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Complete List of Authors:	Uddin, Md Elias; University of Wisconsin Madison, Dairy Science; Bangladesh Agricultural University, Dairy Science Meuwissen, Theo; Norwegian University of Life Sciences, Department of Animal and Aquaqultural Sciences Veerkamp, Roel; Animal Sciences Group, Wageningen University and Research Centre, Animal Breeding and Genomics Centre;
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Adjusting for heterogeneity of experimental data in genetic evaluation of dry matter intake in dairy cattle

Authors: Md Elias Uddin[1], Theodorus Meuwissen[1] and R. F. Veerkamp[2]

[1]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, Aas, Norway

[2]Animal Breeding and Genomics Centre, Wageningen UR, Wageningen, The Netherlands

Corresponding Author: Theodorus Meuwissen, Email: theo.meuwissen@nmbu.no , Cell: + 47 67232674,

Abstract

The objectives of the present study were i) to find the best fitted model for repeatedly measured daily dry matter intake (DMI) data obtained from different herds and experiments across lactations and ii) to get better estimates of the genetic parameters and better genetic evaluations. After editing, there were 572,512 daily DMI records of 3495 animals from 11 different herds across 13 lactations and the animals were under 110 different nutritional experiments. The fitted model for this dataset was a univariate repeated measure animal model in which additive genetic and permanent environmental (within and across lactations) effects were fitted as random. Two different models were fitted based on alternative fixed effects corrections. For unscaled data, each model was fitted as a homoscedastic (HOM) model first and then a heteroscedastic (HET) model. After that, data were scaled by multiplying with particular herd-scaling factors, which were calculated by accounting for heterogeneity of phenotypic within herd variances. Models were selected based on cross-validation and prediction accuracy results. Scaling factors were re-estimated to determine the effectiveness of accounting for herd heterogeneity. Variance components and respective heritability and repeatability were estimated based on a pedigree based relationship matrix. Spearman's rank correlations of estimated breeding values (EBVs) between scaled and unscaled DMI were also calculated. Results indicated that the model fitted for scaled data showed better fit than the models (HOM or HET) fitted for unscaled data. The heritability estimates of the model 2 and 3 fitted for scaled data were 0.30 and 0.08, respectively. The repeatability estimates of the model fitted for scaled data ranged from 0.51 to 0.63. The re-estimated scaling factor after accounting for heterogeneity of residual variances was close to 1.0 indicating the stabilization of residual variances and herd accounted for most of the

heterogeneity. The rank correlation of EBVs between scaled and unscaled data ranged from 0.96 to 0.97.

Keywords: Dry Matter Intake, Heterogeneity, Heritability, Repeatability, Genetic Evaluation, Dairy Cattle

Introduction

Feed cost is one of the major recurring costs of dairy farming. It comprises 43-67% of total farming cost in different countries (Simm et al., 1994; Shalloo et al., 2004; Ho et al., 2005). It is even higher (about 80% of the total recurring cost) if one considers only milk production cost (Board, 1990). Therefore, genetic improvement of feed efficiency traits could make dairy farming economically more profitable and viable. Moreover, the more efficient the cow is, the less methane she emits per kg milk (Hegarty et al., 2007)**.** Although feed efficiency is a complex trait in almost all farm animals it can be considered in selection programs for beef cattle, pigs and poultry. But for dairy cattle, it is even more complex because many physiological processes such as milk production, reproduction, maintenance of health and body and growth in young cows happen simultaneously. More importantly, it is expensive and difficult to measure individual feed intake of dairy animals (Veerkamp & Emmans, 1995; Arthur et al., 2004) and feed intake data are not easily recorded in commercial dairy herds, therefore, most of the previous estimates of the genetic parameters for feed intake and feed efficiency traits were based on small datasets which has made the estimates unreliable due to large sampling errors (Pech et al., 2014). For this reason, the traits that were emphasized in selection strategy for dairy development in the past decades were mainly related to production and health of dairy cows.

With the invention of the genomic selection (GS) (Meuwissen et al., 2001) tool, feed efficiency traits have become of research interest and been considered in selection programs. In GS, only the reference population (sometimes called the training population) needs to have both phenotypic and genotypic information, while genomic estimated breeding values (GEBVs) can be estimated for candidate animals having only genotypic information without phenotype (Meuwissen, 2007). Therefore, GS seems very suited to difficult and expensive to measure traits like feed intake and feed efficiency (Pryce et al., 2014). To achieve satisfactory genetic gain from GS, accuracy of GEBVs is very important. So far, much research have been conducted to evaluate the accuracy of GEBVs (Khansefid et al., 2013). Past research results and theories

reveal that the numbers of animals genotyped and precision of the phenotype measured are the most important factors affecting the reliability of GEBVs (VanRaden et al., 2009). One could increase accuracy of GEBVs by increasing the size of the reference population. Incorporation of multi-breed animals having genotypic and phenotypic information is one of the options to increase the size of reference population. However, multi-breed reference populations did not work well to increase the accuracy of GS (Khansefid et al., 2013) because of i) breed × quantitative trait loci (QTL) interaction ii) variation of linkage disequilibrium (LD) between QTL and single nucleotide polymorphisms (SNPs) among breeds and iii) low LD across the breeds, and it is even limited to SNPs that are close to QTL. Another way to increase reference population size is combining data from different populations from several countries because each country has a small reference population insufficient to achieve satisfactory level of accuracy (Verbyla et al., 2010). Major problems of combining phenotypic data from different countries are genotype × environment interaction and variation of trait's definition among countries (De Haas et al., 2012). There are very limited opportunities to get enough and accurate phenotypic data for difficult-to-measure traits like feed intake, so, for feed intake, another option of increasing the reference population size might be the use of historical nutritional experimental data in which people have already recorded such difficult to measure and expensive trait on dairy animals (Banos et al., 2012; Pryce et al., 2012; Veerkamp et al., 2012). For example, the global Dry Matter Initiative (gDMI) was formed to increase the size of the reference population by combining international research animal's phenotype and genotype (Berry, 2013; Veerkamp, 2013). The main challenge of using experimental data is the wide variability of the phenotypes measured from different nutritional experiments, mainly due to different treatments used in those experiments and animals being from different herds and parities. An approach was developed by Banos et al. (2012) who described in detail how to combine phenotypic data of dairy cattle collected from experimental sources in three different countries. These data were successfully used for genome-wide association study (GWAS) by Veerkamp et al. (2012) to detect the significant QTL of feed intake. For genomic prediction, De Haas et al. (2012) showed the reduction of prediction accuracy assuming feed intake was the same trait across populations. However, estimating genetic correlation between small populations is difficult and prone to large estimation errors. Therefore, looking for an alternative model particularly using within country but across different herds DMI data adjusted for different variances across herds would may be

feasible.The objectives of the present study were i) to find the best fitted model suitable for repeatedly measured DMI data originating from multiple nutritional experiments across experimental herds, years and parities in the Netherlands and ii) to obtain improved estimates of the genetic parameters and genetic evaluation of the animals.

Materials and Methods

Data Description and Editing

The original dataset consisted of 637,471 records repeatedly measured on 3771 Holstein cows from 11 herds across 13 parities in Netherlands. Cows were from 110 different nutritional experiments subjected to different treatments in those experiments. Data were collected from 1991 to 2015 on cows calved between 1990 to 2015. Cows having at least one daily DMI record were kept in the dataset for further analysis and cows without DMI records were removed from the dataset. In addition to feed intake data, other related information on individual cows such as daily milk yield, live weight and calving interval were also available but these data were not used. As data collection were not performed specifically for the present study, there were some extreme values in the dataset and some of the values were even beyond the biological limit. To remove extreme data, editing was performed manually by setting certain biological limits for the different variables or traits as proposed by Banos et al. (2012) (Table 1).

After editing, there were 572,512 daily DMI records from 3495 cows across 11 herds and each cow has at least a single DMI record. After editing, there were 109 experiments retained subjected to 467 different treatments in those experiments. Data retained after editing have been summarized in Table 2.

Pedigree Information

A traditional relationship matrix (A-matrix) was generated based on the available pedigree data. The pedigree file consisted of 18,566 animals among which 15,867 animals were the parents.

Model Fitting

A univariate repeated measure animal model was fitted for this dataset and the model is given below in matrix notation.

$$\boldsymbol{y = Xb + Z_1 p + Z_2 a + e} \quad \text{..... 1(a)}$$

Where, **y** is a vector of n observations, **b** is a vector of fixed effects, **p** is a vector of permanent environmental effects, **a** is a vector of additive genetic effects, **e** is a vector of random residual variances, and **X, Z_1 and Z_2** are incidence matrices which relate **b, p** and **a** to **y**, respectively. The assumptions of random effects of the model have shown below.

$$\begin{bmatrix} \boldsymbol{a} \\ \boldsymbol{p} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} A\sigma_a{}^2 & 0 & 0 \\ 0 & I_d\sigma_c{}^2 & 0 \\ 0 & 0 & I_n\sigma_e{}^2 \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \qquad G = \begin{bmatrix} A\sigma_a{}^2 & 0 \\ 0 & I_d\sigma_c{}^2 \end{bmatrix} \text{.....1(b)}$$

where, $\sigma_a{}^2$ is the additive genetic variance, $\sigma_c{}^2$ is the variance due to permanent environment, and $\sigma_e{}^2$ is the residual variance, $\sigma_p{}^2$ is the phenotypic variance which is the sum of these three variance components, **A** is the pedigree based relationship matrix, I_d is the identity matrix equal to the number of animals included in the pedigree and I_n is the identity matrix equal to the number of observations.

Usually best fitted models have relatively more parameters but available data do not always support the estimation of all these parameters. There were a number of models tried from simple to complex by exploratory exercises but two models (called model 2 and 3) were compared and these are shown below in model terms.

$$DMI = \mu + a + p + \text{Herd} \cdot \sum_{n=1}^{3} DIM^n + \text{TD} + \text{treatment}\,(experiment) + \text{parity}\left(\sum_{n=1}^{2} age\_calving^n\right) + e$$

..... 2

$$\boldsymbol{DMI = \mu + a + p + Herd \cdot \sum_{n=1}^{3} DIM^n + TD \cdot Herd + treatment\,(experiment) + parity\left(\sum_{n=1}^{2} age\_calving^n\right) + e}$$

.....3

Where, DMI is the daily DMI observations, μ is the overall mean, a is the random additive genetic effect, p is the random term for combined permanent environmental effect (within and across lactations), $\text{Herd} \cdot \sum_{n=1}^{3} DIM^n$ is fixed effect for interaction between Herd and third order polynomial of Days In Milk (DIM), TD is fixed effect of Test Day, $\text{treatment}\,(experiment)$ is the fixed effect of treatment nested within experiment, $\text{parity}(\sum_{n=1}^{2} age\_calving^n)$ is fixed effect of parity fitted as co-variate and nested in second order polynomial of age at calving

expressed in months, TD.Herd is fixed effect of herd and test day interaction; e is the random residual error.

At first it was assumed that the residual variances for all the observations are homogeneous. So, the diagonal elements of matrix R in equation 1(b) was equal for all observations which is σ_e^2 and the fitted model is called the homoscedastic model (HOM). As DMI was recorded on animals from 11 different herds across 13 lactations over 25 years (1991 to 2015) and animals were under different nutritional experiments, it was not realistic to assume the residual variances as homogeneous. That is why, the heteroscedastic model (HET) was also fitted assuming different diagonal elements of matrix R for different herds. For example, σ_{ei}^2 is the residual variances of i^{th} herd. Based on homogeneity or heterogeneity of residual variances, we fitted model 2 as two distinct models namely 2A (HOM) and 2B (HET) model, respectively.

In the second step, we fitted 2B model for herds but excluding additive and permanent environmental effect. From this model, we got the heterogeneous phenotypic variances for each herd. A weighting factor (f_i) for each herd was calculated based on the estimated herd phenotypic variances as shown in Equation 4.

$$f_i = \frac{\sqrt{\overline{V_i}}}{\sqrt{V_i}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4$$

Where, f_i is the weighting factor for observations of i^{th} herd (i = 1, 2 ……11); $\sqrt{\overline{V_i}}$ is square root of average phenotypic variances for all herds, $\sqrt{V_i}$ is square root of phenotypic variances for the i^{th} herd,

Observations of each herd were then multiplied by their respective weighting factor f_i to get scaled observations with homogeneous phenotypic variance. Scaled observations were fitted again in model 2 called model 2C. Finally, model 2A, 2B and 2C were compared based on model selection criteria (described below).

The same procedure was followed for model 3 and fitted models were named as model 3A (HOM model), 3B (HET model) and 3C (scaled DMI data).

Heterogeneous herd residual variances and scaling factors were re-estimated in a similar manner for the scaled data to see the effectiveness of scaling for herd heterogeneity.

Criteria for Model Comparisons

Initially Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were used to compare the models. Then prediction accuracy (correlation between DMI observations or scaled DMI and predicted DMI) was used to assess the predictability of the model. Additionally, 10-fold cross-validation was performed for comparing the models. For this purpose, the whole dataset was equally and randomly divided into 10-subsets (disjoint). Each time, 9-subsets were considered as training dataset and the remaining one was called testing set. After training the model in the training set, the model was validated using the testing set and mean squared error (MSE) of each testing fold were recorded for each model. Then, the MSE of the testing folds were averaged across all 10 testing sets. The model giving the lowest average MSE was considered as the best fitted model.

Estimation of Variance Components and Genetic Parameters

Additive genetic ($\hat{\sigma}_a{}^2$), permanent environmental ($\hat{\sigma}_c{}^2$) and residual ($\hat{\sigma}_e{}^2$) variance components were estimated for all the models using the pedigree based relationship matrix. Respective heritability ($\hat{h}^2$) and repeatability ($\hat{t}$) were calculated based on the estimated variance components.

$$\hat{h}^2 = \frac{\hat{\sigma}_a{}^2}{\hat{\sigma}_a{}^2+\hat{\sigma}_c{}^2+\hat{\sigma}_e{}^2} = \frac{\hat{\sigma}_a{}^2}{\hat{\sigma}_p{}^2} \quad \text{.....5}$$

$$\hat{t} = \frac{\hat{\sigma}_a{}^2+\hat{\sigma}_c{}^2}{\hat{\sigma}_a{}^2+\hat{\sigma}_c{}^2+\hat{\sigma}_e{}^2} = \frac{\hat{\sigma}_a{}^2}{\hat{\sigma}_p{}^2} \quad \text{.....6}$$

Comparing Rankings of Animals based on EBVs

Changes of the rankings of the animals based on their EBVs from different models were compared by Spearman's rank correlation coefficients using the SPSS software package.

All the data analyses performed were based on the REML method and the software package used for analysis was ASReml 4.1 (Gilmour et al., 2014) except for Spearman's rank correlation. Heteroscedastic models were fitted by the 'sat' function of ASReml 4.1 package, for example, 'residual sat(Herd).idv(units)' is a function used to partition heterogeneous residual variances by herd.

Results

Model Comparison

AIC, BIC, average MSE of prediction, and prediction accuracy for all fitted models are shown in Table 3. For unscaled data, the HET model showed a better fit than the HOM model according to AIC, BIC and average MSE criteria, and similar trend was found both for model 2 and 3 (Table 3). However, the prediction accuracy of unscaled data was same for both the HOM and HET models. Although AIC and BIC criteria did not favour the model fitted for scaled data but based on average MSE and prediction accuracy, the model fitted for scaled data was found as best fitted model. Scaling of data improved prediction accuracy noticeably regardless of fitting either model 2 or model 3 but MSE and prediction accuracy did not differ due to fitting either model 2 or model 3 for scaled data (Table 3).

Variance Components

Estimates of the variance components and respective standard errors (se) are presented in Table 4. In the case of unscaled data, the estimate of the additive genetic variance ($\hat{\sigma}_a^2$) was slightly higher for the HET model than the HOM model (Table 4). In contrast, when the model 2 was fitted for scaled data, the estimate of the $\hat{\sigma}_a^2$ was approximately 2.5 times higher than for unscaled data. For model 3, there was also a substantial increase of $\hat{\sigma}_a^2$ but the increment was lower in comparison to model 2. On the other hand, permanent environmental variance ($\hat{\sigma}_c^2$) showed an opposite trend for both model 2 and 3. For unscaled data, the estimate of the $\hat{\sigma}_c^2$ was lower for the HET than the HOM model and it was even lower for scaled data (Table 4). Residual error variance ($\hat{\sigma}_e^2$) showed the similar trend to $\hat{\sigma}_c^2$.

Heritability and Repeatability

Both the heritability and repeatability estimates of model 2 were higher for the HET model than the HOM model in the case of unscaled data and it was even higher when the model 2 was fitted for scaled data (Figure 1). Model 3 showed a similar trend but the estimates of the heritability for model 3 were much lower compared to model 2. Estimates of the $\hat{h}^2$(se) for model 2A, 2B and 2C were 0.11 (0.009), 0.15 (0.01) and 0.30 (0.01), respectively. Heritability estimates were 0.05 (0.07), 0.07 (0.008) and 0.08 (0.008), respectively for model 3A, 3B and 3C. Repeatability estimates were very similar between model 2 and 3 and ranged from 0.45 to 0.63.

From the HET model 2B and 3B, within herd $\hat{h}^2$ and $\hat{t}$ were obtained (Figure 2). Although the trend of $\hat{h}^2$ and $\hat{t}$ across herds were similar for both models, the estimates of model 2B was higher for both the heritability and repeatability. Estimates of $\hat{h}^2$ ranged from 0.11- 0.21 and 0.05 -0.09 for model 2B and 3B, respectively. Repeatability estimates ranged from 0.40 to 0.80.

Rank Correlations of EBVs

Table 5 shows the Spearman's rank correlations of EBVs among different models. Rank correlation of EBVs between model 2A and 2B or model 3A and 3B was approximately 1.0 indicating similar ranking of animals between the HOM and the HET models fitted for unscaled data (Table 5). However, EBV ranking of the animals changed after scaling data. Rank correlations for EBVs between scaled and unscaled data were 0.91-0.92 for model 2 and 0.96-0.97 for model 3.

Comparison of Heterogeneous Residual Herd Variance before and after Scaling Data

Heterogeneous residual variances by herds before and after scaling the data are presented in Figure 3. Before scaling the data, there was a wide variability of residual variances across herds found for both models (Figure 3). For scaled data, although there was a little variability of residual variances but it seemed to be similar across herds for both models indicating the stabilization of heterogeneous herd residual

Discussion

Model Selection

For unscaled data, the HET model fitted slightly better than the HOM model based on AIC, BIC and average MSE criteria but the prediction accuracy was same for both the HOM and the HET model (Table 3). Similar trends were noticed for both model 2 and 3. The findings of a previous study on body weight traits in beef cattle by Neves et al. (2012) disagree with our results i.e. they found a better fit for the HOM model than the HET model according to BIC and average MSE criteria. They also found a better fit of the HET model than the HOM model when considering AIC as selection criteria. Moreover, when fitting sex specific models they also found a higher predictive ability (lower average MSE) of the HET model than the HOM model for body weight in females. Although scaling slightly increased AIC and BIC values for the model 2 or 3 fitted

for scaled data but scaling of data decreased the average MSE and increased prediction accuracy of the model. Increase of prediction accuracy was not surprising, because it may be expected that scaled data will fit better than unscaled data. Clearly it indicates that the models fitted for scaled data were the best fitted models. From a past study with swine body weight and backfat thickness trait, it was concluded that the scaled data accounting for heterogeneous herd variances fit better than unscaled data which is consistent with our findings (Pujol et al., 1998).

Estimation of Variance Components

In the case of unscaled data, the estimates of variance components were very similar for the HOM and the HET model. Neves et al. (2012) also found similar estimates of variance components for HOM and HET models for body weight traits in Nellore beef cattle. After scaling data, there was a slight increase of additive genetic variances for model 3 but the increment was much bigger for model 2 (Table 4). In the case of model 2, the fixed effect of TD (Test Day) was fitted within herd which might be one of the reasons for getting higher estimates of additive genetic variance in this model. On the contrary, TD-by-Herd interaction effect was included as fixed term in model 3 which is more realistic because the TD effect may be expected to vary from herd to herd. Another reason for getting model sensitive estimates of heritability might be that models had difficulties in separating fixed effect, permanent environmental effect and additive genetic effect due to a lack of connectedness between TD and Herd. A previous study also pointed to a slight increase of variance components estimate for weight traits of swine after scaling the data which is in complete agreement with the results of model 3 (Pujol et al., 1998). On the other hand, estimates of both permanent environmental and residual variance components decreased after accounting for heterogeneity of herd variances indicating a better fit of the model for scaled data (Table 4).

Heritability and Repeatability

Heritability was doubled to tripled for both model 2 and 3 after scaling the data but repeatability estimates were very similar for both scaled and unscaled data. For the final model (i.e. the model fitted with scaled data), the estimate of the heritability from model 3 (0.08) was much lower than model 2 (0.30). Explanations for this were provided in the previous section on estimates of additive genetic variances. The heritability estimates of model 2 are consistent with the estimates of 0.27 to 0.34 reported by Berry (2013). Although heritability estimates of model 3 were much

lower they fall still in the range of within country heritability estimates (0.08 to 0.52) which were also documented by Berry (2013). Banos et al. (2012) found the heritability ranging from 0.15 to 0.22 for daily DMI in dairy cows however they used only first lactation DMI records. When only first lactation DMI data were included in our analysis, estimates of heritability increased slightly (result not shown). The heritability estimates for the final model (i.e. the model fitted for scaled data from first lactation cows only) were 0.39 and 0.10 for model 2 and model 3, respectively. Berry (2013) also reported a substantial increase of DMI heritability from 0.08 to 0.16 when pedigree based relationship matrix was replaced by a combined pedigree and genomic relationship matrix indicating the potentiality of using genomic information to improve heritability estimates.

In our study, repeatability (within and across lactations) estimates ranged from 0.51 to 0.63 for the final model (i.e. the model with scaled DMI). When within and across lactations repeatability were separated, it did not affect the estimates of repeatability and heritability (data not shown). Although there is not much information available for across lactations DMI repeatability but our finding agrees with the previous repeatability (across lactations) estimate of 0.51 reported by Søndergaard et al. (2002) in Denmark for 293 dairy cows from three different breeds. Findings of Berry (2013) were also consistent to our results and they found across lactations repeatabilities ranging from 0.46 to 0.84 using experimental DMI data collated from 9 different countries of 6,957 dairy cows. They also reported identical repeatability estimates using either only pedigree information or combined pedigree and genomic information for generating relationship matrix.

Scaling of Data

Estimates of scaling factors for 11 different herds varied from 0.68 to 1.29 for model 2 and 0.77 to 1.22 for model 3 indicating a wide variability among herds. This signifies the necessity of taking into account the herd heterogeneity in consideration. Re-estimated within herd residual variances of scaled DMI were similar across herds and this is reflecting that the scaling stabilized the variability (data not shown). In other words, one could say that most of the heterogeneity came from herds. In fact, re-estimated scaling factors using scaled DMI were close to 1.0 which proofs the effectiveness of data scaling.

Comparison of EBV Ranking of Cows

For unscaled data, the spearman's rank correlation between EBVs of the HOM and the HET model was 0.99 (close to 1.0). This indicates that there were limited changes of EBVs due to the heterogeneity of variance correction in the HET model. But, the rank correlations between EBVs before and after scaling the data were 0.92 for model 2 and 0.97 for model 3. This means that the EBV ranking of cows' changes due to scaling of data and the change was more prominent in model 2 than in model 3. The rank correlation of EBVs before and after scaling the data for swine production traits was 0.98 (Pujol et al., 1998) which is similar to the results of our study. The results also suggest that accounting for heterogeneity of within herd variances by scaling of the data improved the precision of the genetic evaluation of dairy cows.

Conclusions

Although the HET model fitted better than the HOM model in the case of unscaled data, the model models for scaled data showed the best fit. The heritability estimates of the model 2 and 3 fitted for scaled data were 0.30 and 0.08, indicating that including a herd by test-date effect explained variance that otherwise was interpreted as genetic variance. The repeatability estimates of the model 2 and 3 fitted for scaled data ranged from 0.51 to 0.63 which is consistent with previous literature findings. The re-estimated scaling factor, after accounting for heterogeneity of residual variances, was close to 1.0 indicating that the stabilization of within herd variances and most of the heterogeneous variances originated from the herds. The rank correlation of EBVs between scaled and unscaled data ranged from 0.96 to 0.97, and the scaled data showed a considerable smaller mean square error of prediction. Thus, scaling data that accounted for the heterogeneity of herd variances, may improve the accuracy of genetic evaluations.

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Adjusting for heterogeneity of experimental data in genetic evaluation of dry matter intake in dairy cattle

Authors: Md Elias Uddin[1], Theodorus Meuwissen[1] and R. F. Veerkamp[2]

[1]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, Aas, Norway

[2]Animal Breeding and Genomics Centre, Wageningen UR, Wageningen, The Netherlands

Corresponding Author: Theodorus Meuwissen, Email: theo.meuwissen@nmbu.no , Cell: + 47 67232674,

Table 1. Biological limits set for editing the original records

Trait/Variable	Unit of Measurement	Acceptable Range
DMI	Kg/d	0.89 to 65
Days in Milk (DIM)	Days	1 to 400
Live Weight	Kg	400 to 1200
Milk Yield	Kg/d	3 to 100
Lactation (Parity)	Number	1 to 13

Table 2. Data summary after editing

Variable	Class Size/Range/Average
Total number of DMI records	572,512
Number of cows having at least single records	3495
Average number of records per cow (Range)	168.80 (1 to 1076)
Number of herds	11
Number of experiments	109
Number of treatments	467
Number of Lactation (Parity)	1 to 13
Year of recording	1991 to 2015
Calving year	1990 to 2015
Average DMI (SD*) Kg/d	17.95 (6.49)
Average age at recording in months (Range)	52.64 (21 to 189)
Average age at calving in months (Range)	47.76 (19 to 175)
Average days in milk (DIM)	126.6

* SD stands for standard deviation

Table 3. AIC, BIC, average MSE and prediction accuracy of the models

Model	Type of model	Data type	AIC[1]	BIC[2]	Average MSE[3] of prediction	Prediction accuracy
2A[4]	HOM[7]	Unscaled[9]	194518.2	194545	14.36	0.81
2B[5]	HET[8]	unscaled	189020.6	189074.3	13.68	0.81
2C[6]		Scaled[10]	192158.4	192185.2	10.46	0.85
3A	HOM	unscaled	194466.4	194493.3	14.36	0.81
3B	HET	unscaled	188995.6	189049.3	13.84	0.81
3C		scaled	192019.5	192046.4	10.46	0.85

[1]Akaike Information Criterion, [2]Bayesian Information Criterion, [3]Mean Squared Error, [4]Homoscedastic model fitted for unscaled data, [5]Heteroscedastic model fitted for unscaled data, Model fitted for scaled data, [7]Homoscedastic model, [8]Heteroscedastic model, [9]Data before adjusting for heterogeneity, [10]Data after adjusting for heterogeneity

Table 4. Variance components and respective standard errors (within parenthesis) estimates of unscaled and scaled data for different HOM and HET models

Model	Type of model	Data type	$\hat{\sigma}_a^2$ (se)[8]	$\hat{\sigma}_c^2$ (se)[9]	$\hat{\sigma}_e^2$ (se)[10]	$\hat{\sigma}_p^2$ (se)[11]
2A[1]	HOM[4]	Unscaled[6]	3.22 (0.30)	11.53 (0.26)	14.68 (0.02)	29.43 (0.30)
2B[2]	HET[5]	Unscaled	3.83 (0.33)	11.31 (0.26)	10.72 (0.19)	25.86 (0.40)
2C[3]		Scaled[7]	8.42 (0.46)	9.42 (0.23)	10.69 (0.02)	28.53 (0.43)
3A	HOM	unscaled	1.29 (0.19)	10.84 (0.23)	14.67 (0.02)	26.80 (0.62)
3B	HET	unscaled	1.45 (0.19)	10.61 (0.23)	10.67 (0.18)	22.72 (0.33)
3C		scaled	1.69 (0.20)	9.32 (0.21)	10.68 (0.02)	21.69 (0.62)

[1]Homoscedastic model fitted for unscaled data, [2]Heteroscedastic model for unscaled data, [3]Model fitted for scaled data, [4]Homoscedastic model, [5]Heteroscedastic model, [6]Data before adjusting for heterogeneity, [7]Data after adjusting for heterogeneity, [8]Additive genetic variance, [9]Permanent environmental variance, [10]Residual error variance, [11]Phenotypic variance

Table 5. Spearman's rank correlation of EBVs

Models	Spearman's rank correlations					
	2A	2B	2C	3A	3B	3C
2A[1]	1.0	0.99**	0.92**	0.77**	0.73**	0.74**
2B[2]	0.99**	1.0	0.91**	0.74**	0.72**	0.73**
2C[3]	0.92**	0.91**	1.0	0.63**	0.61**	0.68**
3A	0.77**	0.74**	0.63**	1.0	0.99**	0.96**
3B	0.73**	0.72**	0.61**	0.99**	1.0	0.97**
3C	0.74**	0.73**	0.68**	0.96**	0.97**	1.0

[1]Homoscedastic model fitted for unscaled data, [2]Heteroscedastic model for unscaled data, [3] Model fitted for scaled data, ** Level of significance at 1%

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Corresponding Author: Theodorus Meuwissen, Email: theo.meuwissen@nmbu.no , Cell: + 47 67232674,

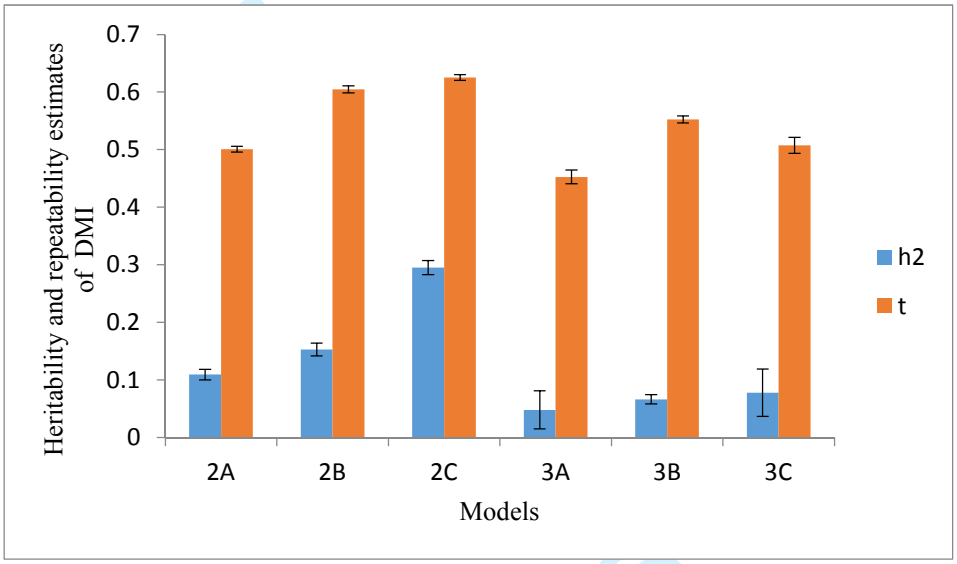

Figure 1. Heritability and repeatability estimates from different models (A: Homoscedastic model fitted for unscaled data, B: Heteroscedastic model for unscaled data, C: Model fitted for scaled data, h2: Heritability, t: Repeatability)

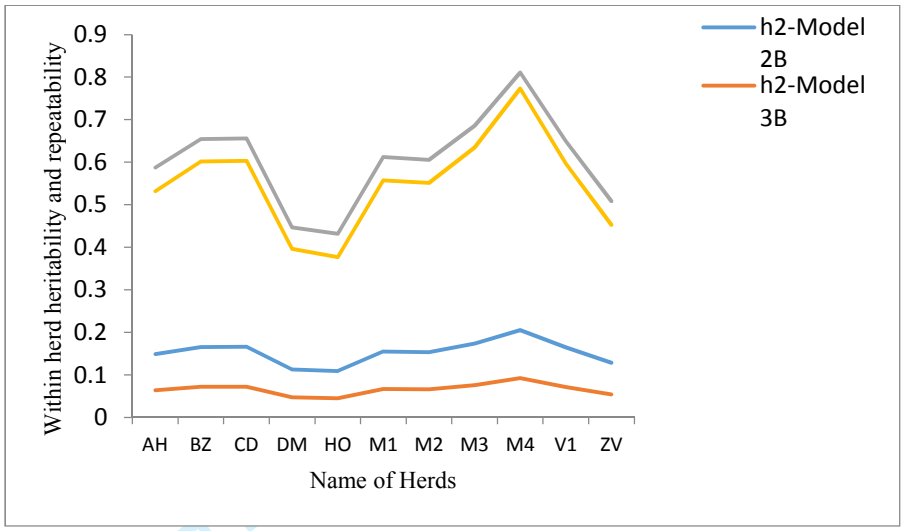

Figure 2. Within herd heritability and repeatability estimates from unscaled data (h2-Model 2B and h2-Model 3B are heritability estimates from model 2B and 3B, respectively; t-Model 2B and t-Model 3B are repeatability estimates from model 2B and 3B, respectively)

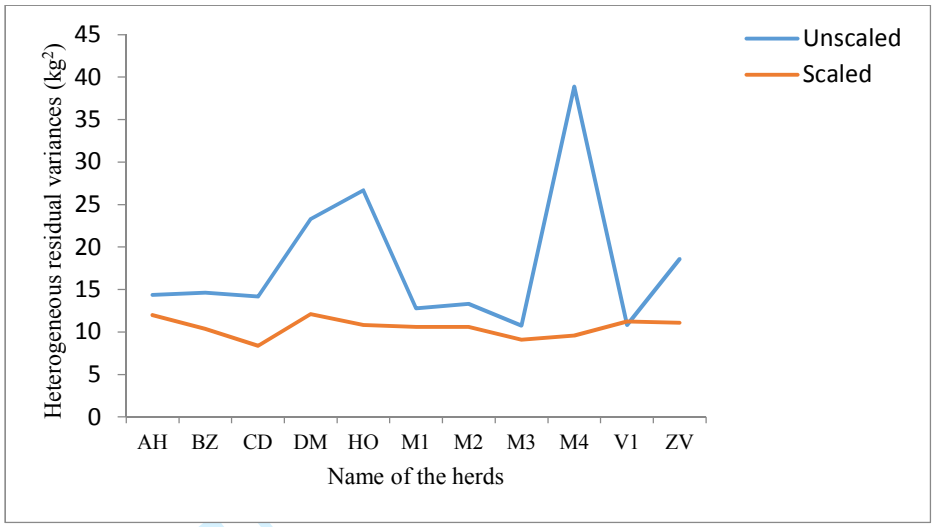

Figure 3 (a). Heterogeneous residual variances by herd before and after scaling of data for model 2 (Unscaled: Data before adjusting for heterogeneity, Scaled: Data after adjusting for heterogeneity)

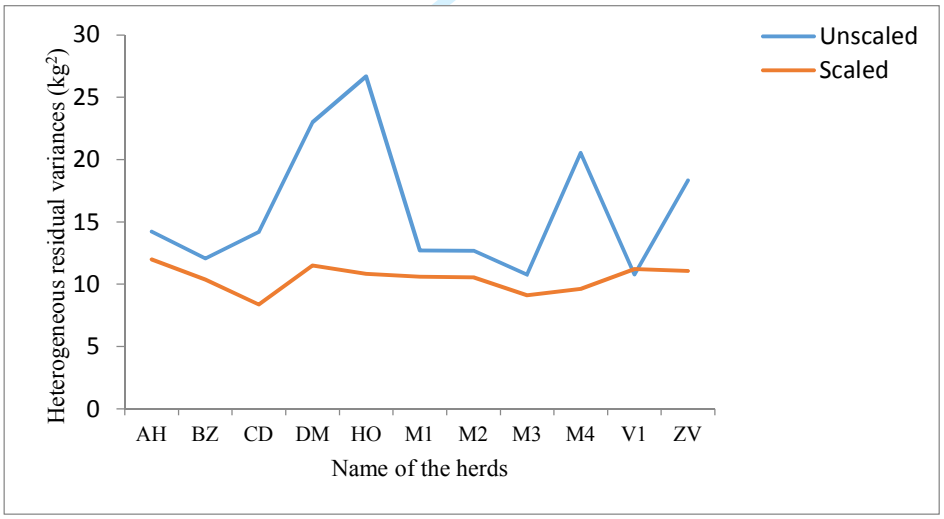

Figure ~~43~~ (b). Heterogeneous residual variances by herd before and after scaling of data for model 3 (Unscaled: Data before adjusting for heterogeneity, Scaled: Data after adjusting for heterogeneity)