

Breeding for feed efficiency in German Holsteins: the new RZFeedEfficiency

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Abstract

A Genomic evaluation has been developed for feed efficiency for German Holsteins and the first official release was in April 2024. As of the release date, more than 327,000 weekly phenotypes of dry matter intake (DMI), body weight (BW) and energy-corrected milk (ECM) were obtained from 14,774 cows from six countries through a collaboration in the resilient dairy genome project. Lactations 1, 2 and 3+ are considered genetically distinct traits. Variance components were estimated with a multi-trait repeatability model, where each of the first three parities was divided into four equal lactation stages. (Co)variance matrices for the random regression model were derived from this multi-trait estimation using the covariance function approach. These are used to obtain genomic estimated breeding values (GEBVs) for DMI, BW and ECM with a single-step random regression model in the routine genetic evaluation. Fixed effects are herd-test-week, inbreeding depression (as a covariate), and calving age by lactation week as a fixed curve (2nd-order Legendre polynomials). The permanent environmental and additive genetic animal effects are fitted as random effects in the model. The averages of heritability estimates for parities 1 to 3, respectively, were 0.19, 0.17, 0.16 for DMI, 0.30, 0.22, 0.20 for ECM and 0.48, 0.45 and 0.50 for BW. The average genetic correlation between parities was 0.79 for DMI, 0.71 for ECM and 0.89 for BW. GEBV for body weight change (BWC) were derived from BW. GEBV correlations of DMI with ECM and BWC were 0.15 and 0.74, respectively. The GEBV correlation between ECM and BWC was -0.07. GEBV for feed saved (FS; expressed in kg DMI), which represents feed efficiency, is then computed from the traits' GEBV as $0.4 \times \text{ECM} + 4.5 \times \text{BWC} - \text{DMI}$. GEBV correlations of FS with the milk production index RZM and other main indices in the total merit index are close to zero. The genetic standard deviation of FS is 247 kg per 305 days in milk, which is roughly 3.5% of total DMI per 305 d. Starting in April 2024, the new GEBV for feed efficiency, RZFeedEfficiency, will be published routinely, expressed on a scale with a mean of 100 and a genetic standard deviation of 12.

Key words: Feed efficiency, dairy cattle, genetic evaluation, Germany, covariance function

Introduction

As feed expenses form the largest single part of the operating costs of dairy farms, enhancing the feed efficiency (FE) of dairy cattle is a major priority for dairy farmers (Connor, 2015). Reducing the environmental impact of dairy production can also be achieved through improving feed efficiency. Animals with higher feed efficiency could generate less greenhouse gas emissions and manure (Bell et al., 2012; Connor, 2015). Furthermore, animals with

lower feed requirements use less land (Connor, 2015).

Compared to many other dairy cattle traits, defining FE is particularly challenging. This is because selecting for FE requires knowledge of how much feed has been used for production. Consequently, several approaches (e.g., Pryce et al., 2015 and VandeHaar et al., 2016) have been developed to account for all components involved and to obtain a phenotype that most accurately identifies animals with favorable genetic merit for FE.

Data on FE is scarce because obtaining feed intake records is both costly and challenging. Hence, the amount of available data is still a limiting factor for achieving highly reliable genetic predictions for FE. Therefore, an international collaboration became essential to expand the reference population (van Staaveren et. al., 2024).

Random regression models (RRM) are well-suited for analyzing longitudinal data with varying variation of traits across the different lactation stages. However, with limited data size, estimation of the variance parameters of an RRM is difficult. Thus, an indirect estimation approach, based on a covariance function, has been proposed (Kirkpatrick et. al., 1994 and Liu et. al., 2000). We describe the German genetic evaluation of FE including variance component estimates, genetic correlations, and the development of the target selection index RZFeedEfficiency.

Materials and Methods

Data

The current data set used in the German genetic evaluation consisted of 327,408 weekly phenotypes of dry matter intake (DMI), body weight (BW), and energy-corrected milk (ECM) from 14,774 cows. The data was obtained through a collaboration with six countries in Europe and North America within the resilient dairy genome project (van Staaveren et al., 2024). These countries are Canada (CAN), Switzerland (CHE), Germany (DEU), Denmark (DNK), Spain (ESP) and the United States of America (USA; Figure 1).

In addition to the phenotypes of the three traits mentioned above, the pedigrees along with the genotypes (50K) of these cows were also obtained. As per quality control for the phenotypes, for each parity, a record was excluded if it exceeded 3 standard deviations either above or below the mean. Animals that had a conflict in the pedigrees and/or the genotypes, had less than 4 records per parity, or had no DMI records were also excluded.

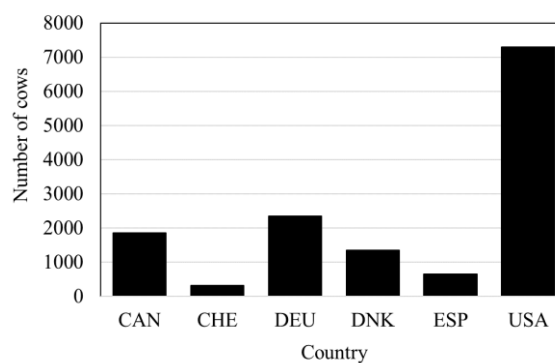


Figure 1. Number of cows with dry matter intake records per country.

Records from higher than the 3rd parity were considered repeated measurements of 3rd parity records. The quality control for the genotypes to clean the genotypic data was the same as for all other German Holstein routine genomic evaluations. For the variance component estimation, the pedigree was limited to the previous five generations of animals with phenotypes. A summary of the final data set is shown in Table 1.

Table 1. Number of records, means and standard deviations for DMI, ECM and BW within the first three parities.

Trait*	Parity	Number of records	Mean	SD
DMI	1	163,833	20.47	3.89
	2	110,419	24.06	4.50
	3+	92,813	24.78	5.06
ECM	1	127,599	32.51	6.25
	2	876,88	39.60	8.38
	3+	759,91	40.68	9.08
BW	1	124,535	605.59	62.84
	2	842,11	669.33	66.86
	3+	721,58	713.03	72.01

*DMI: Dry matter intake.

*ECM: Energy-corrected-milk.

*BW: Live body weight.

Model

The traits DMI, BW, and ECM were analyzed separately, but within trait, the first three parities were analyzed jointly, treating them as genetically distinct traits. Higher parities were considered as repeated measurements of the

third parity. We first fitted a repeatability animal model by dividing each parity into 4 equal stages (11 weeks). Herd-test-week was fitted as a fixed effect, animal as an additive genetic effect, as well as a permanent environmental effect, were fitted as random. The analysis was carried out using WOMBAT (Meyer, 2007).

The variance components obtained from this multivariate model were then used to derive the (co)variances of second-order random regression coefficients (RRC) for the additive genetic, the permanent environmental and the error effects. This was done based on the covariance function approach (Kirkpatrick et al., 1994, Tijani et al., 1999 and Liu et al., 2000). The residual variance was assumed to be homogeneous throughout lactation. Subsequently, a single-step RRM was fitted to estimate the breeding values for each phenotype.

In the single-step random regression model, three fixed effects were fitted: herd-test-week, a fixed curve (2nd order) of calving age by lactation week and a regression on inbreeding. Random effects were animal additive genetic and permanent environmental effects, and the analysis was implemented in MiX99 (Vuori et al., 2006). In the April 2024 routine genetic evaluation run, the number of genotyped animals was 1,518,447 and the number of animals in the pedigree was 3,839,445. Genomic estimated breeding values (GEBV) for BWC were calculated as the weekly change in GEBV of BW, using the derivative of the genetic Legendre function. GEBV from the three parities were aggregated with an equal weight (1/3) into a single GEBV per trait.

Feed efficiency index (RZFeedEfficiency, short: RZFE)

The expected GEBV for DMI was calculated from ECM and BWC. It was assumed that an average ration's energy density is 7.0 MJ NEL per kg DMI. Additionally, it is assumed that 0.4 kg DMI are required to produce 1 kg ECM, and 4.5 kg DMI are required to produce 1 kg

BWC. Hence, feed saved was calculated as follows:

$$\text{GEBV}_{\text{Feed saved}} = 4.5 \times \text{GEBV}_{\text{BWC}} + 0.4 \times \text{GEBV}_{\text{ECM}} - \text{GEBV}_{\text{DMI}}$$

The resulting EBV for feed efficiency is the feed saved, expressed in kg DMI, compared to the average cow. It represents a measure of feed efficiency over the first three lactations, which is roughly the average longevity of Holsteins in Germany. This feed saved GEBV is then expressed as a relative GEBV with a mean value of 100 in the female base population and a genetic standard deviation of 12. The female base population is defined as 4 to 6-year-old genotyped Holstein females at the time of the routine genetic evaluation.

Results and Discussion

The bar chart in Figure 1 shows the number of cows for the six countries whose data is used in the German genetic evaluation of feed efficiency from the resilient dairy genome project database. The United States have the highest number of cows by a significant margin, followed by Germany while Switzerland has the lowest number. Collaboration in the resilient dairy genome project (van Staaveren et al., 2024) with international partners provided the largest possible reference population for feed intake. Modelling the underlying component traits of feed efficiency (DMI, ECM, and BWC) offers flexibility in defining the target trait on the genetic side (based on GEBV), which could be, if necessary, easily adjusted. We found that applying the covariance function approach (Kirkpatrick et al., 1994, Tijani et al., 1999 and Liu et al., 2000) provides stable random regression coefficients, especially as the phenotypic data is limited. Additionally, since feed efficiency varies at different periods of lactation, using an RRM has the advantage of fitting the genetic curves to capture the changes over time. Moreover, switching to daily measurements in this case would be

straightforward, and future improvements can be, if needed, easily implemented.

The heritability estimates obtained from the RRM over the 44 weeks in milk in the first three parities are depicted in Figure 1. In the first parity, heritability starts around 0.1, peaks around 0.25 between 15 to 20 weeks, then slightly decreases and stabilizes around 0.2. In the second parity, it starts around 0.1, peaks slightly below 0.2 around the 15th week, then gradually decreases and stabilizes around 0.15. Finally, in parity 3 heritability estimates were also around 0.1 at the beginning of the lactation and slightly increased to reach 0.2 while remaining relatively stable towards the end of the lactation.

It can be seen that heritability estimates of DMI change over time along the lactation cycle with slight differences between parities showing distinct patterns for each parity group. Heritability for DMI has been intensively reported in the literature based on different methods and in general, it averages between 0.08 and 0.34 (e.g., Berry et al., 2014, Khanal et al., 2022 and Stephansen et al., 2023). Our estimates for the three parities were highly similar and generally slightly lower at the beginning of the lactation, compared to mid-lactation and after. Nevertheless, these estimates are consistent with the most recent reported estimates.

Total heritability estimates for each parity for the three traits are presented on the diagonal of Table 2. Highest estimates were observed in the first parity for all three traits, while the lowest were observed in the third parity for DMI and ECM. The heritability for DMI ranged from 0.30 to 0.39, with an overall total of 0.38. The weekly and the cumulative heritability over parities indicates substantial genetic variation, allowing for better discrimination of genetic differences between animals.

The heatmap in Figure 3 illustrates the correlations between weeks in milk across the first three parities. As expected, adjacent weeks had the highest positive correlations.

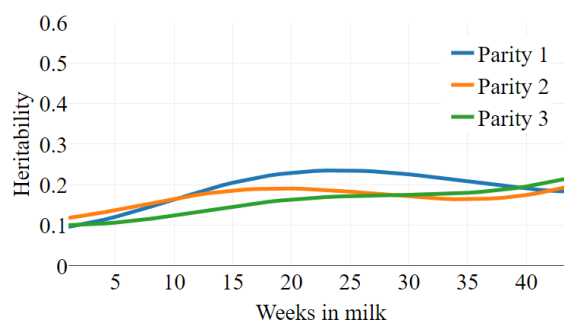


Figure 2. Heritability of DMI over the weeks in milk in the first three parities.

Although genetic correlations between different weeks are all moderately to highly positive, our results show that DMI is genetically not the same trait within and across lactations with minimum genetic correlation estimates within parities of 0.64 (parity 1), 0.52 (parity 2), and 0.70 (parity 3). The minimum genetic correlation between parity 1 and 2 was 0.50, between 1 and 3 was 0.39, between 2 and 3 was 0.49.

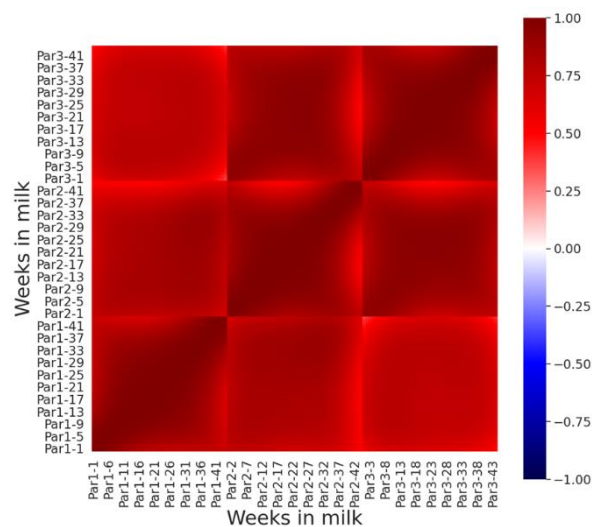


Figure 3. Genetic correlation of DMI over the weeks in milk in the first three parities (Par1, Par2, Par3). Each cell of the matrix represents the correlation between two weeks.

Numerous studies (e.g., Pech et al., 2014) have reported lower genetic correlations for DMI than our estimates, and even negative between mid-lactation and both the start and end of the lactation. It is well known that dairy cattle traits do differ over the course of lactation, but the vast shifts from high positive

to negative correlations could be essentially attributed to the way that RRM estimates are obtained when the data used is small (Kirkpatrick et al., 1994; Liu et al., 2000). For this reason, we implemented the covariance function to reliably estimate random regression coefficients. Genetic correlations within and between entire parities for the three traits are listed below the diagonal in Table 2. Genetic correlation estimates between parities are highly positive, but many values, especially between first and higher parities are below 0.90, indicating a somewhat distinct genetic background of the same trait at different times in the life of the cow.

Table 2. Estimates of heritability (on diagonal) and genetic correlations (below diagonal) for DMI, ECM and BW across the first three parities.

Trait*	Parity#	1	2	3	1/2/3
DMI	1	0.39			
	2	0.88	0.31		
	3	0.79	0.95	0.30	
	1/2/3	0.93	0.99	0.96	0.38
ECM	1	0.43			
	2	0.79	0.31		
	3	0.63	0.97	0.29	
	1/2/3	0.86	0.99	0.94	0.40
BW	1	0.58			
	2	0.94	0.54		
	3	0.88	0.94	0.61	
	1/2/3	0.96	0.99	0.97	0.63

*DMI: Dry matter intake.

*ECM: Energy-corrected-milk.

*BW: Live body weight.

#1/2/3: Combination of parities 1, 2 and 3.

The variance component parameters were then used with the genetic evaluation model to obtain GEBV for the three traits based on a single-step approach, including all available genotyped and pedigree animals.

GEBV of the different traits were then combined to the overall index representing feed efficiency, expressed as feed (DMI) saved. For this index combination, we do not only consider the economically most relevant output of dairy cows, milk (ECM), but also BWC. This is, because body weight is an important storage of energy in the body of the cows. Not respecting BWC could therefore lead to a wrong

estimation of the energy balance of the cows, e.g., when a cow uses energy from her body weight within a lactation, but regains weight between lactations. Additionally, slaughter weight is a secondary output from dairy cows that has also an economic value for the farmers. On average, Holstein cows gain more than 200 kg body weight over the first three parities. Mean genomic reliability is 0.4.

The correlation between GEBV of the different traits was 0.74 (DMI with ECM), 0.15 (DMI with BWC), and -0.07 (ECM with BWC). The values suggest that DMI is genetically highly correlated with ECM and mostly genetically independent of BWC. Many studies have reported a positive genetic correlation of DMI with ECM and typically ranging from moderate to high (e.g., Hüttman et al., 2009 and Li et al., 2018). As selection increases milk production, DMI also tends to increase due to the higher energy demands. The genetic standard deviation of RZFE is 247 kg per 305 days in milk, which is roughly 3.5% of total phenotypic DMI. Correlations of RZFE with GEBV of other trait complexes calculated for 352,692 genotyped females born in 2021 and 2022 are shown in Table 3. Overall, GEBV correlations among RZFE and other trait complexes were low, close to zero. This suggests that genetic improvement for feed efficiency can be targeted without significantly affecting other main dairy traits, including health traits.

To find out how RZFE characterizes the more and the less efficient animals, we obtained the differences in GEBV between the 25% top and the 25% bottom RZFE genotyped females, born in 2021 or 2022 (N = 352,692 per quartile; Table 4). Clear differences exist between the two subgroups in feed efficiency (16.4 for RZFE and 1,264 kg feed saved) while the level for ECM and BWC is very similar between the top and bottom animals. It can be noted that selection for feed efficiency will not decrease ECM and will also not decrease the weight of the cows, because even the top 25% cows for RZFE have a slightly positive breeding value

for body weight. Therefore, most of the difference in RZFE between top and bottom animals stems from the difference in DMI.

Table 3. Correlations of RZFE and GEBVs of other trait complexes

Breeding value	Trait complex	Correlation to RZFE
RZG	Total merit	0.02
RZ€	Total merit (€)	0.05
RZM	Production	-0.07
RZN	Longevity	0.05
RZE	Conformation	-0.11
RZR	Reproduction	0.02
RZHealth	Health	-0.03
RZKm	Calving, maternal	0.03
RZKd	Calving, direct	0.10
RZCalfit	Young stock survival	0.06

Table 4. Differences between the top and the bottom 25% females for feed efficiency (352,692 per quartile) born between 2021 and 2022.

Item	Top 25%	Bottom 25%	Difference
RZFE [#]	107.9	91.5	16.4
FS [*]	607	-657	1,264
DMI [*]	-307	917	-1,224
ECM [*]	743	625	118
BWC [*]	0.6	2.2	-1.5
BW ⁺	4.1	27.1	-23.0

RZFE: Feed efficiency index (RZFeedEfficiency).

FE: Feed saved.

DMI: Dry Matter Intake.

ECM: Energy Corrected Milk.

BWC: Body Weight Change.

[#] On a relative scale (Mean of 100±12)

^{*} Sum of first three parities in kg.

⁺ Mean of first three parities in kg

Conclusions

The German feed efficiency index (RZFeedEfficiency, short: RZFE) was first introduced in April 2024. The international data exchange enables a sufficient data basis for the genetic evaluation of feed efficiency. However, with 0.4, the genomic reliability of the RZFE is at the lower range of genomic reliabilities when compared to other traits under routine genetic evaluation in Holsteins. Applying the covariance function approach facilitated the estimation of variance components for the random regression model. Our results show that underlying traits are heritable with reasonable

estimates of the genetic parameters, allowing for considerable genetic selection. The feed efficiency trait definition considers dry matter intake, energy-corrected milk and body weight change as main energy sources/sinks and refers to three lactations, the average productive life of Holstein cows in Germany. RZFE is mostly independent of production level and health traits. The genetic standard deviation of RZFE is 247 kg per 305 days in milk, which is roughly 3.5% of phenotypic DMI.

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References

- Bell, M. J., Wall, E., Russel, G., Simm, G., Stott, A. W. 2012. The effect of improving cow productivity, fertility, and longevity on the global warming potential of dairy systems. *J. Dairy Sci.* 94, 3662-3678. DOI: <https://doi.org/10.3168/jds.2010-4023>
- Berry, D.P., Coffey, M.P., Pryce, J.E., De Haas, Y., Løvendahl, P., Krattenmacher, N., Crowley, J.J., Wang, Z., Spurlock, D., Weigel, K. and Macdonald, K. 2014. International genetic evaluations for feed intake in dairy cattle through the collation of data from multiple sources. *J. Dairy Sci.* 97(6), 3894-3905. DOI: [10.3168/jds.2013-7548](https://doi.org/10.3168/jds.2013-7548)
- Connor, E. E. 2015. Improving feed efficiency in dairy production: Challenges and possibilities. *Anim* (9), 395-408. DOI: [10.1017/S1751731114002997](https://doi.org/10.1017/S1751731114002997)

- Khanal, P., Gaddis, K.P., Vandehaar, M.J., Weigel, K.A., White, H.M., Peñagaricano, F., Koltes, J.E., Santos, J.E.P., Baldwin, R.L., Burchard, J.F. and Dürr, J.W. 2022. Multiple-trait random regression modeling of feed efficiency in US Holsteins. *J. Dairy Sci.* 105(7), 5954-5971. DOI: [10.3168/jds.2021-21739](https://doi.org/10.3168/jds.2021-21739)
- Kirkpatrick, M., Hill, W. G. and Thompson, R. 1994. Estimating the covariance structure of traits during growth and ageing, illustrated with lactation in dairy cattle. *Genet. Res.* 64(1), 57-69. DOI: [10.1017/S0016672300032559](https://doi.org/10.1017/S0016672300032559)
- Li, B., Fikse, W.F., Løvendahl, P., Lassen, J., Lidauer, M.H., Mäntysaari, P. and Berglund, B. 2018. Genetic heterogeneity of feed intake, energy-corrected milk, and body weight across lactation in primiparous Holstein, Nordic Red, and Jersey cows. *J. Dairy Sci.* 101(11), 10011-10021. -DOI: [10.3168/jds.2018-14611](https://doi.org/10.3168/jds.2018-14611)
- Liu, Z., F. Reinhardt, and R. Reents. 2000. "Estimating parameters of a random regression test day model for first three lactation milk production traits using the covariance function approach. *Interbull Bulletin.* 25, 74-74. <https://journal.interbull.org/index.php/ib/article/view/816>
- Meyer, K. 2007. WOMBAT—A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *J. Zhejiang Univ. Sci.* 8.11, 815-821. DOI: [10.1631/jzus.2007.B0815](https://doi.org/10.1631/jzus.2007.B0815)
- Pech, C.M., Veerkamp, R.F., Calus, M.P.L., Zom, R., Van Knegsel, A., Pryce, J.E. and De Haas, Y. 2014. Genetic parameters across lactation for feed intake, fat-and protein-corrected milk, and liveweight in first-parity Holstein cattle. *J. Dairy Sci.* 97.9, 5851-5862. DOI: [10.3168/jds.2014-8165](https://doi.org/10.3168/jds.2014-8165)
- Pryce, J. E., Gonzalez-Recio, O., Nieuwhof, G., Wales, W. J., Coffey, M. P., Hayes, B. J., Goddard, M. E. 2015. Definition and implementation of a breeding value for feed efficiency in dairy cows. *J. Dairy Sci.* 98. 7340-7350. DOI: [10.3168/jds.2015-9621](https://doi.org/10.3168/jds.2015-9621)
- Stephansen, R. B., Martin, P., Manzanilla-Pech, C. I. V., Gredler-Grandl, B., Sahana, G., Madsen, P., Weigel, K., Tempelman, R. J., Peñagaricano, F., Parker Gaddis, K. L., White, H. M., Santos, J. E. P., Koltes, J. E., Schenkel, F., Hailemariam, D., Plastow, G., Abdalla, E., Vandehaar, M., Veerkamp, R. F., and Lassen, J. 2023. Novel genetic parameters for genetic residual feed intake in dairy cattle using time series data from multiple parities and countries in North America and Europe. *J. Dairy Sci.* 106(12), 9078–9094. DOI: [10.3168/jds.2023-23330](https://doi.org/10.3168/jds.2023-23330)
- Tijani, A., Wiggans, G.R., Van Tassel, C.P., Philpot, J.C. and Gengler, N. 1999. Use of (co)variance functions to describe (co)variances for test day yield. *J. Dairy Sci.* 82(1), 226-e1. DOI: [https://doi.org/10.3168/jds.S0022-0302\(99\)75228-8](https://doi.org/10.3168/jds.S0022-0302(99)75228-8)
- Vandehaar, M. J., L. Armentano, K. Weigel, D. Spurlock, R. Tempelman, and R. Veerkamp. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency. *J. Dairy Sci.* (99), 4941–4954. DOI: [10.3168/jds.2015-10352](https://doi.org/10.3168/jds.2015-10352)
- Vuori, Kaarina, Ismo Strandén, Martin Lidauer, and E. A. Mäntysaari. MiX99-effective solver for large and complex linear mixed models. 2006. *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production.* (9) 27-33.
- van Staaveren, N., Rojas de Oliveira, H., Houlihan, K., Chud, T. C. S., Oliveira, G. A., Hailemariam, D., Kistemaker, G., Miglior, F., Plastow, G., Schenkel, F. S., Cerri, R., Sirard, M. A., Stothard, P., Pryce, J., Butty, A., Stratz, P., Abdalla, E. A. E., Segelke, D., Stamer, E. and Baes, C. F. 2024. The Resilient Dairy Genome Project—A general overview of methods and objectives related to feed efficiency and methane emissions. *J. Dairy Sci.* 107(3), 1510–1522. DOI: [10.3168/jds.2022-22951](https://doi.org/10.3168/jds.2022-22951)