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Estimation of genetic parameters for milk yield traits at different herd production levels in cows milked once- or twice-daily in New Zealand

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Abstract

The objective of this study was to estimate genetic parameters for lactation yields of milk (MY), fat (FY) and protein (PY) for cows milked either once- (OAD) or twice-a-day (TAD) at different production levels (PL), calculated as average milk solids yield (FY + PY) for dairy cattle in New Zealand. Lactation records of 124,620 and 194,631 cows from 298 and 350 herds milked OAD and TAD, respectively were used. Heritabilities (h^2) were lower in low PL herds milked OAD compared to low PL herds milked TAD (0.11-0.18 vs. 0.22-0.37). Across PL, h^2 for MY at medium and high PL were greater than 0.30 at both MF, while for FY and PY, those values were less than 0.30. Genetic correlations (r_G) between MY and PY were greater (>0.70) compared to r_G between FY and any of the other traits (<0.65). The lowest r_G was observed between MY and FY at low PL (0.09±0.087). In conclusion, lower h^2 at low PL from cows milked OAD reveal unequal genetic expression of milk traits genes compared to higher PL. Ignoring the heterogeneity of variance in the genetic evaluation could result in systematic inaccuracies and biases in the estimation of breeding values for cows milked OAD.

Keywords: milking frequency; dairy cattle; New Zealand; genetic parameters; production levels

Introduction

The estimation of genetic parameters for milk traits has been well documented in New Zealand (Ahlborn & Dempfle 1992; Pryce & Harris 2006; Sneddon et al. 2015). In those studies, the parameters were estimated with records from cows milked twice a day (TAD), which is the standard milking frequency (MF) for dairy cattle in New Zealand. However, since the late 1990s, milking once a day (OAD) has been adopted by some farmers for herd management and lifestyle benefits (Clark et al. 2006). There is evidence that Holstein-Friesian (F) cows are more affected than Jersey (J) and crossbred F×J cows by OAD milking because milk yields per cow from F cows show greater reduction than F×J and J cows when they were compared to contemporaries in TAD systems (Cooper 2000; Clark et al. 2006), suggesting that this response is in fact a genotype by environment interaction.

Also, there is evidence that herd production levels (PL) have a significant effect on the genetic evaluation of dairy cattle (Hill et al. 1983; De Veer & Van Vleck 1987; Cromie et al. 1998; Veerkamp & Goddard 1998; Calus et al. 2002). These studies indicated greater variances and genetic parameters at higher PL, due to a more complete expression of the true genetic potential (Vinson 1987).

In dairy cattle, the response to selection is affected by the genetic standard deviation, accuracy of selection, the intensity of selection and generation interval through four selection pathways (bulls to breed bulls, bulls to breed cows, cows to breed bulls and cows to breed cows) (Rendel & Robertson 1950). Genetic standard deviation variation and accuracy of selection are highly dependent on heritability (López-Villalobos 2012).

López-Villalobos & Garrick (2005) detailed the methodology for the implementation of a breeding program for the New Zealand dairy industry. The biggest limitation to implement a breeding program for the OAD systems based on the traditional progeny test is the size of the OAD population (3-5% of the NZ dairy cattle). The latter affects the selection intensity and accuracy of selection of the four selection pathways mentioned previously, and consequently the rate of genetic gain may be different between OAD and TAD population.

The aim of the present study was to estimate genetic parameters for milk yield traits, milked either OAD or TAD at different PL in grazing systems in New Zealand.

Materials and methods

Data

Lactation records of milk (MY), fat (FY) and protein yield (PY) recorded from 2008 to 2012, and pedigree information was provided by Livestock Improvement Corporation (LIC; Hamilton, New Zealand). Data were edited as follows: Firstly, lactation records were sorted based on a MF code to determine if the cow was milked OAD or TAD during the entire lactation. Once-a-day milking herds were those in which 100% of the cows were milked OAD all season. Using the GPS Visualizer (Schneider 2012), TAD herds were selected in a radius of 20 km of the OAD herds. In some cases, at a given single map co-ordinate, an OAD herd was surrounded by several TAD herds. In such cases, all TAD herds were selected. Second, herds with less than 50 cows were deleted from the analysis. Only records from spring-calving cows in their first five lactations with lactation lengths ranged between

150 and 305 days were considered. Lastly, only records from F, J and their crosses were considered, discarding animals with no information on breed composition.

The breed composition of each cow was calculated with the following equation: $\alpha_i^p = \frac{\alpha_i^s + \alpha_i^d}{2}$; where α_i^p is the proportion of genes from breed “i” in the progeny, α_i^s and α_i^d are proportion of breed “i” in the sire and dam, respectively, where “i” is breed F or J. Cows were considered pure-breed cows when their breed composition was $\geq 93.75\%$ from a particular breed (F or J). Coefficient of heterosis in a cow (h_{FJ}) was calculated according to Dickerson (1973): $h_{FJ} = \alpha_F^s \alpha_F^d + \alpha_J^s \alpha_J^d$; where α_F^s and α_J^s are proportion of F or J in the sire and α_F^d and α_J^d are proportion of J and F in the dam, respectively.

The final dataset contained a subset of 124,620 lactations from 298 herds milked OAD and a subset of 194,631 lactations from 350 herds milked TAD. The herds of each subset were grouped in three clusters based on PL calculated as herd-season milk solids (MS) yields (kg/cow). The number of cows and the mean of MS yields per each PL are presented in Table 1. The clusters were formed using the FASTCLUS procedure of SAS (2012) (SAS Institute Inc., Cary, NC, USA). Numbers of herds at low, medium and high PL were 110, 141 and 47 in OAD and 168, 150 and 32 in TAD, respectively.

Estimation of variance and covariance components

Estimation of heritability, repeatability and correlations were obtained using single-trait and bivariate repeatability animal model. These parameters were calculated with restricted maximum likelihood (REML) procedures using the ASReml 3.0 software package (Gilmour et al. 2009) for each subset separately by MF and PL.

A single-trait repeatability animal model was represented as follows (Mrode, 2014):

$$y = Xb + Za + Wp + e,$$

Where y is the vector of observations for each of the traits MY, FY and PY; b is the vector of fixed effects, a is the vector additive genetic effects; p is the vector of random permanent environmental effects; and e is the vector of random residual effects. X , Z and W are incidence matrices relating records to fixed animal, additive genetic, and permanent environmental effects, respectively.

The effects included in b were: contemporary group defined as the combination of herd-season-lactation number; the regression coefficient associated with the linear effect of proportion of F; the regression coefficient associated with the linear effect of coefficient of heterosis; and the regression coefficient associated with the linear effect of deviation days from median calving date of the herd in a given season.

The following expectation (E) of the variables was assumed: $E(y) = Xb$; $E(a) = 0$; and $E(p) = 0$ and $E(e) = 0$. It was also assumed that the residual and permanent environmental effects were independently distributed, therefore, $\text{var}(a) = A\sigma_a^2$; $\text{var}(p) = I\sigma_p^2$; $\text{var}(e) = I\sigma_e^2 = R$ and $\text{var}(y) = ZA\sigma_a^2Z' + WI\sigma_p^2W' + R$, where σ_a^2 is the genetic-

additive variance, σ_p^2 is the permanent environmental variance, σ_e^2 is the random residual variance, and A is the numerator relationship matrix between all cows considered in the data set.

The mixed-model equations used for the estimation of fixed, additive and permanent environmental effects in matrix notation are presented as:

$$\begin{bmatrix} \hat{b} \\ \hat{a} \\ \hat{p} \end{bmatrix} = \begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + A^{-1}\alpha_1 & Z'W \\ W'X & W'Z & W'W + I\alpha_2 \end{bmatrix}^{-1} \begin{bmatrix} X'y \\ Z'y \\ W'y \end{bmatrix},$$

where $\alpha_1 = \sigma_e^2/\sigma_a^2$ and $\alpha_2 = \sigma_e^2/\sigma_p^2$.

The bivariate repeatability animal model was written as (Mrode, 2014):

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

Where y_i is the vector of observation for the i th trait, b_i is the vector of fixed effects for the i th trait, a_i is the vector of additive genetic effects for the i th trait, p_i is the vector of random permanent effects and non-additive genetic effects for the i th trait, e_i is the vector of random residual effects for the i th trait; and X_i , Z_i and W_i are incidences matrices relating records of the i th trait to fixed, random animal effects and random permanent effects and non-additive effects, respectively.

The following assumptions were considered: $E(y_1) = X_1 b_1$; $E(y_2) = X_2 b_2$; $E(a) = 0$; $E(p) = 0$; and $E(e) = 0$. The random effects were assumed to be normally distributed with zero mean and the following co(variance) structure:

$$\text{var} \begin{bmatrix} a_1 \\ a_2 \\ p_1 \\ p_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{a_1}^2 & A\sigma_{a_{12}} & 0 & 0 & 0 & 0 \\ A\sigma_{a_{12}} & A\sigma_{a_2}^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & I_1\sigma_{p_1}^2 & I_1\sigma_{p_{12}} & 0 & 0 \\ 0 & 0 & I_1\sigma_{p_{12}} & I_1\sigma_{p_2}^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_2\sigma_{e_1}^2 & I_2\sigma_{e_{12}} \\ 0 & 0 & 0 & 0 & I_2\sigma_{e_{12}} & I_2\sigma_{e_2}^2 \end{bmatrix},$$

Where $\sigma_{a_1}^2$ is the additive genetic variance for trait 1, $\sigma_{a_2}^2$ is the additive genetic variance for trait 2 and $\sigma_{a_{12}}$ is the additive genetic covariance between both traits;

I_1 is an identity matrix which corresponds to the number of cows with records, $\sigma_{p_1}^2$ is the permanent environmental variance for trait 1, $\sigma_{p_2}^2$ is the permanent environmental variance for trait 2 and $\sigma_{p_{12}}$ is the permanent environmental covariance between both traits;

I_2 is an identity matrix which corresponds to total lactation records, $\sigma_{e_1}^2$ is the residual variance for trait 1, $\sigma_{e_2}^2$ is the residual variance for trait 2 and $\sigma_{e_{12}}$ is the residual covariance between both traits.

Estimation of genetic parameters

Heritability h^2 , repeatability (rep), and genetic (r_g) and phenotypic (r_y) correlations were calculated, respectively, with the following expressions (Falconer & Mackay 1996):

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2); \text{ rep} = (\sigma_a^2 + \sigma_p^2) / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2);$$

$$r_{g_{12}} = \sigma_{g_{12}} / (\sigma_{g_1}^2 \times \sigma_{g_2}^2)^{0.5} \text{ and } r_{y_{12}} = \sigma_{y_{12}} / (\sigma_{y_1}^2 \times \sigma_{y_2}^2)^{0.5}$$

Where σ_a^2 , σ_p^2 and σ_e^2 are the additive, permanent and residual variances, respectively; $\sigma_{g_{12}}$ and $\sigma_{y_{12}}$ are the genetic additive and phenotypic covariance between traits 1 and 2, equivalent to $\sigma_{a_{12}}$ and $\sigma_{a_{12}} + \sigma_{p_{12}} + \sigma_{e_{12}}$, respectively; $\sigma_{g_1}^2$ and

Table 1 Number of cows and herd average of milk solids (fat + protein) yield per cow in once-a-day milking and twice-a-day milking populations in New Zealand dairy cattle.

Production level	Once-a-day milking			Milk solids (kg/cow)	Twice-a-day milking			Milk solids (kg/cow)
	Holstein-Friesian	Crossbred F×J	Jersey		Holstein-Friesian	Crossbred F×J	Jersey	
Low	2,808	9,688	5,581	203.6	7,985	18,366	6,098	272.7
Medium	4,117	18,137	9,618	269.2	12,163	22,836	5,768	353.8
High	2,197	10,355	3,218	339.9	6,091	9,754	1,263	434.1

Table 2 Means, standard deviations, estimates of variance components, heritabilities and repeatabilities for production traits by milking frequency and production level.

MF	PL	Mean (kg)	SD (kg)	σ_a^2	σ_p^2	σ_e^2	h^2	rep
Milk yield								
OAD	Low	2,194	609	28,174	43,583	81,033	0.18 ± 0.02	0.47 ± 0.01
	Medium	2,863	724	91,072	42,364	113,667	0.37 ± 0.02	0.54 ± 0.01
	High	3,650	959	127,515	67,516	231,976	0.30 ± 0.02	0.46 ± 0.01
TAD	Low	3,128	787	108,095	42,759	139,034	0.37 ± 0.02	0.52 ± 0.01
	Medium	4,101	940	171,951	68,564	197,747	0.39 ± 0.02	0.55 ± 0.01
	High	5,121	1,219	233,969	120,832	327,022	0.34 ± 0.02	0.52 ± 0.01
Fat yield								
OAD	Low	115.4	30.7	62.2	113.0	248.3	0.15 ± 0.02	0.41 ± 0.01
	Medium	152.6	36.3	147.1	152.9	371.7	0.22 ± 0.02	0.45 ± 0.01
	High	191.2	44.4	175.2	269.9	656.8	0.16 ± 0.02	0.40 ± 0.01
TAD	Low	153.8	36.6	152.6	129.4	403.1	0.22 ± 0.02	0.41 ± 0.01
	Medium	198.6	42.3	258.6	195.9	545.5	0.26 ± 0.01	0.45 ± 0.01
	High	240.2	52.5	401.8	278.4	810.3	0.27 ± 0.02	0.46 ± 0.01
Protein yield								
OAD	Low	88.2	23.1	22.5	7 0.0	118.2	0.11 ± 0.02	0.44 ± 0.01
	Medium	116.6	27.3	84.8	83.4	176.4	0.25 ± 0.02	0.49 ± 0.01
	High	148.7	35.1	94.7	129.3	357.3	0.16 ± 0.02	0.39 ± 0.01
TAD	Low	118.9	27.5	86.0	64.9	184.1	0.26 ± 0.02	0.45 ± 0.01
	Medium	155.2	32.3	139.1	97.5	264.3	0.28 ± 0.01	0.47 ± 0.01
	High	193.8	42.5	153.5	191.5	444.0	0.19 ± 0.02	0.44 ± 0.01

MF= milking frequency; OAD= once-a-day milking; TAD= twice-a-day milking; PL= production level; SD= standard deviation; σ_a^2 =animal additive variance; σ_p^2 =cow permanent environmental variance; σ_e^2 = residual variance; h^2 = heritability calculated as: $h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2)$; rep = repeatability calculated as: $rep = (\sigma_a^2 + \sigma_p^2) / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2)$.

$\sigma_{y_1}^2$ are the genetic additive and phenotypic variance for trait 1, equivalent to $\sigma_{a_1}^2$ and $\sigma_{a_1}^2 + \sigma_{p_1}^2 + \sigma_{e_1}^2$, respectively; and $\sigma_{g_2}^2$ and $\sigma_{y_2}^2$ are the genetic additive and phenotypic variance for trait 2, equivalent to $\sigma_{a_2}^2$ and $\sigma_{a_2}^2 + \sigma_{p_2}^2 + \sigma_{e_2}^2$, respectively.

Results

Estimates of variance components, h^2 and by MF and PL are presented in Table 2. Overall, estimates of variance increased as PL increased in both, OAD and TAD systems. Estimates of h^2 for milk traits in low PL herds milking OAD were lower than at low PL herds milking TAD, while estimates of rep were similar between MF and PL, although the greatest values were found at medium PL.

In both MF populations, h^2 decreased from medium to high PL (except for FY in TAD). In addition, it is noted that h^2 estimated for MY at medium and high PL were greater

than 0.30 in both MF, while for FY and PY those values ranged between 0.16 and 0.28.

Estimates of rep were similar in TAD compared to the OAD populations. Those values ranged between 0.39 and 0.54, and 0.41 and 0.55 in OAD and TAD populations respectively. Similar to estimates of h^2 , in both MF populations, rep of milk yield traits decreased from medium to high PL.

Correlations (r_g and r_y) are presented in Table 3. In general, correlations were similar across MF and PL, with the exception being the r_g between MY and FY at low PL (0.09 ± 0.087). Phenotypic correlations were greater than r_g , and the correlation between MY and PY was greater than the correlation between FY and any of the other traits. The only r_g between MY and PY less than 0.80 was in the OAD population at the low PL.

Table 3 Estimates of phenotypic and genetic correlations¹ for production traits² by milking frequency (once-a-day and twice-a-day milking) and production level (low, medium and high).

Once-a-day milking											
Low			Medium			High					
MY	FY	PY	MY	FY	PY	MY	FY	PY			
MY		0.75 ± 0.003	0.93 ± 0.001	MY		0.74 ± 0.003	0.93 ± 0.001	MY		0.73 ± 0.003	0.92 ± 0.001
FY	0.09 ± 0.087		0.83 ± 0.002	FY	0.43 ± 0.036		0.82 ± 0.002	FY	0.27 ± 0.063		0.81 ± 0.002
PY	0.74 ± 0.036	0.35 ± 0.082		PY	0.87 ± 0.009	0.61 ± 0.031		PY	0.84 ± 0.017	0.47 ± 0.062	
Twice-a-day milking											
Low			Medium			High					
MY	FY	PY	MY	FY	PY	MY	FY	PY			
MY		0.71 ± 0.003	0.92 ± 0.001	MY		0.68 ± 0.003	0.91 ± 0.001	MY		0.66 ± 0.004	0.91 ± 0.001
FY	0.37 ± 0.038		0.80 ± 0.002	FY	0.34 ± 0.031		0.78 ± 0.002	FY	0.19 ± 0.048		0.76 ± 0.003
PY	0.86 ± 0.010	0.56 ± 0.034		PY	0.84 ± 0.009	0.53 ± 0.028		PY	0.82 ± 0.015	0.39 ± 0.048	

¹Genetic correlations are below the diagonal and phenotypic correlations are above the diagonal, within milking frequency and production level.

Discussion

There is evidence that h^2 for production traits during TAD milking tend to be greater at higher PL (Hill et al. 1983; De Veer & Van Vleck 1987; Cromie et al. 1998). Instead of herd average MS yield, as in this study, those authors mentioned previously considered PL as herd average total lactation MY (Hill et al. 1983 and De Veer & Van Vleck 1987); herd concentrate input per cow per year and herd average MY (Cromie et al. 1998). In contrast with those studies, Table 2 shows that the greatest h^2 for MY and PY were estimated at medium PL in both MF populations, and no difference was observed in the estimated h^2 for FY at medium and high PL in the TAD populations.

Comparison across PL indicates that genetic parameters were different only at low PL. According to Ahlborn & Dempfle (1992), higher yields generally result in higher variances and h^2 . At lower PL, genes responsible for milk yields may be down-regulated or not expressed, hence, the phenotypic variations are mainly explained by difference in the environment (Hammami et al. 2009). Nevertheless, genetic parameters at low PL in the TAD cows did not differ considerably between medium and high PL.

The lower variance components, h^2 and r_g between MY and FY at low PL in the OAD population compared to the other groups are important because the rate of genetic progress is largely influenced by the genetic variance and genetic parameters (López-Villalobos 2012). Based on this, the results of the current study indicate that if selection is applied separately in each of the populations and PL, expected genetic progress in for milk traits in the OAD population at low PL would be lower than the expected genetic progress in the TAD population and OAD at medium and high PL.

Dairy cattle in New Zealand are evaluated without distinction of herd PL and MF. This might lead to genetic evaluation with heterogeneous variances across MF populations and PL. Potential bias due to heterogeneous variances across herds has been simulated (Vinson

1987), indicating that most of the individuals selected are from high-yielding herds, which usually show higher h^2 compared to lower-yielding herds, leading to systematic biases in the EBVs of the individuals.

The problem of heterogeneity of variance has been identified in the animal-evaluation system in New Zealand (Harris et al. 1996). The authors query whether the model used in the animal-evaluation system is robust enough to account for differences in variances due to MF and PL. If the model assumes homogenous variances in the population milked OAD and TAD at different PL, cows milked OAD at low PL will be assigned greater than the actual variances, and hypothetically, overestimating their EBVs.

In conclusion, the results obtained indicate that different h^2 at low PL in cows milked OAD reveals unequal genetic expression of milk traits compared to higher PL, indicating lower genetic variances at low PL and potentially lower genetic progress in those herds.

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