

Implementation of Multiple traits Multi Lactation Random Regression Test Day Model for Production Traits in Australia

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Abstract

Genetic evaluation of dairy cattle using random regression test-day models is now common internationally. In Australia a multiple-trait multi-lactation test day model (MTMLTD) was introduced. Legendre polynomials of second order were used to model the genetic and permanent covariance structure throughout the lactation trajectory. This paper described the results from the implementation of the major components of the Australian test-day model including, co-variance components estimation, reliability calculations, adjustments for herd-year-season variance heterogeneity and simultaneous de-regression of cow's and bull's EBVs to be used in the genomic analyses.

Key words: random regression, multi-trait, de-regression, Australia

Introduction

Until 2015 in Australia, breeding values for milk yield traits are predicted using an animal model with repeated records from all lactations. The records used for prediction are those from individual tests weighted by the length of lactation and parity. The model ignores the genetic and environmental association between milk, fat and protein within and across lactations.

In the last decade most of the countries with advanced breeding programs adopted the so called random regression test-day model for estimation of breeding values in dairy cattle. The advantages of the random regression approach are that cows can be evaluated on any number of tests and the model can account for different genetic, permanent environmental and residual variance over the course of lactation.

The objective of this report is to present some results from the application of multiple trait multi lactation random regression test day model to the genetic evaluation of Australian dairy cattle. The paper is divided into four categories:

1. Estimation of co-variance matrices and related genetic parameters
2. Adjustment for heterogeneous herd-year-seasons variances
3. Reliability approximations
4. De-regression of 305 days final breeding values

Materials and Methods

Estimation of co-variance components

The data used for estimation of co-variance components were test-day yields of milk, fat and protein yield from the first 3 lactations of Australian Holstein cows collected from 1985 to 2012. Several data sets were randomly extracted from the ADHIS database. The number of cows with records varied from 20,000 to 30,000 and the minimum number of required tests ranged from 5 to 10. Sires with less than 10 daughters were excluded from the data as well as herd-test-days with less than 5 contemporaries. Days in milk ranged from 6 to 305 days. Cows were required to have first lactation record to be included in the study. All 3 traits were required on each test day. Two seasons were defined: January to June and July to December. The age at calving was converted to 22 age classes.

The model used for co-variance and breeding values estimation can be written in matrix notation as follows:

$$y = Xb + Z_1a + Z_2p + e \quad (1)$$

where y is the vector of observations; b is a vector of systematic effects including herd-test-day, year-season, age at calving, and fixed regression on days in milk using Legendre polynomials of order 4; a is the vector of random regression coefficients of the additive genetic animal effect; p is the vector of random regression coefficients of permanent environmental effects; e is the vector of residuals; and X , Z_1 and Z_2 are incidence matrices corresponding to the observations for fixed and random effects. The rows of the Z matrices are Legendre polynomials on DIM of order 2. The assumptions of the model are:

$$y|b, a, p, \sigma_{e_i}^2 \sim MVN(Xb + Z_1a + Z_2p, R) ,$$

$$Var[a', p', e'] = \begin{bmatrix} G \otimes A & 0 & 0 \\ 0 & P \otimes I & 0 \\ 0 & 0 & R \end{bmatrix},$$

where G is the co-variance matrix of the additive genetic regression coefficients, A is the relationship matrix among all animals, and P is the co-variance matrix of the permanent environmental regression coefficients.

$$R = \Sigma^+ \begin{bmatrix} R_{11} & 0 & 0 \\ 0 & R_{22} & 0 \\ 0 & 0 & R_{33} \end{bmatrix}_i, \text{ where } R_{jj} \text{ is the}$$

residual co-variance matrix for j traits and $i = 1, \dots, n$ residual classes.

Blocks within R contain (3 x 3) co-variances among traits with elements that depend on lactation 1, 2 or 3, over 10 time intervals of approximately 30 days.

The assumptions regarding prior distributions for the unknown parameters were:

$$\begin{aligned} G|v_a, S_a^2 &\sim W^{-1}(v_a, v_a S_a^2), \\ P|v_p, S_p^2 &\sim W^{-1}(v_p, v_p S_p^2), \\ R|v_e, S_e^2 &\sim W^{-1}(v_e, v_e S_e^2), \end{aligned}$$

where v_a, S_a^2, v_p, S_p^2 , and v_e, S_e^2 correspond to the degree of belief and prior values for co-

variances of additive genetic and permanent environmental regression coefficients and for residual variances, respectively. The term W^{-1} corresponds to the inverse Wishart distribution.

The analyses were performed by Gibbs sampling algorithm using GIBBS3F90 program (Misztal, 2010).

Adjustment for heterogeneous herd-year-season variances

The data used to estimate the correlation between consecutive year-seasons within a herd; herd-year-season and residual variances contained test-day records of cows with calving date from 1990 to 2005 from 506 randomly selected herds. There was 22 year-season's subclasses.

The following model was used:

$$y = Xb + Zhy + e \quad (2)$$

where y is a vector containing test-day records for milk, fat and protein yields for lactations 1, 2 and 3; X and Z are incidence matrices; b is a vector containing fixed age at calving effect and fixed regression on days in milk using Legendre polynomials of order 4; hy is a random effect containing herd-year-season effect; and e is a random residual vector.

The covariance structure of the model was assumed to be:

$$Var \begin{bmatrix} hy \\ e \end{bmatrix} = \begin{bmatrix} H & 0 \\ 0 & R \end{bmatrix}$$

where H is a block diagonal matrix of first order autoregressive correlations matrices, i.e. for i^{th} herd having records in rs_i year-seasons and it takes the form:

$$\sigma_{hy}^2 \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix}$$

where ρ is the correlation between consecutive year-seasons within a herd and σ_{hy}^2 is the herd-year-season variance. Nine separate analyses

were performed for each trait within lactation. Model (2) was fitted by the AR(1) procedure in ASReml (Gilmore, 2003).

The method to adjust for heterogeneous herd-year-season variances was similar to those reported by Kistemaker & Schaeffer (1998) and Strabel *et al.* (2006).

Data from three extractions March 2012, 2013 and 2014 were used to assess the method. Nine separate sparse BLUP equations were constructed using model (2) and solved separately using PCG method with iteration on data. The autoregressive matrix was constructed using the rules described by Wade and Quaas (1993). The observations were adjusted by using correction factors with different weights. After adjustments breeding values were estimated using multi-trait multi-lactation RR model. Differences between each bull's EBV and average breeding value of the parents (PA) were calculated and basic statistics for these quantities were derived.

Reliability approximations

The sample data used for evaluation of the procedure for reliability approximations contained 24,677 cows with records, daughters of 1,135 sires.

The model for the approximate and true reliability was as follows:

$$y = Xb + Za + Wp + e \quad (3)$$

where y was a vector of observations; b was a vector containing herd-test-day fixed effect; a was a random vector of animal genetic effects; p was a random vector containing permanent environmental effects; and e was a random residual vector. The co-variances matrices were the same as for the full model.

The true reliability was calculated from prediction error co-variance matrices obtained from the sparse inverse of the mixed model coefficient matrix. The approximated reliabilities were calculated using an adaptation of the information source method (Ducrocq and Schneider, 2007).

De-regression of cow and bull breeding values

The data used for the de-regression analyses contained 305 days EBVs for milk, fat and protein yield obtained from the routine RR March 2015 run. There were 13,589 genotyped cows and 4,134 genotyped bulls from the Holstein and Jersey breeds. The relationship matrix contained 57,605 relatives of these animals. The number of phantom parent groups was 53.

The de-regression procedure is based on the following mixed-model equations:

$$\begin{bmatrix} 1'R_i^{-1}1 & 1'R_i^{-1} & 0 \\ R_i^{-1}1 & R_i^{-1} + A_{aa}^{-1}\alpha & A_{apg}^{-1} \alpha \\ 0 & A_{pga}^{-1}\alpha & A_{pgpg}^{-1}\alpha \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{a} \\ \hat{pg} \end{bmatrix} = \begin{bmatrix} 1'R_i^{-1}y_i \\ R_i^{-1}y_i \\ 0 \end{bmatrix} \quad (4)$$

where R^{-1} is a diagonal matrix containing EDCs for all animals we want to de-regress, A^{-1} is the numerator relationship matrix which includes unknown parents groups and α is the ratio of residual to additive genetic variance. A small constant was added to the diagonal of A_{pgpg}^{-1} to make the system positive definite. The relationship matrix is a subset of a larger matrix used in the national evaluation. The A_{aa}^{-1} part contains only animals that are genotyped and included in the reference set. A_{apg}^{-1} is the part that contains all non-genotyped animals that are related to the animals in the reference set. The matrix on the left in the above system is sparse but unordered. In order to facilitate the solution to the equations, the system is ordered by using a permutation matrix P such that the product PCP^{-1} is ordered, where C is the left hand side in (4). The de-regressed proofs were obtained in a similar way described elsewhere (Jairath *et al.*, 1998). The part pertaining to the un-genotyped animals and groups was solved by using PCG method. Three different R matrices were used: 1). EDC based on own and progeny performance only (OP); 2). The total reliabilities were de-regressed and converted to EDC using the procedure described by Harris and Johnson (2010) (HJ); EDC obtained from

the final full reliabilities. The de-regressed proofs were used as a phenotype for estimation of DGV and related reliabilities (RL).

The DGVs were calculated from marker effects and the reliabilities were obtained from the inverse of the G-BLUP coefficient matrix. Regressions of DGV on phenotype were calculated as well as average reliabilities using different EDCs and de-regressed proofs.

Results and Discussion

Co-variance estimates

The combined estimates of the daily additive genetic variances for milk, fat and protein yields had the highest values at the beginning of the lactation and the lowest at the end. The

first lactation daily estimates had lower values compared to the values for the second and third lactations. The estimates reported here were in line with most of the literature estimates obtained from Gibbs sampling (Jamrozik *et al.*, 1997; Strabel and Jamrozik, 2006; Muir *et al.*, 2007).

The shape of the curves of the daily permanent environmental variances for all yield traits throughout lactations was similar to the majority of the studies found in the literature. The highest values were observed in the beginning and at the end of lactation. The values for first lactation were the lowest followed by second and third lactation.

The estimates of heritabilities from combined MCMC estimates are presented in Figures 1 to 3.

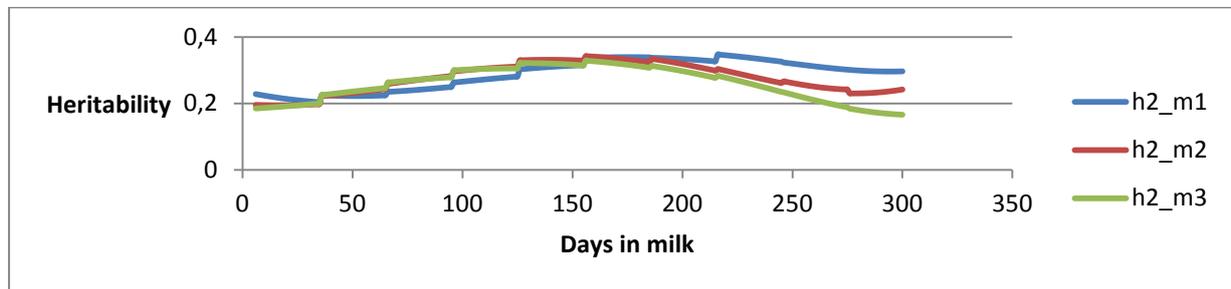


Figure 1. Estimates of daily heritabilities for milk yield obtained from combined MCMC analyses.

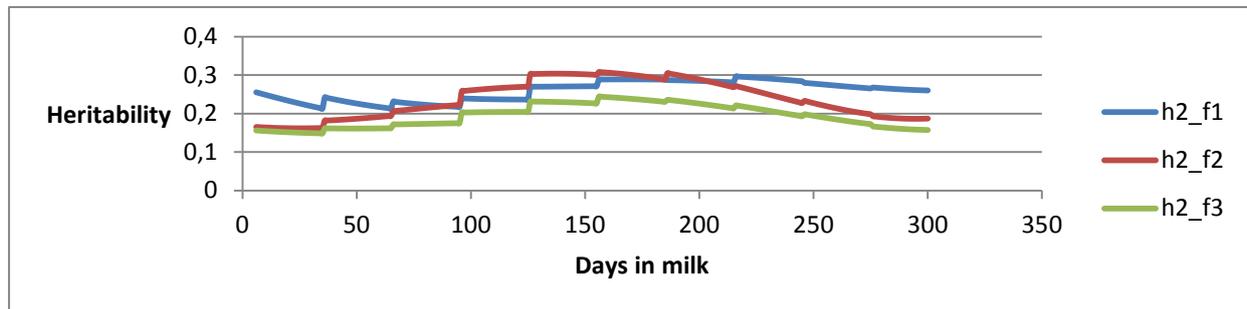


Figure 2. Estimates of daily heritabilities for fat yield obtained from combined MCMC analyses.

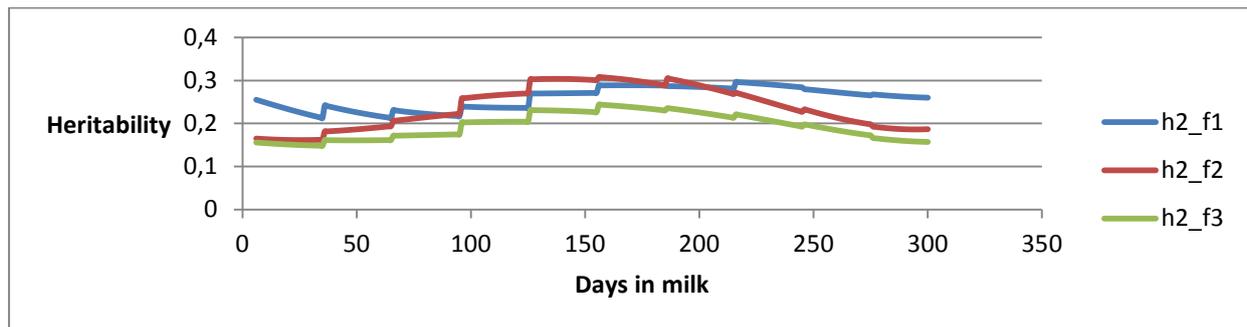


Figure 3. Estimates of daily heritabilities for protein yield obtained from combined MCMC analyses.

The literature estimates of heritabilities obtained from Gibbs sampling analyses with random regression models were also very heterogeneous considering both magnitude and shape of heritability curve. The heritability estimates obtained from this study ranged from 0.14 to 0.35 with average daily heritability of 0.29, 0.26 to 0.23 for milk, fat and protein yields, respectively. The values of 305 days heritabilities in first lactation were 0.44, 0.48, and 0.39 for milk, fat and protein, respectively. Similar estimates were reported by Muir *et al.* (2007).

For all traits higher values were observed in the middle part of the lactation. These findings are in line with the findings reported by other

authors (e.g. Swalve, 1995; Rekaya *et al.* 1999; Liu *et al.* 2000; Druet *et al.* 2003).

The estimates of the residual co-variances were higher in the beginning of the lactation period compared to the estimates at the end of lactation. This pattern is in a good agreement with most of the studies in the literature. However, the estimates in period 10 were higher compared to those from period 9. This pattern has not been found in any of the literature reports dealing with random regression.

Table 1 presents the estimates of the genetic correlations between selected days in milk for milk, fat and protein yield that are obtained from MCMC analyses.

Table 1. Estimates of genetic (above diagonal) and permanent environmental correlations (*100) (below diagonal) between protein yields on selected days in milk from combined Gibbs sampling analyses.

DIM	Lactation 1					Lactation 2					Lactation 3							
	15	45	125	205	265	305	15	45	125	205	265	305	15	45	125	205	265	305
15		95	53	36	44	51	94	64	55	53	41	96	72	55	38	19		
45			77	61	59	54	97	86	75	57	31	96	88	73	48	17		
125				95	76	50	68	83	95	61	17	61	80	94	64	20		
205					90	64	44	59	89	81	42	41	59	90	84	46		
265						91	35	43	65	90	87	39	47	64	88	87		
305							32	34	44	74	96	39	38	40	69	95		

The genetic correlations across lactations within traits were all positive and ranged from 0.19 to 0.97, 0.25 to 0.97, and 0.17 to 0.96 for milk, fat and protein yield, respectively. The correlations between yields on days that were close together were higher compared to those for days that were further apart. The lowest correlations were observed for test days recorded at the beginning of a lactation and at the very end. Many other studies reported similar findings. It should be noted that in this case there were no negative estimates between any of the selected days in milk. Negative genetic correlations for selected days in milk were reported in several studies (Zavadiлова *et al.* 2005; Rekaya *et al.* 1999; Liu *et al.* 2000; Kettunen *et al.* 2000).

The problem of selecting the best random regression model and related co-variance

components is not trivial, and has been discussed in several studies (Druet *et al.* 2003; Lopez-Romero and Carabano, 2003; Strabel and Misztal, 1999). On one hand the difficulty comes from the fact that different countries used different functions to describe the random curves. Although Legendre polynomials have become a standard for this part of the model, there are differences in their order between different countries. For the fourth order is used in Canada (Kistemaker, 2003) and the fifth in the United Kingdom (Mrode *et al.* 2003).

Some authors argue that higher order polynomials improve model plausibility. This may be true for certain data sets and structures but it leads to several problems. The use of higher order polynomials results in extreme values for additive genetic co-variances at the peripheries of the lactation and a negative

correlation for the extremes of lactation (Pool *et al.* 2000; Strabel *et al.* 2005; Zavadilova *et al.* 2005). Moreover, analyses of the eigenvalues of the co-variance matrices shows the diminishing importance of adding further parameters. Additionally, the more parameters that are used, the less accurately they are estimated, because fewer records are available for each estimate. The use of unreasonably high estimates of genetic variances may cause considerable overestimation of the accuracy of the genetic evaluations.

Overall the estimates of the genetic parameters in this study were in a good agreement with the literature values.

Herd-year-season heterogeneity adjustments

Variance components for herd-year-season, residual and the correlation coefficient between consecutive year-seasons within a herd are presented in Table 2.

Table 2. Variance components estimates using model (2).

Component	Milk 1	Fat 1	Protein 1	Milk 2	Fat 2	Protein 2	Milk 3	Fat 3	Protein 3
σ_e^2	9.795	0.017	0.010	13.522	0.024	0.013	16.600	0.032	0.016
ρ	0.671	0.635	0.567	0.741	0.756	0.640	0.745	0.773	0.621
σ_{ny}^2	14.321	0.017	0.015	18.325	0.021	0.019	19.083	0.023	0.020

The estimates of the correlation coefficients between consecutive year-seasons within a herd are significantly less than 1 which suggests that there is heterogeneity of variances within a herd.

calculated as a difference between their EBVs and their parent average (PA). For all traits the weight of 1.5 was the most effective. Table 3 contains results of analyses of differences between EBV of bulls having at least 20 daughters and their parent average.

A measure of improvement of the evaluation method using adjustments is the bias of the EBVs of selected animals

Applying the data adjustment decreased the average difference between EBVs and PA. The

Table 3. Basic statistics for the difference between estimated ABVs of bulls obtained from models with and without correction for heterogeneous variance.

Method	Mean	SD	Minimum	Maximum
No adjustment				
Milk yield	-75.9	284.6	-1284.1	1912.2
Fat yield	-3.2	9.9	-56.6	38.8
Protein yield	-2.7	7.6	-41.3	30.1
Adjustment w=1.5				
Milk yield	-68.8	259.2	-1156.1	1403.3
Fat yield	-2.9	9.1	-43.4	30.5
Protein yield	-2.5	6.9	-31.3	24.4

decrease in differences found for weight = 1.5 was 9.4%, 7.5% and 8.6% for milk, fat and protein yield, respectively. These percentages were slightly higher than those reported by Kistemaker and Schaeffer (1998) in Canada.

suggesting very little re-ranking of the EBVs. This result is in line with the majority of the studies reported in the literature.

The correlations between EBV without adjustment and EBV with adjustment for bulls with more than 20 daughters were very high

To investigate the effect of HV adjustment on the data for cows, the best cows with EBVs without adjustment were extracted and compared with the same cows from EBVs with HV adjustment. The “best” cow was defined as

a cow having at least 3 progeny, EBV for milk > 1000 and EBV for fat and protein > 50 kg. The correlations between EBVs with and without adjustments were 0.97, 0.94, and 0.94 for milk, fat and protein yield, respectively. Clearly the adjustment for HV resulted in some re-ranking of the cow's EBVs. The correlations were considerably lower compared to those for bulls. Again these results are consistent with the literature findings (Kistemaker and Schaeffer, 1998).

Reliability approximation

The information source method for approximating the reliabilities corresponded well to the true values derived from the inverse of the MME matrix. The results for bulls are shown in figure 4.

The mean values for the true and the approximate reliability were 27 and 30, respectively. The intercept from the regression

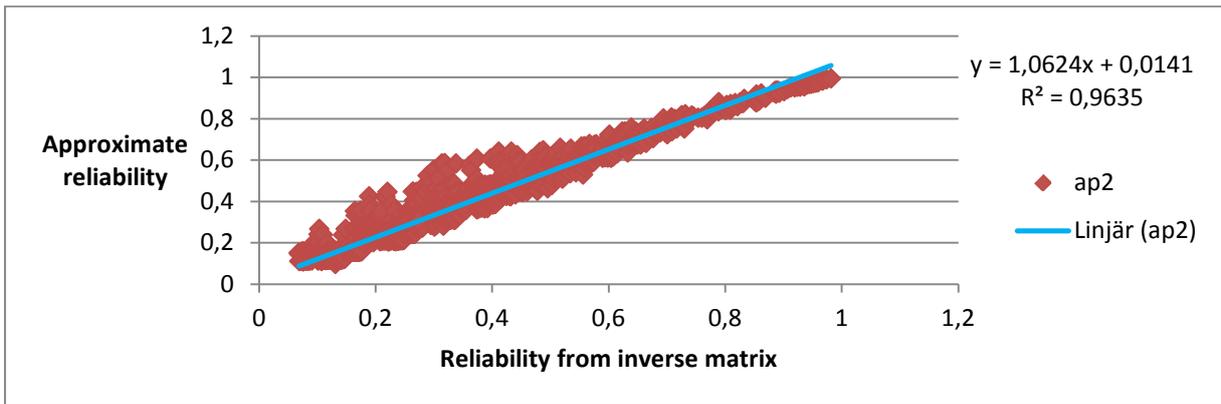


Figure 4. Relationship between true and approximate reliability for bulls.

analysis was 0 and the linear coefficient was greater than one and the regression model accounts for almost all (96.35%) of the variation.

For all cows with records the mean values for the true and the approximate reliability were 28 and 34, respectively. The intercept from the regression analysis was 0.1 and the regression model accounts for 92.25% of the variation.

For all dams the mean values for the true and the approximate reliability were 26 and 28, respectively. In this category of animals the results are very similar to those obtained for the sires. The intercept from the regression analysis was zero and the linear coefficient was greater than one, indicating that the higher the reliability the more it is overestimated. The regression model accounts for (96.34%) of the variation.

From these results it is evident that the approximate method slightly overestimates the higher reliabilities (> 0.5). Similar findings were reported by Tier and Meyer (2004). The

results for the cows with records were not unexpected since their reliabilities were based only on the inverse of the diagonal block EDC matrices. In contrast some of the dams have their reliability based on own performance as well as the performance of their progeny and collateral relatives.

De-regression of breeding values

The de-regression procedure used in this study adjusts for ancestral information, such that the DRP contain only own and progeny information on each animal. It also eliminates shrinkage contained in the EBVs. The DRP have unequal variances and are used in a weighted analyses in both ridge regression and G-BLUP. The weights used were similar to those reported by Garrick *et al.* (2009). The effect of using different EDCs on DGVs was evaluated by regressing DGVs on DRPs and calculation the average prediction error variances from G-BLUP.

The results from the regression analyses for Holstein are shown in table 4.

Table 4. Regression of DGV on DRP for Holstein.

RHS for DGV	Trait						
	Milk		Fat		Protein		
	\hat{b}	R^2	\hat{b}	R^2	\hat{b}	R^2	
DRP/HJ for bulls and cows	1.318	0.531	1.386	0.530	1.309	0.52	
DRP/HJ for bulls	1.401	0.520	0.913	0.628	1.069	0.761	
DRP/HJ for cows	0.985	0.740	1.484	0.537	1.400	0.475	
DRP/RL for bulls and cows	1.342	0.670	1.360	0.670	1.280	0.657	
DRP/RL for bulls	1.386	0.678	1.341	0.781	1.326	0.690	
DRP/RL for cows	1.114	0.780	0.960	0.690	1.172	0.790	
DRP/OP for bulls and cows	1.294	0.726	1.334	0.684	1.250	0.687	
DRP/OP for bulls	1.011	0.904	0.989	0.842	1.060	0.926	
DRP/OP for cows	1.360	0.717	1.440	0.683	1.330	0.653	

The highest R^2 for bulls were obtained when OP EDCs were used. The regression coefficients were 1.011, 0.989 and 1.060 for milk, fat and protein yield, respectively. The regression coefficients for the HJ and RL EDCs were considerably higher than 1.0 and ranged from 0.913 to 1.401. The corresponding R^2 values ranged from 0.520 to 0.781. Similar picture was observed for the Jersey bulls.

The lowest average prediction error variance for Holstein bulls was obtained when OP EDCs were used. The average PEVs were 0.141, 0.145 and 0.141 for milk, fat and protein yield, respectively. The corresponding figures for Jersey were 0.175, 0.168 and 0.173 for milk, fat and protein yield, respectively. The standard errors for Holstein ranged from 0.038 to 0.046 and for Jersey the range was from 0.064 to 0.066. The average PEVs from HJ and RL EDCs were much higher ranging from 0.200 to 0.250 with standard deviations

in the range of 0.066 to 0.091. Similar figures were observed for the Jersey breed.

Further evaluation of the predictive ability of each approach on the reliability of the genotyped validation animals is under way.

Conclusion

The multiple-trait multi-lactation test day model was successfully implemented for the Australian dairy industry. It is an important development towards improving the accuracy of genetic evaluations, including new procedure for reliability calculations and herd-year-season variance heterogeneity. The de-regressed proofs using the final 305 days EBVs obtained from EDCs based on own and progeny contributions seem feasible for use as a phenotypes in the genomic analyses for production traits.

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