agree with Veerkamp et al. (9) who reported 8.23 MJ (1.97 Mcal) of ME per day for REI. This may be due to differences in, among others, calculation methods, structure of studied populations, production level, and efficiency of the studied population and diets used. Veerkamp et al. (9) calculated the REI considering maintenance, energy yielded as milk and body condition score change, based on partial efficiency values of $k_m$, $k_l$ and $k_f$, respectively, as suggested by Agricultural and Food Research Council (14), whereas, in the present study, the REI was calculated based on the models from National Research Council (13).

Heritability estimates for REI in this study (0.21 from multivariate and 0.15 from univariate analysis) are almost in agreement with heritability estimates of 0.28, 0.19 and 0.14 reported by Madgwick et al. (19), Van Arendonk et al. (8) and Kennedy et al. (7), respectively. However, these estimates are much less than the reported estimation of 0.46 by Archer et al. (20), and higher than the estimates of 0.016 by Ngwerume and Mao, (10) and 0.00 – 0.11 by Svendsen et al. (11). These differences in estimated values of heritability for REI could be attributed to different

Table 1. Overall means, estimates of phenotypic, additive genetic and permanent environment variances ($\sigma^2_P$, $\sigma^2_A$ and $\sigma^2_{PE}$, respectively) and coefficients of additive genetic variation ($CV_A$) for different traits, estimated from multivariate models.

| Traits | Mean | $\sigma^2_P$ | $\sigma^2_A$ | $\sigma^2_{PE}$ | $CV_A$% | $h^2$ | r |
|---|---|---|---|---|---|---|---|
| Residual energy intake (Mcal/d) | 4.64 | 20.6 | 4.41 | 7.88 | 45 | 0.21 ± 0.02 | 0.60 |
| Dry matter intake (kg/d) | 17.79 | 4.6 | 0.57 | 1.94 | 4 | 0.12 ± 0.02 | 0.55 |
| Milk yield (kg/d) | 23.08 | 23.3 | 6.04 | 10.24 | 11 | 0.26 ± 0.06 | 0.70 |
| 4% Fat corrected milk yield (kg/d) | 20.92 | 14.4 | 4.29 | 5.36 | 10 | 0.29 ± 0.03 | 0.67 |
| Fat yield (kg/d) | 0.78 | 0.045 | 0.004 | 0.031 | 9 | 0.15 ± 0.05 | 0.78 |
| Protein yield (kg/d) | 0.69 | 0.019 | 0.006 | 0.007 | 12 | 0.34 ± 0.02 | 0.66 |

Table 2. Estimates of phenotypic, additive genetic and permanent environment variances ($\sigma^2_P$, $\sigma^2_A$ and $\sigma^2_{PE}$, respectively) and coefficients of additive genetic variation ($CV_A$) for different traits, estimated from univariate models.

| Traits | $\sigma^2_P$ | $\sigma^2_A$ | $\sigma^2_{PE}$ | $CV_A$% | $h^2$ | r |
|---|---|---|---|---|---|---|
| Residual energy intake (Mcal/d) | 18.49 | 2.74 | 7.15 | 36 | 0.15 ± 0.06 | 0.53 |
| Dry matter intake (kg/d) | 4.81 | 0.65 | 2.11 | 5 | 0.13 ± 0.03 | 0.57 |
| Milk yield (kg/d) | 26.69 | 13.63 | 6.85 | 16 | 0.51 ± 0.03 | 0.77 |
| 4% Fat corrected milk yield (kg/d) | 18.65 | 8.02 | 6.24 | 14 | 0.42 ± 0.03 | 0.76 |
| Fat yield (kg/d) | 0.032 | 0.011 | 0.015 | 13 | 0.35 ± 0.03 | 0.81 |
| Protein yield (kg/d) | 0.021 | 0.009 | 0.007 | 14 | 0.44 ± 0.03 | 0.76 |

Table 3. The estimations of genetic and phenotypic correlations for residual energy intake (REI), dry matter intake (DMI), milk yield (MY), 4% fat corrected milk (FCM), fat yield (FY) and protein yield (PY), estimated from multivariate models*

| | REI | DMI | MY | FCM | FY | PY |
|---|---|---|---|---|---|---|
| REI | | 0.13 | -0.07 | -0.05 | -0.09 | -0.05 |
| DMI | 0.61 | | 0.15 | 0.13 | 0.06 | 0.08 |
| MY | -0.05 | 0.54 | | 0.39 | 0.19 | 0.44 |
| FCM | -0.08 | 0.43 | 0.94 | | 0.19 | 0.41 |
| FY | -0.07 | 0.15 | 0.41 | 0.69 | | 0.23 |
| PY | -0.05 | 0.25 | 0.96 | 0.95 | 0.56 | |

* Genetic correlations below diagonal and phenotypic correlations above diagonal; approximated standard errors of genetic correlations ranged from 0.01 to 0.05.

calculating methods for REI, different algorithms and models of analysis, and properties of the studied animals and the samples of the population.

As mentioned before, estimates of genetic and phenotypic correlation of REI with yield traits were negative but small; REI had genetic correlations from -0.08 to -0.05, and phenotypic correlations from -0.09 to -0.05 with yield traits. These values of correlation coefficient are so small that REI and yield traits can be considered as independent traits. Low negative genetic correlations of REI with yield traits is confirmed by findings of Van Arendonk et al. (8) who estimated a genetic correlation of -0.12 between REI and milk yield, Veerkamp et al. (9) who reported weak correlations between REI and all yield traits, both genetically and phenotypically, and Madgwick et al. (19) who reported the estimate of -0.05 for genetic correlation of residual feed intake with yield traits. However, Kennedy et al. (7), using simulated data, showed that residual feed intake, based on genotypic regression of feed intake on production, is genetically independent of production.

Residual energy intake had somewhat high positive genetic correlation (0.61) and low positive phenotypic correlation (0.13) with DMI (Table 3). High genetic correlation of REI with DMI in this study (0.61) agrees with the findings of Veerkamp et al. (9), who reported genetic correlations from 0.63 to 0.69, depending on the methods used for calculating REI.

Generally, the aim for providing the genetic parameter estimates is to enable animal breeders to develop strategies for genetic improvement of the whole production system efficiency. Most of the feed efficiency criteria, such as gross efficiency, net efficiency, feed conversion ratio, or milk yield per unit of dry matter intake, are expressed as ratios of 2 or more component traits, while REI is a linear subtraction index. The use of ratio traits (e.g., feed conversion ratio, gross efficiency etc.) for genetic selection represents some problems related to the prediction of change in the component traits in future generations. This is due to the disproportionate fashion by which selection pressure is exerted on the component traits (21). Gunsett (22) compared the efficiency of direct selection for a 2-component trait with a linear index trait derived from the same two components. It was concluded that the use of a linear index increases selection responses as compared with direct selection on the ratio trait.

Little effort has been focused on the amount, or causes, of individual variation in the efficiency of energy utilization by cattle, even though differences among individuals have long been recognized. Observed maintenance requirements and energetic efficiencies, for example, have not been substantially altered during the last 100 years. Reasons for the lack of change in energetic efficiencies include a lack of a consistent selection goal, loose and inconsistent definitions of efficiency, concentration on output characteristics, and emphasis on population similarities rather than individual variation (23). It is time to assess new or different tools and concepts to enhance the efficiency of dietary energy use by dairy cattle.

Hegarty et al. (24) reported that steers selected for residual feed intake did not only have lower daily methane production, but also reduced methane cost of growth. A recent work (25) on Angus steers has provided evidence of increased rate of mitochondrial respiration in low REI steers compared with high RFI steers. Kahi and Hirooka (26) reported that additional genetic gain and profitability are generated when RFI of the cow and feedlot animals are included in the breeding objective with nonzero economic values.

Moreover, genetic correlations between milk yield and reproductive measures in dairy cows are unfavorable. In early lactation, high producing cows are generally in negative energy balance and mobilize body reserves for milk production (27). Negative energy balance may be associated with a higher incidence of metabolic disorders, impaired fertility, and other health problems (28), which suggests that successful selection for higher yields may have led to some problems such as a decline in fertility (29). Thus, selection for improvement of energy efficiency might have some advantages for reducing fertility problems and health disorders.

In this study, low negative or close to zero correlations of REI with yield traits (Table 3) indicate that, by selection on yield traits, reduction of REI is very unlikely. In other words, indirect improvement of REI through selection on yield traits is not easily accessible. On the other hand, REI had a high positive genetic correlation with DMI; however, with regard to positive genetic correlation of DMI with yield traits (Table 3), it seems that selection against DMI reduces yield traits and does not improve feed efficiency.

These evidences show the importance of residual energy intake as a selection criterion for genetic improvement of feed efficiency. However, this is possible where measuring the actual feed intake is feasible, such as some of the dairy farms involved in progeny test schemes.

For a trait to be used as a selection criterion it must present genetic variance and be heritable. Heritability estimate of 0.21 for REI in this study, which is equivalent to an average of previous reports (7,8,10,11,20) and high additive genetic coefficient of variation (45%) for REI, in comparison to other traits (Table 1), might indicate that direct selection against REI has the potential to improve feed efficiency in lactating dairy cows. Moderate heritability estimate for REI, along with negligible genetic correlations with yield traits and high genetic correlation with dry matter intake, might reveal that selection against REI improves feed efficiency by reducing feed intake and little increase in yield traits. Therefore, genetic selection to reduce REI can result in progeny that eats less without sacrificing production performance. This is in agreement with Herd and Bishop (30) who proposed that selection against RFI has the potential to increase the efficiency of beef production by reducing feed intake without changing the growth rate of the young animal, or increasing mature cow size. Moreover, it has been shown that, compared with other measures of feed efficiency, RFI should have a greater potential to improve overall production efficiency and energetic efficiency for average daily gain above maintenance, without altering the growth and body size of different animals (31).

In this study, RFI was genetically independent of yield traits, so it seems that RFI could not be easily improved by a selection index on feed intake and yield traits. Therefore, REI could be combined with yield traits as a selection index for improving both yield and feed efficiency. Therefore, multi-trait selection is recommended to ensure that selected animals have appropriate EBVs for both REI and yield traits. However, factors such as cost of feedstuffs and price of yields and mean energy concentration of rations used in each region might affect the weights of REI and other traits in the concerned selection index. This could be a subject for a future research.

Residual energy intake, estimated using NRC models, is moderately heritable and has negligible correlations with yield traits. Selection against REI might result in a moderate improvement of feed efficiency by reducing feed intake and increasing yield traits a little. The fertility problems and health disorders, which are the results of direct selection for production traits, might be reduced by selection against RFI. REI can be combined with yield traits as a selection index for improving both yield and feed efficiency. The weight coefficients of REI and other traits in selection index might depend on the price of feedstuff and yields, and energy level of the rations consumed.

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