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Genetics of alternative definitions of feed efficiency in grazing lactating dairy cows

AM Hurley[ab*], N Lopez-Villalobos[b], S McParland[a], E Lewis[a], E Kennedy[a], M O'Donovan[a], J L Burke[b], and DP Berry[a]

[a]*Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Co. Cork, Ireland;* [b]*Institute of Veterinary, Animal and Biomedical Science, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand*

**Corresponding author:* Email: a.hurley@massey.ac.nz

Abstract

The objective of this study was to estimate genetic parameters for measures of energy conversion efficiency (ECE), energy balance (EB), net energy intake (NEI), net energy of lactation (NEL) and body weight (BW), within lactation stages in grazing dairy cows. Individual measurements of NEI (n=7,675) from 2,445 lactations on 1,245 grazing cows were available. Residual energy intake (REI) was defined as NEI minus predicted energy requirements; residual energy production (REP) was defined as net energy of lactation (NEL) minus predicted energy requirements. Energy conversion efficiency was defined as NEL divided by NEI; EB was defined as the difference between intake and energy required for maintenance plus lactation. Lactation was divided into three stages (8-90, 91-180, and >180 days in milk [DIM]). Genetic and phenotypic (co)variances for EB, NEL and BW were estimated using univariate and bivariate animal repeatability models. The models included the fixed effects of contemporary group (treatment and test-date), parity, DIM, as well as a random additive genetic effect of animal, a within-lactation stage random permanent environmental effect and an across-lactation permanent environmental effect. Heritability across-lactation stages varied from 0.13 (8-90 DIM) to 0.28 (91-180 DIM) for NEI, from 0.16 (8-90 DIM) to 0.33 (91-180 DIM) for NEL, from 0.04 (8-90 DIM) to 0.10 (91-180 and >180 DIM) for EB, from 0.03 (8-90 DIM) to 0.11 (>180 DIM) for REI, and from 0.04 (8-90 DIM) to 0.18 (>180 DIM) for ECE. A strong genetic association between REI and EB was evident when average BW change was close to zero. These genetic parameters from Holstein-Friesian dairy cows fed predominantly grazed grass imply that genetic improvement in selected efficiency traits is achievable.

Keywords: genetics; heritability; feed efficiency; residual energy intake

Introduction

The efficiency of converting feed energy to milk has more than doubled over the past century in dairy cattle, largely as an indirect consequence of selection and management changes that have provided for increased milk output per cow (Oltenacu 2010). Recognition of the importance of feed efficiency in the dairy industry has resulted in large-scale, global efforts to further improve this attribute by selection (Pryce et al. 2012). Although selection for feed efficiency is common in pigs and poultry (Emmerson 1997), it is not explicitly considered in most breeding objectives for dairy cows. This is due to numerous reasons, such as the lack of available feed intake data, but also the lack of a consensus on the most appropriate definition of feed efficiency in dairy cattle. Several definitions of feed efficiency have been proposed and have been the subject of extensive discussion. Hurley et al. (2016) described the phenotypic covariances among a range of different definitions of feed efficiency in grazing lactating dairy cows. What is not known, however, is the genetic covariance structure among these different definitions of feed efficiency. The existence of genetic variation among alternative definitions of feed efficiency, as well as the estimation of precise inter-trait genetic correlations needs to be quantified, to enable estimation of breeding values as well as to decide the trait for inclusion in the breeding objective.

The objective of the present study was to estimate genetic parameters for energy conversion efficiency (ECE), energy balance (EB), net energy intake (NEI), and net energy of lactation (NEL) within stages of lactation in grazing lactating Holstein-Friesian dairy cows.

Materials and methods

Data

Data were available from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Fermoy, Co. Cork, Ireland, for cows lactating between the years 1995 to 2014, inclusive. All studies were undertaken on two adjacent farms, namely, Curtin's Research Farm and the Moorepark Research Farm both located in southern Ireland (latitude 52°9N; longitude 8°16W). Cows originated from several controlled experiments which evaluated alternative grazing strategies, nutritional strategies, or strains of Holstein-Friesian animals; see Hurley et al. (2016) for a description of the database. Individual animal grass dry matter intake (DMI) at pasture was estimated using the n-alkane technique (Mayes et al. 1986). Details on the procedures used to collect and analyze the fecal grab samples have been provided elsewhere (Kennedy et al. 2008).

Cows were milked twice daily at 0700 and 1500 h and individual cow milk yield was recorded at each milking. Individual cow milk samples were taken at consecutive p.m. and a.m. milkings once weekly. Net energy requirement for lactation (NEL) was calculated as (Jarrige et al. 1986):

$$NEL = (0.054 * FC) + (0.031 * PC) + (0.028 * LC) - 0.015$$

where FC is fat concentration (%), PC is protein concentration (%), and LC is lactose concentration (%).

Individual animal body weight was generally measured weekly following the a.m. milking using an electronic scale (Tru-Test Limited, Auckland, New Zealand). Body condition score on a scale of 1 to 5 (BCS; scale 1 = emaciated, 5 = obese) was assessed by trained scorers every two to three weeks in increments of 0.25 (Edmonson et al. 1989). Cubic splines were fitted through individual BW and BCS test-day records as described by Hurley et al. (2016).

Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available, on average, 4.5 times per lactation. Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (UFL) is the net energy requirements for lactation equivalent to 1 kg standard air-dry barley (Jarrige et al. 1986) which represents 7.11 MJ net energy or 11.85 MJ metabolisable energy.

Net energy intake from pasture and concentrate intake was estimated up to eight times per lactation on 2,445 lactations from 1,245 Holstein-Friesian cows. A total of 8,139 individual feed intake test-day measurements were available. Only intake measures with at least five test-day records in the contemporary group (i.e., an amalgamation of the test-date of measure and the experimental treatment the cow was on) and in the first 280 days of lactation were retained; 7,675 individual feed intake measurements remained. No test-day records were available before eight days in milk (DIM). Milk yield and composition during the week of each intake measure were retained. Lactations were divided into three stages (8–90, 91–180, and >180 DIM), while five parity classes (1, 2, 3, 4, and 5+) were considered.

Pedigree information was extracted from the Irish Cattle Breeding Federation (ICBF) database. Animals with no sire or dam records were excluded from the analysis; the final pedigree contained 1025 dams and 217 sires. The pedigrees of all dams and sires were traced back at least four generations, where available. The average number of daughters per sire was 5.74.

Efficiency traits

Energy balance for each test day was calculated in accordance with the net energy system outlined by Jarrige (1989) and modified for Irish dairy systems by O'Mara (1996) as in Hurley et al. (2016).

Residual energy intake (REI) and residual energy production (REP) for each day of lactation were calculated as:

$$\mathrm{REI} = \mathrm{NEI} - [\mathrm{NEL} + \textstyle\sum_{i=1}^{2}\mathrm{DIM}^{i} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75}\times\mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+}\times\mathrm{BCS} + \Delta\mathrm{BW}^{-}\times\mathrm{BCS}]$$

$$\mathrm{REP} = \mathrm{NEL} - [\mathrm{NEI} + \textstyle\sum_{i=1}^{2}\mathrm{DIM}^{i} + \mathrm{BW}^{0.75} + \mathrm{BCS} + \mathrm{BW}^{0.75}\times\mathrm{BCS} + \Delta\mathrm{BW}^{+} + \Delta\mathrm{BW}^{-} + \Delta\mathrm{BCS}^{+} + \Delta\mathrm{BCS}^{-} + \Delta\mathrm{BW}^{+}\times\mathrm{BCS} + \Delta\mathrm{BW}^{-}\times\mathrm{BCS}]$$

where REI is daily residual energy intake, REP is daily residual energy production, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, $\sum_{i=1}^{2}\mathrm{DIM}^{i}$ is days in milk included as a continuous variable with a linear (i=1) and quadratic (i=2) effect, $\mathrm{BW}^{0.75}$ is metabolic live weight, BCS is body condition score, $\Delta\mathrm{BW}^{+}$ describes animals gaining body weight, $\Delta\mathrm{BW}^{-}$ describes animals losing body weight, $\Delta\mathrm{BCS}^{+}$ describes animals gaining BCS, $\Delta\mathrm{BCS}^{-}$ and describes animals losing BCS.

Energy conversion efficiency (ECE) for each day of lactation was defined as the daily net energy requirements for lactation (NEL) divided by the daily net energy intake (NEI).

Data analysis

Components of (co)variances for the estimation of heritabilities, repeatabilities, genetic and residual correlations were obtained using single-trait and bivariate animal models in ASREML (Gilmour et al. 2009). Fixed effects in the models included contemporary group (i.e., defined as the amalgamation of treatment and test-date), parity (1, 2, 3, 4, and 5+), DIM (centred within stage of lactation) and the interaction between parity and DIM. The random effects considered in the model included the additive genetic effect of animal, the within lactation stage permanent environmental effect and across-lactation permanent environmental effect. Both permanent environmental effects were used in the estimation of the total permanent environmental effect for use in the calculation of repeatabilities.

Results

Mean milk fat, protein and lactose yields were 0.89 kg/d, 0.77 kg/d and 1.04 kg/d, respectively. The average test-day milk yield was 22.39 kg/d with a standard deviation of 6.82 kg/L. Mean BW, ΔBW, BCS, ΔBCS and REI were 523.50 kg, 0.18 kg, 2.84, -0.0008 and 0.00 UFL/d, respectively. Regression coefficients derived for the REI and REP models are in Hurley et al. (2016).

Estimated residual variances from univariate analyses were greater in early lactation, decreasing steadily as lactations progressed. Within lactation stage, heritability estimates are in Table 1. Heritability estimates for all efficiency traits increased consistently with DIM.

Genetic and phenotypic correlations among the efficiency and performance traits within lactation stages are in Table 2. The genetic correlation between EB and REI was moderate (0.65) in early lactation, while near unity correlations existed in mid (0.91) and late lactation (0.87). The genetic correlation between NEL and REP was strongest in early lactation (0.76), weakening in mid (0.67) and late (0.64) lactation. Net energy of lactation was positively genetically correlated with all efficiency traits, as well as with NEI and BW in all lactation stages, but was negatively correlated (-0.28) with EB in early lactation (Table 2). Body weight was moderately negatively genetically correlated with REP in all lactation stages (-0.53 to -0.41).

Table 1 Mean, genetic standard deviation (SDg), heritabilities (h^2) and repeatabilities (t) with their associated standard errors among the efficiency and performance traits

Lactation stage	Traits[1]	Mean	SDg	h^2	t
Early (8 – 90 DIM)	EB (UFL/d[2])	-2.18	0.86	0.04 ± 0.02	0.12 ± 0.04
n = 2,341	ECE	73.73	2.70	0.04 ± 0.03	0.15 ± 0.04
	REI (UFL/d)	0.15	0.37	0.03 ± 0.03	0.05 ± 0.04
	REP (UFL/d)	0.85	27.73	0.16 ± 0.05	0.39 ± 0.03
	NEI (UFL/d)	16.59	0.80	0.13 ± 0.04	0.25 ± 0.04
	NEL (UFL/d)	11.90	0.61	0.16 ± 0.05	0.55 ± 0.03
	BW (kg)	506.38	26.13	0.39 ± 0.08	0.64 ± 0.01
	BCS	2.86	0.14	0.33 ± 0.07	0.70 ± 0.01
Mid (91 – 180 DIM)	EB (UFL/d)	2.88	1.10	0.10 ± 0.03	0.17 ± 0.03
n = 3,366	ECE	57.05	2.24	0.09 ± 0.03	0.26 ± 0.03
	REI (UFL/d)	-0.08	0.56	0.10 ± 0.03	0.18 ± 0.03
	REP (UFL/d)	-2.15	23.00	0.19 ± 0.05	0.49 ± 0.02
	NEI (UFL/d)	16.79	1.08	0.28 ± 0.06	0.41 ± 0.03
	NEL (UFL/d)	9.50	0.69	0.33 ± 0.06	0.70 ± 0.02
	BW (kg)	521.15	26.02	0.30 ± 0.06	0.66 ± 0.01
	BCS	2.81	0.17	0.49 ± 0.07	0.75 ± 0.01
Late (>180 DIM)	EB (UFL/d)	1.56	1.12	0.10 ± 0.04	0.25 ± 0.05
n = 1,968	ECE	48.11	2.94	0.18 ± 0.06	0.38 ± 0.04
	REI (UFL/d)	0.03	0.54	0.11 ± 0.04	0.25 ± 0.05
	REP (UFL/d)	3.16	25.62	0.24 ± 0.06	0.61 ± 0.03
	NEI (UFL/d)	16.20	0.84	0.20 ± 0.06	0.44 ± 0.04
	NEL (UFL/d)	7.74	0.58	0.30 ± 0.08	0.72 ± 0.02
	BW (kg)	548.87	25.89	0.41 ± 0.09	0.69 ± 0.001
	BCS	2.81	0.15	0.41 ± 0.08	0.76 ± 0.01

[1]EB = energy balance; ECE = energy conversion efficiency; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy of lactation; BW = test-day body-weight; BCS = test-day body condition score.
[2]One UFL is defined as the net energy content of 1 kg standard air-dry barley (Jarrige et al., 1986)

The phenotypic correlations between REI and NEL were close to zero in all lactation stages, yet moderate genetic correlations were evident (0.29 to 0.55). Residual energy production was strongly phenotypically correlated with NEL in early (0.84), mid (0.76) and late (0.74) lactation.

Discussion

Feed efficiency is of economic importance, but as a trait it is explicitly overlooked in national dairy-cow breeding goals. This is due primarily to a lack of accurate feed intake data on commercial animals, but also a lack of clarity on the most appropriate definition of the feed intake and utilization complex. In the present study, in which pasture NEI was estimated using the n-alkane technique (Mayes et al. 1986), ample genetic variation clearly exists for the range of efficiency traits investigated.

Variance components

The large residual variance in early lactation for the efficiency traits and EB is consistent with results of previous research (Veerkamp & Thompson 1999), suggesting that environmental variation not appropriately accounted for in the statistical model can impact the fit of models to observed phenotypic performance, especially in early lactation. This is, however, not surprising. Factors such as dystocia and other possible subclinical diseases not recorded and included in the model will contribute to this residual variability.

Heritability estimates for EB from cows fed indoors on TMR or conserved forages range from 0.08 to 0.43 (Veerkamp et al. 1995), corroborating the heritability estimates from the present study for cows fed predominantly grazed grass. The heritability estimates for NEI in the present study are also consistent with heritability estimates previously published from DMI in grazing dairy cows and cows fed in confinement systems (Berry & Crowley 2013). The ample genetic variation and moderate heritability estimates for NEI suggests genetic improvement is certainly achievable should the necessary information be available from which to make selection decisions. The low heritability estimates for REI in our study contrasts with results from other studies (Berry & Crowley 2013). Possible reasons for low heritability around the transition period in our study could also be a result of inter-cow variability in predisposition to different diseases such as metabolic and infectious diseases (i.e., hypocalcaemia, ketosis, fatty liver syndrome) especially in the transition period Huzzey et al. (2007), thereby contributing to the residual as these were not accounted for in the statistical model. Another factor contributing to the residual variation, especially in early lactation, could be dystocia which results in both reduced DMI and reduced milk yield (Proudfoot et al. 2009). If these factors are taken into account in the statistical model these effects at least partially contribute to residual effects thereby depressing heritability. A possible explanation for higher heritability for REI in mid and late lactation stages is the reduced mobilisation of body reserves. Conversely, another explanation for low heritability is variation in EB in early lactation.

Genetic and phenotypic correlations

The moderate genetic correlations between REI and NEI is in agreement with several published studies, for example, 0.63 to 0.69 in Veerkamp et al. (1995) and 0.45 in Lin et al. (2013). These results indicate that lower REI (increased efficiency) is associated with decreased energy intake and improved gross efficiency. Genetic correlations between NEL and ECE are often strong; suggesting selection for milk yield improves gross efficiency as depicted by ECE. Possible explanations for the increase in

Table 2 Estimates of phenotypic and genetic correlations[1] among the efficiency[2] and performance traits in early, mid and late lactation

Lactation stage	Traits	EB	ECE	REI	REP	NEI	NEL	BW
Early (8 – 90 DIM)	EB		-0.92	0.90	-0.70	0.72	-0.41	-0.04
n = 2,341	ECE	-0.81 ± 0.21		-0.78	0.73	0.54	0.48	-0.01
	REI	0.65 ± 0.26	-0.22 ± 0.55		-0.48	0.20	-0.05	0.00
	REP	-0.59 ± 0.21	0.85 ± 0.14	0.07 ± 0.46		0.82	0.84	-0.12
	NEI	0.35 ± 0.26	0.23 ± 0.27	0.09 ± 0.22	0.63 ± 0.16		0.33	0.29
	NEL	-0.28 ± 0.37	0.55 ± 0.26	0.40 ± 0.43	0.76 ± 0.09	0.67 ± 0.16		0.26
	BW	0.25 ± 0.30	-0.54 ± 0.33	0.06 ± 0.41	-0.48 ± 0.17	0.59 ± 0.14	0.18 ± 0.19	
Mid (91 – 180 DIM)	EB		-0.88	0.95	-0.63	0.75	-0.25	-0.02
n = 3,366	ECE	-0.56 ± 0.14		-0.74	0.84	0.43	0.57	-0.02
	REI	0.91 ± 0.04	-0.20 ± 0.21		-0.44	0.31	0.00	0.01
	REP	-0.21 ± 0.20	0.81 ± 0.08	0.18 ± 0.22		0.83	0.76	-0.23
	NEI	0.66 ± 0.11	-0.11 ± 0.19	0.62 ± 0.11	0.78 ± 0.06		0.44	0.31
	NEL	0.15 ± 0.19	0.59 ± 0.13	0.55 ± 0.15	0.67 ± 0.09	0.83 ± 0.06		0.26
	BW	0.02 ± 0.19	-0.12 ± 0.20	0.14 ± 0.18	-0.41 ± 0.15	0.53 ± 0.11	0.37 ± 0.13	
Late (>180 DIM)	EB		-0.81	0.90	-0.61	0.72	-0.25	0.10
n = 1,968	ECE	-0.81 ± 0.09		-0.72	0.86	0.38	0.63	-0.15
	REI	0.87 ± 0.08	-0.51 ± 0.18		-0.48	0.25	0.00	0.15
	REP	-0.49 ± 0.19	0.75 ± 0.09	-0.20 ± 0.23		0.84	0.74	-0.42
	NEI	0.56 ± 0.16	0.06 ± 0.23	0.41 ± 0.18	0.66 ± 0.13		0.39	0.34
	NEL	0.15 ± 0.19	0.63 ± 0.02	0.29 ± 0.22	0.64 ± 0.11	0.67 ± 0.12		0.13
	BW	0.29 ± 0.23	-0.19 ± 0.20	0.41 ± 0.20	-0.53 ± 0.15	0.62 ± 0.14	0.33 ± 0.16	

[1]Genetic correlations are below the diagonal and phenotypic correlations are above the diagonal.
[2]EB = energy balance; ECE = energy conversion efficiency; REI = residual energy intake; REP = residual energy production; NEI = net energy intake; NEL = net energy of lactation; BW = body weight.
All standard errors of phenotypic correlations were 0.03.

ECE as a consequence of selection for milk yield include the dilution of the maintenance costs where high producing animals are grossly more efficient, the pleiotropic effect of genes affecting both yield and efficiency, and also where high ECE is a result of increased tissue mobilisation at higher yields (Veerkamp & Emmans 1995).

The strong genetic association between REI and EB in the present study was particularly noticeable in mid lactation when average ΔBW was close to zero. When every individual ΔBW is zero, then ΔBW does not contribute to the REI model; therefore, REI is mathematically equivalent to energy balance (Veerkamp 2002). The positive genetic correlations between EB and NEI in the current study suggest animals consuming less NEI are catabolising body reserves resulting in more negative EB. Larger and fatter cows were less efficient during lactation than smaller and thinner cows as indicated by the moderate genetic correlation between BW and REP in the present study. The weak genetic correlations between EB and NEL within lactation stages in the current study imply that different genes influence these traits in the progress of lactation.

The phenotypic correlation between REI and BW in the present study was close to zero but was not always zero due to the effect of stage of lactation. A moderately positive phenotypic correlation between REI and NEI in our study is in agreement with other studies (Lin et al. 2013, Kelly et al. 2010). This indicates that high energy intake animals either use energy less efficiently for growth compared with those with lower intakes or have a higher rate of food passage with relatively less time for digestion and nutrient uptake.

Conclusion

Genetic parameters presented from Holstein-Friesian dairy cows fed predominantly grazed grass imply that genetic improvement in selected efficiency traits is achievable. Therefore, these traits will likely respond to selection pressure; the selection of which trait to use will depend on the preference of the end-user but in some circumstances the response in over genetic gain can be equivalent irrespective of which definition is used. Nonetheless, the estimation of precise correlations between the efficiency traits with both reproduction and health traits (as well as other traits) needs to be quantified.

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References

Berry DP, Crowley JJ 2013. Genetics of feed efficiency in dairy and beef cattle. Journal of Animal Science 91: 1594-1613.

Edmonson AJ, Lean IJ, Weaver LD, Farver T, Webster G 1989. A body condition scoring chart for Holstein dairy cows. Journal of Dairy Science 72: 68-78.

Emmerson DA 1997. Commercial approaches to genetic selection for growth and feed conversion in domestic poultry. Poultry Science 76: 1121-1125.

Gilmour AR, Cullis BR, Welham SJ, Thompson R 2009. "ASREML Reference Manual". New South Wales Agriculture, Orange Agricultural Institute, Orange, NSW, Australia, 145 pages.

Hurley AM, López-Villalobos N, McParland S, Kennedy E, Lewis E, O'Donovan M, Burke JL, Berry D 2016. Inter-relationships among alternative definitions of feed efficiency in grazing lactating dairy cows. Journal of Dairy Science 99: 468-479.

Huzzey JM, Veira DM, Weary DM, Von Keyserlingk MAG 2007. Prepartum behavior and dry matter intake identify dairy cows at risk for metritis. Journal of Dairy Science 90: 3220-3233.

Jarrige R 1989. Ruminant nutrition: Recommended allowances and feed tables. Libbey, London.

Jarrige R, Demarquilly C, Dulphy JP, Hoden A, Robelin J, Beranger C, Geay Y, Journet M, Malterre C, Micol D, and Petit M. 1986. The INRA "fill unit" system for predicting the voluntary intake of forage-based diets in ruminants: A review. Journal of Animal Science 63: 1737-1758.

Kennedy E, O'Donovan M, Delaby L, O'Mara F 2008. Effect of herbage allowance and concentrate supplementation on dry matter intake, milk production and energy balance of early lactating dairy cows. Livestock Science 117: 275-286.

Lin Z, Macleod I, Pryce JE 2013. Short communication: estimation of genetic parameters for residual feed intake and feeding behavior traits in dairy heifers. Journal of Dairy Science 96: 2654-2656.

Mayes RW, Lamb CS, Colgrove PM. 1986. The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. Journal of Agricultural Science 107: l-170.

Oltenacu PA, Broom DM 2010. The impact of genetic selection for increased milk yield on the welfare of dairy cows. Animal Welfare 19: 39-49.

O'Mara F 1996. A net energy system for cattle and sheep. University College Dublin. Department of Animal Science and Production, Dublin.

Proudfoot KL, Huzzey JM, Von Keyserlingk MAG 2009. The effect of dystocia on the dry matter intake and behavior of Holstein cows. Journal of Dairy Science 92: 4937-4944.

Veerkamp R 2002. Feed intake and energy balance in lactating animals. 7th World Congress on Genetics Applied to Livestock Production, Session 10, 19-23 August, Montpellier, France, pp. 0-8.

Veerkamp RF, Emmans GC 1995. Sources of genetic variation in energetic efficiency of dairy cows. Livestock Production Science 44: 87-97.

Veerkamp RF, Emmans GC, Cromie AR, and Simm G 1995. Variance components for residual feed intake in dairy cows. Livestock Production Science 41: 111-120.

Veerkamp RF, Thompson R 1999. A covariance function for feed intake, live weight, and milk yield estimated using a random regression model. Journal of Dairy Science 82: 1565-1573.