Calculation and Use of Daughter Yield Deviations and Associated Reliabilities of Bulls Under Multiple Trait Models

Z. Liu, A. Bünger, F. Reinhardt, and R. Reents
VIT, Heideweg 1, D-27283 Verden, Germany

Abstract

A method was presented for calculating daughter yield deviations of bulls and average yield deviations of cows under general multiple trait models. Reliabilities associated with the yield deviations were approximated using the multiple trait effective daughter contribution method. The presented daughter yield deviation formula was verified to be correct in a simulation study with a random regression test day model and high accuracy of daughter yield deviations was also confirmed based on their correlations with proofs from a routine genetic evaluation using a random regression test day model. The daughter yield deviations and associated reliabilities can be used for international bull comparison based on a multiple trait multiple country model, marker assisted genetic evaluation and validation of national genetic evaluation system.

1. Introduction

Daughter yield deviations (DYD) of a bull are, by definition, average of daughters' performance adjusted for fixed and non-genetic random effects of the daughters and genetic effects of his mates. Because DYD are not regressed on bull's breeding values, they are the most independent and accurate measure of phenotypic performance of bull's daughters (VanRaden and Wiggans, 1991). Thanks to this property, DYD are widely used in genetic analyses, such as mapping quantitative trait loci (Szyda *et al.,* 2002), validating national genetic trends (Boichard *et al.,* 1995), a two-step multiple trait genetic evaluation (Ducrocq *et al.,* 2001), and international bull comparison (Ducrocq *et al.,* 2003, Gengler, 2002; Schaeffer, 2001; Weigel *et al.,* 2001). For repeatability animal model applied to lactation records, VanRaden and Wiggans (1991) showed the calculation of DYD. Mrode and Swanson (2002) extended the method to a random regression test day model (RRTDM), however, computation of reliability associated with DYD, estimability of lactation DYD and short lactation problem were not addressed. The objectives of this study were 1) to develop a method for calculating DYD under general multiple trait models, 2) to verify the DYD calculation under a RRTDM, and 3) to apply the DYD method in a routine genetic evaluation.

2. Materials and Methods

2.1. Methods

A multiple trait model is assumed:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_p\mathbf{p} + \mathbf{Za} + \mathbf{e} \qquad [1]$$

where $\mathbf{y}$ is a vector of records of a cow, **b** represents all fixed effects assigned to the records, **p** and **a** represent non-genetic random effects, e.g. permanent environmental (p.e.) and additive genetic effects of the cow, respectively. **e** is a vector of random error effects, and $\mathbf{X}$, $\mathbf{Z}_p$ and **Z** are design matrices. In case of RRTDM **p** and **a** are random regression coefficients. Further more it is assumed that the random effects are not correlated with each other. Let $\mathbf{G}_0$ represent genetic (co)variance matrix. Denote **R** as error (co)variance matrix for the records of the cow.

Calculation of DYD of a bull represents a process of absorbing his daughters' genetic effects using their records adjusted for all other effects and his mates' breeding values. Denote a_*^{ii} as diagonal element of the inverse of numerator relationship matrix corresponding to daughter i of a bull under the assumption that the daughter has no own progeny, and d_i as diagonal element pertinent to daughter *i* in the inverse of (co)variance matrix of Mendelian sampling $\mathbf{D}^{-1}$ (Mrode, 1996, pp28). DYD of the bull under the general multiple trait model [1] are computed with

$$\mathbf{q} = \mathbf{B}^{-1}\boldsymbol{\xi} = 2\left(\sum_{i=1}^{n} d_i\, \mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i\right)^{-1} \sum_{i=1}^{n} d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}(\mathbf{y}_i - \mathbf{X}_i\hat{\mathbf{b}} - \mathbf{Z}_{pi}\hat{\mathbf{p}}_i - \tfrac{1}{2}\mathbf{Z}_i\hat{\mathbf{a}}_d), \qquad [2]$$

where subscript *i* represents the *i*-th daughter of the bull, *n* is number of daughters with records, $\hat{\mathbf{a}}_d$ is a vector of estimated breeding values (EBV) of dam of daughter *i* obtained from a complete genetic evaluation like routine national evaluation, $\mathbf{y}_i$ is a vector of the *i*-th daughter's trait values adjusted for heterogeneous herd variances,

$$\mathbf{Q}_i = (\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + a_*^{ii}\mathbf{G}_0^{-1})^{-1}, \mathbf{B} = \sum_{i=1}^{n} \tfrac{1}{4} d_i\, \mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i, \text{ and}$$

$$\boldsymbol{\xi} = \sum_{i=1}^{n} \tfrac{1}{2} d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}(\mathbf{y}_i - \mathbf{X}_i\hat{\mathbf{b}} - \mathbf{Z}_{pi}\hat{\mathbf{p}}_i - \tfrac{1}{2}\mathbf{Z}_i\hat{\mathbf{a}}_d).$$

See Appendix for the derivation of DYD Formula [2].

Formula [2] for calculating DYD is equivalent to the one by VanRaden and Wiggans (1991) developed for repeatability animal model and also similar to the one by Mrode and Swanson (2002) for RRTDM. For repeatability animal model the DYD vector **q** becomes a scalar that is a weighted average DYD over all lactation records. For multiple lactation/trait models **q** consists of DYD for each lactation/trait. As genetic effects are modelled in regression coefficients on days in milk (DIM) in RRTDM, **q** is expressed in the form of regression coefficients too (Mrode and Swanson, 2002). With those regression coefficients, any linear function of the DYD regression coefficients can be calculated. For RRTDM, the inverse of matrix **B** does not always exist. For instance, when all daughters of a bull have fewer test day records in a given lactation than the order of fit for genetic effects, DYD are not estimable for the bull. However, when at least one daughter has at least as many test day records in a lactation as the order of fit for genetic effects, DYD of the bull are defined for this lactation. Likewise, lactation yield deviations (LYD) for cows (see Appendix) are estimable when there are at least so many test day records available for a lactation as the order of fit for genetic effects. In case of estimable DYD, all data from daughters with defined as well as daughters with undefined LYD can be used. Records without contemporaries must be excluded from the DYD calculation. In case of unknown mates $\hat{\mathbf{a}}_d$ is replaced with solutions of corresponding genetic groups. The DYD Formula [2] for bulls and Formula [A3] in Appendix for average yield deviations (AYD) of cows show how information on test day level should be summarized to lactation level for test day models for the purpose of national and international genetic evaluations (Gengler, 2002).

In contrast to the derivations by VanRaden and Wiggans (1991) and Mrode and Swanson (2002), the DYD Formula [2] was derived from bull equations (see Appendix), but not from cow equations. Additionally, bulls and their mates are allowed here to be inbred. Factor 2 in Formula [2] reflects the fact that the derived DYD are expressed on animal basis, not on sire basis as in VanRaden and Wiggans (1991) and Mrode and Swanson (2002). Formula [2] always gives zero DYD values for missing lactations/traits. The DYD Formula [2] developed for general multiple trait models is directly applicable to any RRTDM and single trait models.

Because fixed effects, non-genetic random effects and EBV of mates are subtracted from daughters' records, but not absorbed in daughters' genetic effects, in DYD calculation, no reliability associated with DYD can be derived from the DYD Formula [2]. However, the multiple trait effective daughter contribution (MTEDC, Liu *et al.,* 2001*a* and 2001*b*) can be implemented to compute reliability associated with DYD. The procedure of reliability calculation for DYD using the MTEDC differs with normal procedure of reliability approximation in that only first two steps of the MTEDC are needed: calculation of data contribution for daughters with records and collecting EDC of daughters adjusted for mates' contribution. Summing up EDC matrices of all daughters gives EDC matrix ($\mathbf{\Psi}_\mathbf{q}$) associated with bull's DYD

$$\mathbf{q}\text{: } \mathbf{\Psi}_\mathbf{q} = \sum \mathbf{\Psi}_{\text{P–M}} , \qquad [3]$$

with $\mathbf{\Psi}_{\text{P–M}}$ being EDC matrix contributed by a daughter adjusted for her dam's contribution. Reliability matrix associated with **q** is computed with

$$\mathfrak{R}_\mathbf{q} = \mathbf{I} - (\tfrac{1}{4}\mathbf{\Psi}_\mathbf{q}\mathbf{G}_0 + \mathbf{I})^{-1} . \qquad [4]$$

2.2. Data for an application study

The presented DYD Formula [2] and associated reliability Formula [4] were applied to the data set used in official May 2003 genetic evaluation of production traits for Austrian, German and Luxembourgish Holstein, Red and Jersey dairy cattle breeds. The data set included about 179 million test day records from approximately 22 millions of lactations of about 11 million cows.

2.3 A verification study on the DYD and reliability calculation methods

The rationale of the verification study is that EBV of a bull obtained from DYD and associated reliabilities must be equal to those obtained from a complete mixed model equations (MME) system including equations of genetic and non-genetic effects of the bull, his daughters and mates. Also approximated reliability values of the bull's EBV must be equal to their true reliability value. The selected model for this verification study was a RRTDM (Liu *et al.,* 2001*b*) applied to test day milk yield.

2.3.1. Pedigree and data

A single half-sib family structure was assumed in the verification study. As parental contribution is irrelevant for validating the DYD formula and its associated reliability method, both parents of the bull were assumed to be unknown. All daughters of the bull had known dam and own performance records. All mates of the bull had both parents missing and full performance information, i.e. three complete lactations with 10 test day records each. Each mate had only one progeny, namely a daughter of the bull. Between daughter-dam pairs there was no additional genetic connection except the bull. With p.e. effects included in the study, correctness of the method of adjusting records for other effects and accuracy of the reliability calculation method could be examined, therefore, no fixed effects were included in the simulation. Monthly testing scheme was assumed to generate test day records for daughters and dams, with first tests done at DIM 10 for mates or first-crop daughters and DIM 15 for second-crop daughters. A new test day record was added every 30 days for daughters or mates.

Various scenarios were investigated on the accuracy of the DYD and reliability methods. Different number of daughters was used to simulate the bull in progeny testing program and with second-crop daughters. The daughters may have one to three lactations. Lactation progress of the daughters was simulated with number of test day records. Test day yields of all mates of the simulated bull were set to zero, implicating that phenotypic performance of the mates was equal to comparison group average. All daughters' phenotypic records on all test days were simulated as deviations from their comparison groups and expressed in phenotypic standard deviations. Test day yield deviation at any chosen DIM was assumed to be 0.10 phenotypic standard deviation of that DIM for all daughters. Parameters of test day milk yield (Liu *et al.,* 2000) were used in generating and analysing data.

2.3.2. Solving a complete MME system

Genetic effects of the daughters, mates and bull, and p.e. effects of the daughters and mates were included in the complete genetic evaluation system. The effects were estimated by directly solving the MME system using partitioned matrix inversion technique. All effects of a daughter and her dam were absorbed jointly into genetic effects of the sire. True reliabilities of the sire were calculated using the inverse matrix and compared to those approximated with the MTEDC. In order to ensure correct computation, the MME were solved in another way. For each daughter or dam, p.e. effect was absorbed on a within animal basis, and then the MME after the absorption were solved using the matrix inversion by partitioning method too.

2.3.3. Estimating bull's breeding values using DYD and associated reliabilities

The solutions from the complete MME system were used to calculate DYD with Formula [2]. For estimating the bull's breeding values using his DYD, the following MME are to be solved:

$$(\boldsymbol{\Psi}_{\mathrm{b}} + \mathbf{G}_0^{-1})\hat{\mathbf{a}}_s = \boldsymbol{\Delta}_{\mathrm{b}}, \tag{5}$$

where

$$\boldsymbol{\Psi}_{\mathrm{b}} = [(\mathbf{I} - \boldsymbol{\Re}_{\mathbf{q}})^{-1} - \mathbf{I}]\mathbf{G}_0^{-1}, \tag{6}$$

and

$$\boldsymbol{\Delta}_{\mathrm{b}} = \boldsymbol{\xi} + (\boldsymbol{\Psi}_{\mathrm{b}} - \mathbf{B})(\mathbf{B} + \mathbf{G}_0^{-1})^{-1}\boldsymbol{\xi}. \tag{7}$$

Reliability matrix of sire EBV was calculated with

$$\boldsymbol{\Re}_{\hat{\mathbf{a}}_s} = \mathbf{I} - \mathbf{G}_0^{-1}(\boldsymbol{\Psi}_{\mathrm{b}} + \mathbf{G}_0^{-1})^{-1}. \tag{8}$$

For international genetic evaluations, DYD can be used as dependent variables and are comparable to de-regressed proofs (Schaeffer 2001) for multiple trait models. However, setting up MME of multiple across country evaluation based on DYD differs with the multiple trait bull comparison procedure based on de-regressed proofs (Schaeffer, 2001). Least squares part of left-hand-side of MME corresponding to a bull with daughters having performance is $\boldsymbol{\Psi}_{\mathrm{b}}$. Right-hand-side of MME pertinent to the bull in MACE equations is $\boldsymbol{\Delta}_{\mathrm{b}}$.

3. Results and Discussion

The Formula [2] for calculating DYD and Formula [4] for approximating associated reliability are valid for general multiple trait models, including RRTDM. Calculation of DYD using Formula [2] requires estimates of all fixed effects and non-genetic random effects and EBV of mates of bulls from a genetic evaluation. Size of contemporary groups and absorption of non-genetic random effects are considered in computing data contribution of daughters in reliability calculation, and reliability values of mates of bull are adjusted for as well. For the calculation of DYD of a bull, only records of his own daughters have to be considered, male progeny must be excluded, because they do not have own performance records for production traits. The contribution of female descendents of his daughters, e.g. grand-daughters of the bull, to his DYD must be ignored, otherwise the contribution would be double counted, because the grand-daughters would contribute their data to DYD of his sons. In DYD calculation, only the path, cow to sire, is considered, other paths, such as son to sire, are ignored. This is because the contribution of male progeny to the bull will be accounted for in subsequent genetic analyses, e.g. international bull evaluations (Ducrocq *et al.,* 2003; Fikse and Banos, 2001), marker assisted genetic evaluation (Szyda *et al.,* 2002), and two-step multiple trait evaluations based on evaluation results from single trait models (Ducrocq *et al.,* 2001). Because DYD of one bull do not affect DYD of other bulls, DYD calculation can be done on a within-bull basis. Parental contribution to bull is irrelevant for the calculation of DYD of bulls.

For genetic analyses, DYD on 305-day lactation basis are more useful than the DYD vector **q** expressed on daily basis in the form of regression coefficients, therefore, DYD on daily basis need to be converted to 305-day lactation basis. Due to the mathematical function for modelling genetic effects in RRTDM, there is an estimability issue for lactation DYD. In case that there are no data available in some lactations or some lactation DYD are not estimable, only a sub-matrix of matrix **B** needs to be inverted and the other parts of the inverse of matrix **B** are set to zero for obtaining a generalized inverse of **B**. Lactation DYD estimated from shorter lactations are more influenced by extrapolation than lactation DYD from longer lactations. In order to minimize the impact of extrapolation, at least 10 daughters are required to pass 120 DIM in a lactation in order to make DYD of this lactation official for a bull, which was determined in the application study using the data from May 2003 evaluation. Similarly, LYD of a lactation of a cow will be publishable, if her lactation pass 210 DIM and she has at least seven tests. Computer resources required for the calculation DYD of bulls and LYD of cows and their associated reliabilities were rather limited, total CPU was equivalent to eight rounds of iteration for solving MME (Liu *et al.* 2001*b*) for May 2003 production trait genetic evaluations.

The verification study was conducted using Maple 6 software. EBV and reliabilities of the bull obtained from the DYD based MME system were identical to those from the complete MME system in all scenarios. And the reliability values calculated using the MTEDC equalled to their true values. EBV of the daughters obtained from the two solving procedures for the complete MME system were equal too. The results proved that the DYD Formula [2] and the reliability Formula [4] are correct. A few combinations of other DYD formulae and reliability methods had been developed but none of them passed the verification test until this DYD and reliability Formulae. A similar verification study was done for a repeatability model and the DYD and associated reliability formulae were confirmed to be correct for the single trait model as well. Table 1 shows lactation DYD and EBV of the simulated bull during the course of lactation of his daughters. When all daughters had only two test day records in a lactation, which was fewer than the order of fit for genetic effects, DYD of the bull could not be estimated for this lactation. Even in this case EBV of the bull could be estimated, because both left- and right-hand-sides of the DYD based MME system existed in spite of the unestimable DYD. For short lactations DYD were greater than EBV, with the exception that both were nearly equal in cases of at least 100 daughters. Due to the way of simulation, greater DYD values than EBV indicated greater DYD variance than variance of EBV. As lactation made progress, the difference between DYD and EBV became smaller, and this was more evident with higher numbers of daughters. DYD of missing lactations were zero but corresponding EBV not. Adding 1000 lactations with one test each from second-crop daughters caused changes in both DYD and EBV for the bull. However, these changes were much smaller than those caused by short lactations of first-crop daughters.

It can be seen in Table 2 that, as lactations of daughters became longer or more complete, correlation of lactation DYD with EBV of bulls increased significantly. After average number of test day records of daughters reached five, the correlation was stabilized. DYD and EBV of later lactations were less correlated than first lactation, in particular when daughters had on average only three tests in a lactation. This can be explained by the fact that later lactation EBV were estimated from more sources of information including daughter information of earlier lactations, whereas first lactation EBV were influenced by first lactation daughter information and parental average only. Table 3 shows that correlation between lactation DYD and EBV increased slightly with the number of daughters. In Table 4 correlations of lactation DYD with EBV were close to unity, except for the youngest birth year, where bulls tended to have fewer daughters and higher percentage of daughters with incomplete lactations. Due to shorter lactations of second-crop daughters, bulls born in 1994, 1993, and 1991-1992, had slightly lower correlations for first, second and third lactation, respectively. Across all birth years of bulls, correlation between lactation DYD and EBV was 0.996 for all three lactations. Summarizing the correlations in Tables 2, 3, and 4, we can conclude that the DYD Formula [2] is accurate.

Table 1. Lactation DYD and EBV of the simulated bull from the verification study, expressed in genetic standard deviations.

No. of daughters	No. of tests by lactation			Lactation 1		Lactation 2		Lactation 3	
				DYD	EBV	DYD	EBV	DYD	EBV
50	2/	0/	0	§	.23	0	.17	0	.18
	3/	0/	0	.52	.25	0	.19	0	.19
100	3/	0/	0	.53	.27	0	.20	0	.21
	10/	0/	0	.34	.33	0	.27	0	.27
	10/	2/	0	.35	.34	§	.35	0	.34
	10/	3/	0	.35	.34	.63	.35	0	.35
	10/	10/	0	.35	.34	.42	.40	0	.39
	10/	10/	2/	.35	.34	.42	.41	§	.40
	10/	10/	3/	.35	.34	.42	.41	.67	.40
	10/	10/	10	.35	.34	.43	.42	.43	.42
+1000	1/	0/	0	.36	.36	.43	.42	.44	.43
	10/	1/	0	.36	.36	.45	.45	.45	.45
	10/	10/	10	.36	.36	.45	.45	.46	.46

§ DYD of this lactation could not be computed for the bull.

Table 2. Correlation of milk yield lactation DYD with EBV by average number of test day records of daughters for Black and White Holstein bulls that had at least 10 daughters with lactation passed 120 DIM and in at least 10 herds in May 2003 genetic evaluation.

Average no. of tests of daughters	Lactation 1		Lactation 2		Lactation 3	
	No. of bulls	Correlation	No. of bulls	Correlation	No. of bulls	Correlation
3	171	0.943	88	0.901	38	0.903
4	217	0.983	208	0.976	197	0.971
5	233	0.997	338	0.993	291	0.989
6	368	0.996	390	0.996	512	0.996
7	1210	0.997	1266	0.998	2080	0.997
8	7131	0.998	6220	0.998	4604	0.997
9	2111	0.998	1966	0.997	1131	0.997
10	35	0.993	41	0.997	17	0.987

Because the DYD Formula [2] expresses DYD in form of regression coefficients for RRTDM, any linear function of the regression coefficient estimates can be derived for individual bulls. For routine genetic evaluations, 305-day lactation DYD values and DYD lactation curves are published for bulls satisfying the requirement for official DYD mentioned above, in addition to lactation EBV and genetic lactation curves for bulls.

Table 3. Correlation of milk yield lactation DYD with EBV by number of daughters for Black and White Holstein bulls that had at least 10 daughters with lactation passed 120 DIM and in at least 10 herds in May 2003 genetic evaluation.

No. of daughters	Lactation 1		Lactation 2		Lactation 3	
	No. of bulls	Correlation	No. of bulls	Correlation	No. of bulls	Correlation
10-19	446	0.989	600	0.988	859	0.992
20-29	545	0.994	870	0.994	1216	0.994
30-39	528	0.996	824	0.994	1211	0.995
40-49	472	0.992	789	0.994	1105	0.996
50-59	409	0.994	967	0.995	976	0.996
60-69	523	0.991	1026	0.996	726	0.996
70-79	750	0.993	979	0.996	566	0.997
80-89	958	0.996	837	0.997	395	0.998
90-99	986	0.997	625	0.998	303	0.998
100-199	4182	0.998	1936	0.998	785	0.998
200-499	847	0.998	473	0.998	344	0.998
> 499	844	0.998	596	0.998	385	0.998

Table 4. Correlation of milk yield lactation DYD with EBV by birth year for Black and White Holstein bulls that had at least 10 daughters with lactation passed 120 DIM and in at least 10 herds in May 2003 genetic evaluation.

Birth year	Lactation 1		Lactation 2		Lactation 3	
	No. of bulls	Correlation	No. of bulls	Correlation	No. of bulls	Correlation
1986	746	0.996	1122	0.996	1094	0.995
1987	1021	0.996	1010	0.996	960	0.995
1988	1063	0.997	1053	0.997	1013	0.996
1989	775	0.997	759	0.997	720	0.997
1990	808	0.997	790	0.997	755	0.997
1991	835	0.998	818	0.996	783	0.994
1992	888	0.997	863	0.996	814	0.995
1993	945	0.996	904	0.994	874	0.995
1994	970	0.994	933	0.996	910	0.995
1995	1039	0.997	1025	0.996	863	0.987
1996	1075	0.998	1001	0.992	85	0.953
1997	1036	0.990	244	0.941		
1998	289	0.960				
All	11,490	0.996	10,522	0.996	8871	0.996

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Appendix. Derivation of the formula for computing daughter yield deviations of bulls under multiple trait models

Formula [2] is used for computing DYD of bulls under general multiple trait models, including RRTDM. To derive the DYD formula for multiple trait models, we apply here a similar approach as used by VanRaden and Wiggans (1991) for single trait model. Assuming a cow i has own performance records and no progeny, equations of genetic effects for the cow i can be written in a general way as follows

$$\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{X}_i\hat{\mathbf{b}} + \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_{pi}\hat{\mathbf{p}}_i + (\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + a_*^{ii}\mathbf{G}_0^{-1})\tilde{\mathbf{a}}_i - \tfrac{1}{2}d_i\mathbf{G}_0^{-1}(\tilde{\mathbf{a}}_s + \hat{\mathbf{a}}_d) = \mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{y}_i, \quad \text{[A1]}$$

where EBV of dam of the cow ($\hat{\mathbf{a}}_d$) are obtained from a complete evaluation system, e.g. from a national genetic evaluation. $\tilde{\mathbf{a}}_i$ is EBV of the cow *i* that were estimated as if only her own performance and her parents made contribution to her EBV. $\tilde{\mathbf{a}}_s$ is EBV of sire of the cow *i* that were estimated as if only his daughters contributed to his EBV. For computing the contribution of the cow to her sire's DYD, only performance records of her own are considered, and the contribution of her progeny to her EBV must be ignored, because her daughters' records make contribution to her mates' DYD and her grand-daughters' to her sons. d_i is diagonal element pertinent to cow *i* in inverse of (co)variance matrix of Mendelian sampling $\mathbf{D}^{-1}$ (Mrode, 1996, pp28). Without own progeny, $d_i = a_*^{ii}$. Note that the sire and his mate are allowed to be inbred. Re-writing Equation [A1] gives EBV of the cow based on her own records and parental information $\tilde{\mathbf{a}}_i = \mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\boldsymbol{\varepsilon}_i + \tfrac{1}{2}d_i\mathbf{Q}_i\mathbf{G}_0^{-1}(\tilde{\mathbf{a}}_s + \hat{\mathbf{a}}_d)$, [A2]
where $\boldsymbol{\varepsilon}_i = \mathbf{y}_i - \mathbf{X}_i\hat{\mathbf{b}} - \mathbf{Z}_{pi}\hat{\mathbf{p}}_i$ and $\mathbf{Q}_i = (\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + a_*^{ii}\mathbf{G}_0^{-1})^{-1}$.

Define average yield deviations for the cow *i* as $\mathbf{c}_i = (\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i)^{-1}\mathbf{Z}_i'\mathbf{R}_i^{-1}\boldsymbol{\varepsilon}_i$. [A3]
For RRTDM $\mathbf{c}_i$ are expressed in form of regression coefficients. Lactation or average yield deviations do not exist for a lactation of the cow *i* when she has fewer tests in the lactation than the order of fit for genetic effects. Replacing $\boldsymbol{\varepsilon}_i$ in Equation [A2] with $\mathbf{c}_i$ gives

$$\tilde{\mathbf{a}}_i = \mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i\mathbf{c}_i + \tfrac{1}{2}d_i\mathbf{Q}_i\mathbf{G}_0^{-1}(\tilde{\mathbf{a}}_s + \hat{\mathbf{a}}_d) . \quad \text{[A4]}$$

Because no other sources of information are involved, $\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i + d_i\mathbf{Q}_i\mathbf{G}_0^{-1} = \mathbf{I}$. [A5]

Genetic effect equations for a bull without own performance can be written as

$$a^{ss}\mathbf{G}_0^{-1}\tilde{\mathbf{a}}_s = \tfrac{1}{2}d_s\mathbf{G}_0^{-1}(\hat{\mathbf{a}}_{ss} + \hat{\mathbf{a}}_{ds}) + \sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}(\tilde{\mathbf{a}}_i - \tfrac{1}{2}\hat{\mathbf{a}}_d), \quad \text{[A6]}$$

where $\hat{\mathbf{a}}_{ss}$ and $\hat{\mathbf{a}}_{ds}$ represent EBV of sire and dam of the bull, respectively. d_s is diagonal element of matrix $\mathbf{D}^{-1}$ (Mrode, 1996, pp28) for the bull. Note that no male progeny of the bull is considered, because his sons do not have own production records. $a^{ss} = d_s + \sum_{i=1}^{n}\tfrac{1}{4}d_i$, [A7]
where *n* is number of daughters with data. Substituting Equation [A4] into [A6] by treating the cow *i* as one of *n* daughters of the bull gives

$$a^{ss}\mathbf{G}_0^{-1}\tilde{\mathbf{a}}_s = \tfrac{1}{2}d_s\mathbf{G}_0^{-1}(\hat{\mathbf{a}}_{ss} + \hat{\mathbf{a}}_{ds}) + \sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}(\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i\mathbf{c}_i + \tfrac{1}{2}d_i\mathbf{Q}_i\mathbf{G}_0^{-1}(\tilde{\mathbf{a}}_s + \hat{\mathbf{a}}_d) - \tfrac{1}{2}\hat{\mathbf{a}}_d) . \quad \text{[A8]}$$

Accumulating the terms involving $\tilde{\mathbf{a}}_s$ to the left side of Equation [A8] leads to

$$\mathbf{G}_0^{-1}(a^{ss}\mathbf{I} - \sum_{i=1}^{n}\tfrac{1}{4}d_i^2\mathbf{Q}_i\mathbf{G}_0^{-1})\tilde{\mathbf{a}}_s = \tfrac{1}{2}d_s\mathbf{G}_0^{-1}(\hat{\mathbf{a}}_{ss} + \hat{\mathbf{a}}_{ds}) + \sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}[\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i\mathbf{c}_i - (\mathbf{I} - d_i\mathbf{Q}_i\mathbf{G}_0^{-1})\tfrac{1}{2}\hat{\mathbf{a}}_d] \quad \text{[A9]}$$

Based on Equation [A5], right side of Equation [A9] can be simplified to

$$\tfrac{1}{2}d_s\mathbf{G}_0^{-1}(\hat{\mathbf{a}}_{ss}+\hat{\mathbf{a}}_{ds})+\sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i(\mathbf{c}_i-\tfrac{1}{2}\hat{\mathbf{a}}_d).$$

Let $\mathbf{B}=\sum_{i=1}^{n}\tfrac{1}{4}d_i\ \mathbf{G}_0^{-1}(\mathbf{I}-d_{a_i}\mathbf{Q}_i\mathbf{G}_0^{-1})=\sum_{i=1}^{n}\tfrac{1}{4}d_i\ \mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i$, [A10]

$$\boldsymbol{\xi}=\sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i(\mathbf{c}_i-\tfrac{1}{2}\hat{\mathbf{a}}_d)=\sum_{i=1}^{n}\tfrac{1}{2}d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}(\mathbf{y}_i-\mathbf{X}_i\hat{\mathbf{b}}-\mathbf{Z}_{pi}\hat{\mathbf{p}}_i-\tfrac{1}{2}\mathbf{Z}_i\hat{\mathbf{a}}_d), \quad \text{[A11]}$$

thus DYD formula for general multiple trait models is obtained as

$$\mathbf{q}=\mathbf{B}^{-1}\boldsymbol{\xi}=2(\sum_{i=1}^{n}d_i\ \mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}\mathbf{Z}_i)^{-1}\sum_{i=1}^{n}d_i\mathbf{G}_0^{-1}\mathbf{Q}_i\mathbf{Z}_i'\mathbf{R}_i^{-1}(\mathbf{y}_i-\mathbf{X}_i\hat{\mathbf{b}}-\mathbf{Z}_{pi}\hat{\mathbf{p}}_i-\tfrac{1}{2}\mathbf{Z}_i\hat{\mathbf{a}}_d). \quad \text{[A12]}$$