

Genetic Parameters of Estimated Net Energy Efficiencies for Milk Production, Maintenance, and Body Weight Change in Dairy Cows¹

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ABSTRACT

Net efficiencies of converting intake energy into energy for maintenance, milk production, and body weight change in a lactation were estimated for each of 79 Holstein cows by a two-stage multiple regression model. Cows were from 16 paternal half-sib families, which each had members in at least two of the six herds. Each cow was recorded for milk yield, net energy intake, and the three efficiency traits. These traits were analyzed in a multitrait model containing the same 14 fixed subclasses of herd by season by parity and a random factor of sires for each of the five traits. Restricted maximum likelihood estimates of sire and residual (co)variance components were obtained by an expectation maximization algorithm with canonical transformations. Between milk yield and net energy intake, net energy efficiencies for milk yield, maintenance, and body weight change, the estimated phenotypic correlations were .36, -.02, .08, and -.06, while the genetic correlations were .92, .56, .02, and -.32, respectively. Both genetic and phenotypic correlations were zero between net energy efficiency of maintenance and that of milk yield and .17 between net energy efficiency of body weight change and that of milk yield. The estimated genetic correlation between net efficiency for lactation and milk yield is approximately 60% of that

between gross efficiency and milk yield. With a heritability of .32~.49, net energy efficiency for milk yield may be worth consideration for genetic selection in certain dairy cattle populations.

INTRODUCTION

Improving cows' efficiency of converting energy intake to produce milk should be an important goal for the dairy industry. Distinction must be made between gross and net efficiency. Gross efficiency is defined as the ratio of energy contained in the milk over the total energy input from feed, and net efficiency is the ratio of energy contained in the milk over the portion of energy intake used to produce it above maintenance requirements.

To measure gross efficiency of individual cows, data on milk yield, feed intake, and their compositions are necessary. Feed information is not normally collected on commercial dairy farms but can be collected relatively easily for research purposes. Literature (2, 4, 9, 10, 13, 14) on gross efficiency has indicated a high heritability ranges from .36 to .86, a high positive phenotypic correlation with milk yield from .66 to .86, and a very high genetic correlation with milk yield from .92 to .95. The high phenotypic correlation may be caused by the decreasing proportion of energy intake that is used for maintenance as milk production increases. However, the high correlations might be partly due to the practice of feeding according to production. The correlations may be lower under an ad libitum feeding practice. High producing cows tend to be larger but the increase in yield is proportionally greater than the increase in maintenance energy requirement (6, 7). For a genetic correlation as high as reported, genetic improvement in gross efficiency by selection for milk yield would be between 70 to 95% of the improvement ob-

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tainable by direct selection on gross efficiency (4).

Net efficiency is a better biological indicator of a cow's productivity than gross efficiency, because it measures the efficiency of energy used to produce milk while correcting for energy required for maintenance and for changes in body reserve status.

Unlike gross efficiency, few results are available on (co)variability of net efficiency and milk yield in dairy cattle. The lack of such research activity is due to the difficulties in gathering data. To obtain exact measure of net energy efficiencies of an animal, the partitioning of total energy intake into proportions for various usages must be determined first. This would require the use of calorimetric chambers, but the cost and complexity severely limit the number of animals needed for meaningful quantitative studies.

Alternative approaches of measuring net energy efficiencies that are less costly, more convenient, and most important, can generate efficiency data on cattle kept under normal farm conditions, would be highly desirable. Walter and Mao (20) studied several multiple regression models using daily energy intake as dependent variable and daily solid-corrected milk, metabolic body weight, body weight change, and pregnancy as independent variables. Partial regression coefficients from these models gave reciprocal of net energy efficiency estimates.

The objectives of this study were to estimate heritability values of net energy efficiency for milk production, for maintenance, and for body weight change in dairy cows that are kept in dairy herds and to estimate phenotypic and genetic correlations between these efficiency characteristics, net energy intake, and milk yield.

MATERIALS AND METHODS

Data

An experiment involving seven herds distributed across the US provided records of daily milk yield (MY), daily intake of net energy (NEI), biweekly analysis results of milk components, 10 BW during a lactation, and breeding information on 357 cows of various ages. In each of the seven herds, cows were assigned to

three groups based on their projected production, which was determined by their average milk production during the first 3 wk in lactation. Heifers were in another group regardless of production. Total mixed rations were fed to all heifers and cows with varying forage to concentrate ratio according to production group and stage of lactation. In each case, energy provided was 10% more than the estimated cow's energy requirements according to NRC (17). Milk production was expressed as kilograms solid-corrected milk (SCM) (19). Daily BW and BW change (WC) were estimated by fitting the data with a fourth degree polynomial.

Metabolic body weight (MBW) was computed as BW to the power of .75. Walter and Mao (20) used factors tabulated by NRC (17) to compute NE required for maintenance (NE_{MBW}) from MBW and NE required for WC (NE_{WC}) from WC. They used the following two-stage regression model to fit observations on the j^{th} day of a lactation of cow i :

Stage 1:

$$NEI_{ij}/SCM_{ij} = b_{L,i} + b(NE_{MBW,ij} + NE_{WC,ij})/SCM_{ij} + e_{ij}$$

Stage 2:

$$(NEI_{ij} - b_{L,i}SCM_{ij})/MBW_{ij} = b_{M,i} + b_{B,i}WC_{ij}/MBW_{ij} + e_{ij}$$

where:

- $b_{L,i}$ denotes the megacalories (Mcal) of NEI that the i^{th} cow required to produce 1 kg of SCM in a lactation while holding MBW and WC constant;
- $b_{M,i}$ denotes the Mcal of NEI that the i^{th} cow required to maintain 1 kg of MBW while holding SCM production and WC constant during a lactation;
- $b_{B,i}$ represents the Mcal of NEI that the i^{th} cow retrieved from, or stored away in, 1 kg of WC while holding SCM production and maintenance constant throughout a lactation.

For the 357 cows, the average of b_L was .774, of b_M was .085, and of b_B was 2.483

with standard errors of means of .02, .003, and .333, respectively. From calorimetric experiments, requirement of NE to produce caloric content of 1 kg SCM is .748 Mcal (19), requirement for maintenance plus activity allowance is .073 Mcal NE/kg MBW (17), requirement for 1 kg BW increase is 5.12 Mcal NE, and energy retrieved from 1 kg BW losses is 4.92 Mcal NE (19). Therefore, Walter and Mao's (20) estimates of energetic costs averaged over experimental cows are in close agreement with the expected values from energy chamber results. The average estimated energy involved in WC is lower than the chamber values. The discrepancy could be due to the differences between cows in field conditions and cows in chambers and could be partially attributed to the difficulty of estimating energy content of WC without knowing the cow's rumen fill (15) and body composition.

The reciprocals of b_L , b_M , and b_B give, respectively, measures of net energy efficiency for milk yield (NE_L), for maintenance (NE_M), and for body weight change (NE_B).

For the 357 cows, a total of 16 sires were identified to have one or more daughters in at least two of the six herds. Data on the 79 daughters of these sires were used for the genetic analysis.

Model and Procedure

Each cow had records on all five characteristics, which are MY, NEI, and net energy efficiencies of NE_L , NE_M , and NE_B . The same linear mixed model was assumed for each of the traits. For the i th trait, with $i = 1, 2, 3, 4, 5$,

$$y_i = Xb_i + Zs_i + e_i$$

where:

y_i is a vector of the 79 observations for the i th trait;

b_i is a vector, for trait i , of unknown fixed constants for 14 filled subclasses of six herds by three calving seasons (December to February, March to September, and October to November), and four parity numbers (1, 2, 3, and 4 or greater);

s_i is a vector of unknown random effects of 16 sires on the i th trait. Sires are connected with herds, seasons, and parities in the data set. The (co)variance matrix of s_i is $I_{g_{ij}}$;

X and Z are incidence matrices corresponding to b_i and s_i , respectively; and

e_i is a vector of 79 random residuals for the i th trait corresponding to y_i . The (co)variance matrix of e_i is $I_{r_{ij}}$.

The effective progeny group size in this model was 3.26. When this model was used to analyze one trait at a time [single-trait analysis (STA)], the sire and residual covariances between traits were ignored. Variance components of sire and residual were estimated by the expectation maximization (EM) REML algorithm (8). The convergence criterion was set that the absolute difference between sire variance estimates of two consecutive iteration rounds were less than 10^{-3} . Depending on the trait analyzed, 243 to 1,743 rounds of iteration were required to meet the criterion, but convergence did occur in every case. Shapiro-Wilk test of normality of distribution (5) was conducted on residuals after the analysis for each of the five traits.

Based on the STA model described, the five-trait multitrait model was used:

$$y = (I_5 * X)b + (I_5 * Z)s + e$$

where $*$ is the direct product operator, and y , b , s , and e are consisted of y_i , b_i , s_i , and e_i for i from 1 through 5, respectively. The (co)variance matrices of s and e , respectively, are

$$I_{16} * G = I_{16} * \begin{bmatrix} g_{11} & g_{12} & \dots & g_{15} \\ g_{12} & g_{22} & \dots & g_{25} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ g_{15} & g_{25} & \dots & g_{55} \end{bmatrix}$$

and

$$I_{79} * R = I_{79} * \begin{bmatrix} r_{11} & r_{12} & \dots & r_{15} \\ r_{12} & r_{22} & \dots & r_{25} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ r_{15} & r_{25} & \dots & r_{55} \end{bmatrix}$$

where g_{ii} and g_{ij} are sire variances and covariances, and r_{ii} and r_{ij} are residual variances and covariances. Canonical transformation of y was implemented in the iterative multitrait EM-REML algorithm (11) to estimate all elements in G and R . A total of 1613 rounds of iteration was needed to meet the convergence criterion, which was that the percent difference in the Frobenius norm of estimated G of two consecutive iteration rounds was less than 10^{-6} .

Phenotypic (co)variances are $p_{ij} = g_{ij} + r_{ij}$ for $i \leq j = 1, 2, 3, 4, 5$. Heritability estimates are $4g_{ii}/p_{ii}$, the genetic correlations between traits are $g_{ij}/(g_{ii} \cdot g_{jj})^{1/2}$, and phenotypic correlations between traits are $p_{ij}/(p_{ii} \cdot p_{jj})^{1/2}$ for $i \neq j$.

Standard errors for estimated heritabilities and genetic and phenotypic correlations were approximated by a simulation procedure. A total of 50 random data sets was generated from a simulated population with (co)variances of estimates from the experimental data. Each replicate data set was of the same size and structure as the experimental data, and was analyzed by the same model and procedure described earlier. Converged estimates from the 50 replicates were used to compute the standard errors. Correlations whose estimates exceed two times the magnitude of approximate standard errors may be assumed to be nonzero with confidence (5).

RESULTS AND DISCUSSION

Table 1 presents estimates of sire and residual variance components and heritability values from both STA and multitrait analysis (MTA) for each of the five traits. Residual variance components from MTA were slightly greater than those from STA, while sire variance components were consistently much greater. These differences were not expected and they could be due to the small experi-

TABLE 1. Estimates of additive genetic and phenotypic standard deviations and heritability values for milk yield, net energy intake, and net energy efficiencies ($\pm 10^8$) from single (STA)- and multiple-trait (MTA) models.

	Standard deviation				Heritability		SE
	Additive genetic		Phenotypic		STA	MTA	
	STA	MTA	STA	MTA			
Milk yield	568.9	723.3	1076.4	1080.8	.28	.45	.39
Net energy intake	249.1	681.6	1102.7	1112.4	.05	.38	.29
Net energy efficiency for milk yield	864.1	1078.3	1529.9	1542.7	.32	.49	.36
Net energy efficiency for maintenance	167.7	288.3	458.6	462.7	.13	.34	.35
Net energy efficiency for body weight change	13,496.4	13,623.5	17,904.9	17,909.9	.57	.58	.50

mental data size and statistical properties of the estimation algorithm. Discrepancy between STA and MTA estimates was not consistent across traits but seems to be inversely related to the magnitude of the estimates and directly related to the skewness of the distribution of residuals. For example, NEI has the largest difference between STA and MTA estimates and also has a most severely skewed distribution of residuals.

Among the net energy efficiency traits, NE_M has the smallest variances, NE_L is nearly 11 times more variable than NE_M , and NE_B is the most variable. The relatively small variance in energy required by individual cows to produce one unit of milk or to maintain one unit of metabolic body weight is consistent with literature reports (1, 16). The large variability found for the amount of energy stored in or retrieved from one unit of WC could be due to the unreliability of BW as indicator of body energy reserves (15).

Heritability Estimates

The STA heritability estimate for MY was .28, which is well within the range typically reported in literature for field collected data (13). However, the MTA estimate of .45 was nearly twice as great, which is on the high side of the range reported. In agreement with Hooven et al. (9), the estimated heritability for NEI was smaller than that for MY. These estimates are also smaller than those cited by Freeman (4) of .21 for first lactation based on 170 daughter-dam pairs and .43 for all lactations of 255 daughter-dam pairs.

Literature does not provide comparable estimates of genetic parameter involving NE efficiencies. The only heritability estimate of NE efficiency cited (4) was for milk fat and was .23. Several heritability estimates of gross efficiency have been reported and range from .36 to .89 (4, 9, 10, 14). Table 2 shows phenotypic and genetic correlation estimates between the traits from MTA EM-REML estimation of (co)varinace components.

Correlation Between Milk Yield and Net Energy Intake

A high positive phenotypic correlation between MY and NEI was expected since cows were fed with a ration based on their produc-

TABLE 2. Estimates of phenotypic correlations (above diagonal) and genetic correlations (below diagonal) with standard errors between milk yield, net energy intake, and net energy efficiencies.

Trait	MY		NEI		NE _L		NE _M		NE _B	
	SE		SE		SE		SE		SE	
Milk yield (MY)										
Net energy intake (NEI)	.92	.40	.36	.11	-.02	.11	.08	.12	-.06	.15
Net energy efficiency for milk yield (NE _L)	.56	.52	.72	.39	-.01	.12	-.61	.10	.12	.15
Net energy efficiency for maintenance (NE _M)	.02	.55	-.30	.64	-.07	.54	-.01	.16	.17	.11
Net energy efficiency for body weight change (NE _B)	-.32	.55	.07	.61	.18	.59	-.88	.36	-.69	.06

tion but slightly more than estimated requirement. Instead, the phenotypic correlation was a moderate .36, which is significantly different from zero, but smaller than the .68 reported by Hooven et al. (10) from data of 425 first lactations by 31 sires. The genetic correlation was .92, which is in agreement with the .86 by Hooven et al. (10).

Correlations Between Milk Yield and Net Energy Efficiencies

Phenotypic correlation between MY and NE efficiency for milk yield was found to be essentially nil, but genetic correlation between the two was .56. This is smaller than that between MY and gross efficiency for MY, which reportedly ranges from .92 to .95 (9, 10, 12, 14).

Between MY and NE_M , neither phenotypic nor genetic correlation appear to be different from zero. This implies that energetic expenditure for maintenance per unit of metabolic weight is independent from milk yield. This agrees with results by Davey et al. (3) who found no influence of genetic merit for MY on maintenance requirements.

The NE efficiencies for WC showed no significant phenotypic correlation with MY, but a genetic correlation of -0.32 . However, the importance of body reserve mobilization for milk production has long been recognized (1, 2, 14).

Correlations Between Net Energy Intake and Net Energy Efficiencies

Between NEI and NE_L , there is no evidence of a phenotypic correlation, but there is a strong positive genetic correlation of .72. This indicates that cows with high genetic potential for energy intake are also those with high genetic potential in net energy efficiency for producing milk. This result is analogous to that reported for gross efficiency (4, 9, 10). The same researchers have consistently found that gross efficiency is not as highly correlated genetically with energy intake as with milk production. The reverse is true for net energy efficiency as we have found in this study.

A fairly high significant negative phenotypic correlation and a moderate negative genetic correlation were found between NEI and NE_M , implying that cows that are efficient for maintenance tend to require less intake of energy. This is in agreement with the negative

correlation reported between the upper limit of an animal's appetite and its maintenance efficiency (18).

No substantial phenotypic and genetic correlations were found between NEI and net efficiency of energy loss or retrieval in WC.

Correlations Between Net Energy Efficiencies

Net efficiency of energetic expenditure for production of one unit of SCM was not correlated to that for maintenance of one unit of MBW, either phenotypically or genetically. This is consistent with the results reported earlier that MY is not correlated with NE_M but is moderately highly correlated with net energy efficiency for milk production. Both phenotypic and genetic correlations are low between net efficiency of energy conversion for MY and that for WC.

Net efficiency of energy expenditure for maintenance was highly but negatively correlated both phenotypically and genetically with the net efficiency of energy conversion for WC. This observation may indicate that cows that use less energy for maintaining 1 kg of MBW tend to require more energy to store 1 kg of body fat and tend to retrieve more energy from mobilizing 1 kg of body fat.

CONCLUSIONS

In Holstein cows, MY and net efficiency in converting available energy into energy in SCM have similar heritability values when the energy conversion efficiencies for maintenance and WC are held constant. The two traits are not correlated phenotypically for all practical purposes, but their genetic correlation is a high positive .56. This genetic correlation is not as high as that between NEI and NE efficiency for MY, which was estimated to be .72. However, neither of these genetic correlations is as high as that between MY and gross efficiency, which is reported as above .90. Therefore, although direct genetic response in gross efficiency is expected to be similar to correlated genetic response in gross efficiency with selection emphasis on MY, the same cannot be expected in terms of NE efficiency. The implication is that, as we strive for a more efficient dairy production system to meet the market situation, cow's NE efficiency in producing milk

may be worthy for consideration as a selection criterion.

Future estimation involving more data is needed to confirm our results and to expand inferences. The NE efficiency measures on individual cows used in this study were those generated from a model, which is one of many, by Walter and Mao (20). The model was chosen since the averages over cows coincide with the expected values based on results from calorimetric experiments. One needs to be mindful, however, that partitioning of energy intake of cows under normal field conditions may not be the same as those in calorimetric chambers. An alternative model or models may give NE efficiency measures that better describe the variances, even if their averages do not approximate the expected values as closely.

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