Two approaches to account for genotype-by-environment interactions for production traits and age at first calving in South African Holstein cattle

Vincent Ducrocq1,2*, Astrid Cadet1, Clotilde Patry1, Lene van der Westhuizen2,3, Jacob B. van Wyk2 and Frederick Wilhelm Cornelius Neser2

Abstract

Background: If not accounted for, genotype x environment (GxE) interactions can decrease the accuracy of genetic evaluations and the efficiency of breeding schemes. These interactions are reflected by genetic correlations between countries lower than 1. In countries that are characterized by a heterogeneity of production systems, they are also likely to exist within country, especially when production systems are diverse, as is the case in South Africa. We illustrate several alternative approaches to assess the existence of GxE interactions for production traits and age at first calving in Holsteins in South Africa. Data from 257,836 first lactation cows were used. First, phenotypes that were collected in different regions were considered as separate traits and various multivariate animal models were fitted to calculate the estimates of heritability for each region and the genetic correlations between them. Second, a random regression approach using long-term averages of climatic variables at the herd level in a reaction norm model, was used as an alternative way to account for GxE interactions. Genetic parameter estimates and goodness-of-fit measures were compared.

Results: Genetic correlations between regions as low as 0.80 or even lower were found for production traits, which reflect strong GxE interactions within South Africa that can be linked to the production systems (pasture vs total mixed ration). A random regression model including average rainfall during several decades in the herd surroundings gave the best goodness-of-fit for production traits. This can be related to a preference for total mixed ration on farms with limited rainfall. For age at first calving, the best model was based on a random regression on maximum relative humidity and maximum temperature in summer.

Conclusions: Our results indicate that GxE interactions can be accounted for when genetic evaluations of production traits are performed in South Africa, by either considering production records in different regions as different correlated traits or using a reaction norm model based on herd management characteristics. From a statistical point of view, climatic variables such as average rainfall over a long period can be included in a random regression model as proxies of herd production systems and climate.

© The Author(s) 2022. Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/. The Creative Commons Public Domain Dedication waiver (http://creativecommons.org/publicdomain/zero/1.0/) applies to the data made available in this article, unless otherwise stated in a credit line to the data.
climate in the interior plateau, a subtropical climate in the east and a small area in the northwest with a desert climate, all with summer rainfall. With an average rainfall of only 464 mm, it is a relatively dry country. Most of the country has warm, sunny days and cool nights. Winters in South Africa occur between June and August [1, 2].

The total number of dairy cattle in South Africa is estimated at about 1.37 million [3] with a majority of Holstein cows. These cows are kept under a total mixed ration (TMR) or under a pasture-based production system or a combination of both, depending on the geographical region [4]. Currently between 65 and 75% of the milk production is based on pasture. However, many of these pasture-based systems increasingly incorporate additional feeding such as concentrates or forage crops as hay or silage [5].

In South Africa, breeding values for production traits are computed three times a year [6]. Currently, no consideration is given to the different production environments or climatic conditions when bulls are evaluated. In most national genetic evaluations, local genotype x environment (G×E) interactions are considered negligible for production traits in dairy cattle [7]. However, if these interactions are present but ignored [8], they can substantially decrease the accuracy of the estimated breeding values (EBV) of bulls, generate biases according to the production environment of their daughters, and ultimately decrease the efficiency of selection at the farmer or country level, i.e. the lower true reliability of the genetic evaluations will reflect negatively on the genetic gain because bull selection for a particular environment is based on inadequate information.

G×E interactions in dairy cattle are most often studied by defining phenotypic expressions in various environments as separate traits [9–15] (say, N traits for N environments) and by estimating the genetic correlations between these N separate traits. An estimate that is significantly different from 1 is interpreted as a signature of a G×E interaction. This is, in particular, the basic assumption underlying the multiple across-country evaluations (MACE) that are routinely calculated by Interbull [10] for national dairy cattle traits. A drawback of the MACE approaches is that the number of (co)variance genetic components (CGC) to be estimated increases quadratically with N. For MACE of milk production in the Holstein breed, this represents 435 CGC for 29 countries [10], which requires significant postprocessing in order to obtain results that are both realistic and consistent.

An intermediate option is to consider only n (< N) underlying traits, in which case the number of CGC increases quadratically only with n. Particular strategies have been proposed to find an optimum number n of underlying traits in international genetic evaluations, such as rank reduction [16, 17] and principal components and factor analyses [18, 19].

At the national level, G×E interactions also exist (e.g., [11–13]), and a particular approach to reveal them consists in adding an interaction term to the traditional quantitative genetic model. For example, a random regression mixed linear model can be built including a reaction norm function of a continuous variable [11, 20, 21], such as a climatic or herd management variable, to reflect the fact that the observed phenotype is the result of a genetic component which differs according to the local environmental conditions [22]. Other strategies consist in constructing structural models in which environmental and genetic variables are used to describe and measure similarities (e.g., between geographical regions). In fact, when modelling G×E interactions, there is a continuum between the two extreme alternatives to describe the link between the genetic component and the environment of the animal, i.e. “one trait stands for one environment” up to “the genetic component is a continuous function of environmental parameters”.

The purpose of this study was to illustrate the wide range of potential genetic evaluation models along this continuum in the particular context of G×E interactions in South African Holstein cows for production traits and age at first calving. The same phenotypes will be described as separate traits in different regions, or by including in the model a reaction norm involving climatic characteristics of the herds averaged over a long period. For simplicity, only first lactation records are considered in this study, to focus more easily on the detection of potential G×E interactions. This is in contrast with the current genetic evaluation model in South Africa, which is based on a 3-lactation fixed regression test-day model [6, 23].

Methods
Data from 378,782 first lactation Holstein cows recorded over a period of 30 years (1982–2012) were used in the analysis. The traits analyzed were first lactation milk, fat and protein yields (corrected to a 305-day equivalent) and age at first calving (AFC) in months. Only herds in the seven major administrative regions (provinces) with dairy production were considered. Cows were required to have a known sire and an age at first calving between 20 and 40 months. Contemporary groups were defined within herd and included at least 20 cows that were the progeny of sires with at least 20 recorded daughters each in the complete data set. After editing, records from 257,836 first lactation cows from 702 herds were first grouped into four regions according to global climatic characteristics: Western Cape...
(1), Eastern Cape (2), Free State, Gauteng, North West and Limpopo (3), Kwazulu-Natal (4). Table 1 shows the number of observations and average performances in each region. The data of 10 global climatic variables (yearly rainfall, maximum and minimum temperature, maximum and minimum relative humidity, solar radiation, evapotranspiration, maximum temperature in summer, maximum humidity in summer and maximum solar radiation in summer) from the closest weather station, based on the GPS position of the herd, were averaged over a period of 50 years and added to each herd. To this list, it would have been interesting to add a composite climatic variable such as the average or extreme daily temperature-humidity index (THI) [24] but this was not possible as only yearly averages of temperature and humidity were available. Overall, these variables are used to reflect the long-term climatic characteristics of the herds and not temporary events such as a heat wave or a period of drought. Table 2 presents the average and standard deviation of each climatic variable in the four groups of regions. For all the herds, the feeding system that is categorized in three possibilities (pasture-based, total mixed ration (TMR) or a mixture between the two) had to be known. In a first set of analyses, three linear models (summarized in Table 3) were fitted and analyzed using restricted maximum likelihood, as implemented in the Wombat software [25]. The fixed effects included were the same for all analyses: herd-year, calving season (quarter) and age at first calving in months (except for the analyses considering age at first calving as the trait under study).

The first model was a univariate model: the phenotype was considered for the whole population as a unique trait with homogenous variance parameters across environments. This is basically the same assumption as in the current fixed regression test-day model used to estimate breeding values of Holstein cows in South Africa [6, 14]. The second model investigated G×E interactions between regions using a multivariate model: the same phenotypes in each of the four regions were considered as four distinct traits, without preconceived hypotheses about the source of potential G×E interactions. Genetic correlations between traits (here, between regions) were estimated as well as the specific genetic and residual

| Table 1 | Descriptive statistics of the data set after edits for the four traits studied |
|---------|-------------------------------------------------------------|
| Region (code) | N | Mean (± SD) |
|          | | Milk yield (kg) | Fat yield (kg) | Protein yield (kg) | Age at first calving (months) |
| Western Cape (1) | 70,864 | 8119 ± 2513 | 297 ± 99 | 249 ± 80 | 26.6 ± 3.6 |
| Eastern Cape (2) | 40,559 | 6072 ± 1529 | 218 ± 59 | 194 ± 50 | 28.8 ± 3.7 |
| Free State, Gauteng, North West and Limpopo (3) | 75,388 | 7464 ± 2458 | 273 ± 93 | 237 ± 77 | 28.1 ± 4.0 |
| KwaZulu Natal (4) | 71,025 | 5894 ± 1461 | 211 ± 53 | 187 ± 45 | 28.6 ± 3.8 |
| Number of animals | 70,864 | 40,559 | 75,388 | 71,025 |
| Rainfall (mm) | 554 ± 186 | 609 ± 107 | 613 ± 85 | 853 ± 103 |
| Max temperature (°C) | 22.7 ± 0.9 | 23.0 ± 0.7 | 23.7 ± 1.2 | 23.0 ± 1.4 |
| Min temperature (°C) | 11.1 ± 0.7 | 12.2 ± 1.7 | 8.4 ± 1.3 | 9.9 ± 1.8 |
| Max relative humidity (%) | 88.0 ± 4.4 | 88.9 ± 2.5 | 88.9 ± 5.2 | 91.7 ± 2.9 |
| Min relative humidity (%) | 47.2 ± 6.1 | 49.8 ± 6.3 | 38.7 ± 5.1 | 47.3 ± 5.2 |
| Solar radiation (MJ m⁻² day⁻¹) | 163 ± 0.9 | 156 ± 1.5 | 193 ± 0.7 | 178 ± 1.2 |
| Evapotranspiration (mm) | 3.3 ± 0.3 | 3.1 ± 0.3 | 3.8 ± 0.3 | 3.4 ± 0.3 |
| Max temperature in summer (°C) | 26.3 ± 1.6 | 25.4 ± 1.1 | 27.4 ± 2.2 | 25.5 ± 1.6 |
| Max humidity in summer (%) | 85.2 ± 6.0 | 91.6 ± 2.9 | 88.9 ± 7.0 | 94.5 ± 2.0 |
| Max solar radiation in summer (MJ m⁻² day⁻¹) | 25.1 ± 1.6 | 24.5 ± 1.9 | 25.0 ± 1.8 | 25.9 ± 1.6 |

N number of animals; SD standard deviation
Table 3  Overview of the different models tested

| Analysis by region         | Univariate       | Multivariate |
|----------------------------|------------------|--------------|
| Analysis including climatic variables | Univariate with heterogeneous residual | Reaction norm on 1 variable | Reaction norm on > 1 variables |

\[ y_i = \sum f + a_i + \epsilon_i \]
\[ y_i = \sum f + a_{im} + \epsilon_{im} \]
\[ y_i = \sum f + a_i + \epsilon_{im} \]
\[ y_i = \sum f + a_i + \lambda_j b_{ij} + \epsilon_{im} \]

\( y_{im} \): performance of animal \( i \) in region \( r \); \( \sum f \): sum of fixed effects (herd-year, calving season and age at first calving for production traits); \( a_{im} \): additive genetic value for animal \( i \) in region \( r \); \( \lambda_j \): reaction norm coefficient for climatic variable \( j \); \( b_{ij} \): standardized value of climatic variable \( j \) for animal \( i \) in region \( r \); \( \epsilon_{im} \): residual for animal \( i \) in region \( r \).

variances from which a heritability could be derived for each region.

The third model was also a multivariate model, but with a reduction of the rank of the correlation matrix that was imposed a priori. The Wombat software [25] reparametrizes the genetic (co)variance matrix in order to force a matrix of rank inferior to the number of traits (i.e., 3, 2 or 1, in our case). This results in a more parsimonious description of the correlation between traits and forces an increased resemblance between regions. The extreme situation is a final rank equal to 1, which implies that all the genetic correlations between regions are equal to 1 but the genetic and residual variances—and therefore heritability—may vary. Goodness-of-fit of the various models were compared using the Bayesian information criterion (BIC), which is recommended when comparing non-nested mixed models with a large number of observations [26]. A lower BIC represents a better model after accounting for the number of parameters to be estimated.

A second group of analyses was set up in order to assess whether the observed differences between regions in terms of production could be related to the climatic conditions that prevailed in each herd. Only milk yield was analyzed and a random regression analysis on climatic variables was used. First, as a base model, a unique (homogeneous) genetic variance and heterogeneous residual variances (one per region) were estimated. This is equivalent to the univariate analysis with a specific residual variance for each region. Then, the model was extended to a random regression model by including each climatic variable as a reaction norm variable: as a result, the genetic parameters of the random regression model included two genetic effects: a fixed term and a regression coefficient on the climatic variable (one at a time). The comparison of these models should reveal which climatic variables contribute to a G×E interaction. Then, two climatic variables were included simultaneously together with the fixed term and the most relevant combination of the two climatic variables was chosen. These random regression analyses were initially run assuming a full rank genetic variance–covariance matrix. This rank was then reduced to 1. In such a case, the first eigenvector of the resulting genetic covariance matrix can be interpreted as the optimal linear combination of the climatic variables describing the environmental component of the genetic variability.

Results
A summary of the statistics describing first lactation milk, fat and protein yield and age at first calving in the four regions is in Table 1. The mean value of the three production traits differed between the four regions, but for age at first calving, it only differed between Western Cape and the three other regions. The climatic characteristics of the four (groups of) regions are in Table 2. Average rainfall is the variable that varies the most between regions, with the lowest average in the Western Cape.

Genetic parameter estimates for production traits and age at first calving measured in each of the four regions are in Table 4, under six models: two univariate genetic models assuming either a common (U1) or four different (U4) residual variances for the four different regions, and four multivariate models assuming different genetic and residual variances in each region and different assumptions about the rank of the genetic variance matrix (from full (MTR4) to rank 1 (MTR1)). The heritability estimates are generally in agreement with the range of values found in the literature [27–30]. They are lower for protein yield and even more so for fat yield than for milk yield (see Additional file 1: Table S1), possibly because of less accurate on-farm measurements of fat and protein contents compared to milk yield (records are collected by the farmers themselves). Regardless of the trait, rank reductions of the genetic variance matrix did not modify the estimated heritabilities significantly. Heritability estimates varied between regions or models used, especially for production traits. All the genetic correlations estimated using the multivariate models without rank reduction (MTR4) ranged from 0.619 to 0.868 and were usually lower than 0.8. They were all statistically different from 1. These results underline the existence of important G×E interactions, not only as scale effects but also inducing strong bull re-rankings. The effect of rank reduction on genetic correlations was substantial,
Table 4  Estimates of heritability (in bold) and genetic correlations (below the diagonal) for each region sorted according to Table 1 depending on the trait studied and the model used (± SE)

| Trait              | Univariate analyses | Multivariate analyses |
|--------------------|---------------------|-----------------------|
|                    | Residual variance(s)| Rank 4 (MTR4)         |
|                    | Unique (U1) By region (U4) | Rank 3 (MTR3) | Rank 2 (MTR2) | Rank 1 (MTR1) |
| Milk yield        | 0.194 (0.004)       | 0.234 (0.001)         |
|                   | 0.254 (0.006)       | 0.286 (0.009)         |
| Age at first calving | 0.177 (0.006)     | 0.207 (0.010)         |

U1 univariate model, one residual variance; U4 univariate model, four residual variances; MTRi multiple traits genetic variance matrix of rank i
NA not available due to singularities

especially for reduction to a rank of 2 (MTR2), or—obviously—1 (MTR1). The inclusion of these interactions in the genetic evaluation model could be more precise by using climatic variables: they appear to define more accurately the variety of environments than the geographical limits, e.g., regions. It appears that including region

Table 5  Contribution of the second eigenvalue of the genetic covariance matrix, correlation between the two genetic effects (± SE) and goodness-of-fit (BIC was set to 0 for the model without climatic variable) for reaction norm models including a constant and a regression on one climatic variable at a time, in the case of milk yield and age at first calving traits

| Climatic variable | Milk yield | Age at first calving |
|-------------------|------------|----------------------|
|                   | Eigenvalues (%) | Correlation (SE) | BIC          | Eigenvalues (%) | Correlation (SE) | BIC          |
| C1: Average rainfall | 9.93        | −0.637±0.016         | −28.1        | 8.97         | 0.236±0.035         | 202.6        |
| C2: Max temperature          | 2.64        | 0.599±0.041         | 726.9        | 7.30        | −0.366±0.040         | 241.5        |
| C3: Min temperature          | 0.37        | −0.499±0.107       | 1199.6       | 3.07        | −0.692±0.037       | 66.9         |
| C4: Max relative humidity    | 1.78        | −0.837±0.029       | 188.3        | 18.82       | 0.439±0.023       | 52.0         |
| C5: Min relative humidity    | 1.01        | −0.880±0.025       | 204.0        | 23.25       | −0.061±0.027       | 106.2        |
| C6: Solar radiation (SR)    | 1.13        | 0.797±0.032       | 748.5        | 10.26       | 0.115±0.039       | 234.5        |
| C7: Evapotranspiration      | 1.07        | 0.867±0.026       | 315.7        | 12.14       | −0.119±0.038       | 206.3        |
| C8: Max temperature in summer | 0.99        | 0.895±0.029       | 400.9        | 26.11       | 0.895±0.029       | −26.3        |
| C9: Max relative humidity in summer | 1.06        | −0.911±0.022       | 65.5         | 16.09       | −0.346±0.025       | −100.7       |
| C10: Max solar radiation in summer | 1.35        | 0.692±0.048       | 876.8        | 16.43       | 0.692±0.048       | 110.5        |

RH relative humidity; SR solar radiation; T temperature
as a factor of heterogeneity for residual variances already greatly improved the goodness-of-fit of the model.

Table 5 shows the respective importance of the two eigenvectors of the genetic variance matrix when a reaction norm model was used with one climatic variable included at a time for each studied trait (C1–C10). Given the eigenvector coordinates, it follows that the first eigenvalue roughly represents the part of the total genetic variance that is explained by the average genetic effect regardless of the environment. The second eigenvalue represents the part explained by the reaction norm on the climatic variable.

The most important climatic variable for all production traits is the average rainfall, contributing to about 10% of the total genetic variance (C1). In fact, the other climatic variables did not lead to any improvement of the BIC. In contrast, age at first calving was more influenced by the average maximum temperature in summer (C8) and by the average minimum relative humidity (C5), representing about a quarter of the total genetic variance, i.e., the two components related to THI.

To highlight the impact of average rainfall, cows were partitioned into four groups depending on the average rainfall of their herd and a multivariate analysis was performed for milk production (RF4). The results are in Table 6. This analysis showed that a higher level of rainfall was often associated with a lower milk production but also a reduced residual variance and a higher proportion of pasture-based herds (among the herds for which this information was available). However, and quite surprisingly, the heritability was higher in herds with an above-average rainfall level, in spite of their lower average production.

All the models used were compared according to their goodness-of-fit [BIC, see Table 7 and (Additional file 1: Table S2)]. It can be first concluded that including a heterogeneous residual variance according to the region (U4) strongly increased the goodness-of-fit for the univariate model. However, for milk yield, a reaction norm model including average rainfall (C1) led to a better fit (lower BIC) than models based on regions. Including more climatic variables in the model (C2V, C5V) did not necessarily increase the goodness-of-fit, but greatly increase computation time. The best model was clearly the multivariate model that groups herds according to rainfall level (RF4), with distinct residual variances by region. For age at first calving, the best model was the model that included a reaction norm on maximum relative humidity in summer, followed by the model with a reaction norm on maximum temperature in summer, suggesting again that a model including a reaction norm on temperature-humidity index

### Table 6
Herd characteristics, estimates of heritability (in bold) and genetic correlations (below the diagonal of bold figures) for milk yield when herds are grouped according to average rainfall (Model RF4)

| Level of average rainfall (mm) | Proportion of herds with pasture | Milk production | Heritability and genetic correlations |
|-------------------------------|----------------------------------|----------------|--------------------------------------|
|                               | Mean Residual standard deviation | Heritability     |                                      |
| > 755                         | 5962 783                        | 0.268           |                                      |
| > 659 and < 755               | 6070 797                        | 0.909; 0.306    |                                      |
| > 547 and < 659               | 7746 1016                       | 0.779; 0.991; 0.257 |                                      |
| < 547                         | 7989 1062                       | 0.829; 0.858; 0.862; 0.250 |                                      |

*Information on feeding system was available only on a limited fraction of the herds

### Table 7
Goodness-of-fit of analyses based on different models for milk production

| Model | BIC – BICmin |
|-------|--------------|
| U1: Univariate | 11,190 |
| U4: Univariate + specific residual variances by region | 2016 |
| MTR4: Multivariate by region, rank 4 | 773 |
| MTR1: Multivariate by region, rank 1 | 967 |
| C1: Reaction norm on average rainfall | 745 |
| C2V: Reaction norm on average rainfall and maximum temperature with genetic correlation = 0 and reduced rank | 956 |
| C5V: Reaction norm on 5 variables with genetic correlation between “average production” and a linear regression term on climatic variables | 967 |
| RF4: Multivariate, grouping herds according to level of rainfall | 0* |

*Best model
Europe—where genetic variance and heritability tend to increase with level of production, the highest heritability was found in the group of herds with substantially lower average production levels (Table 6), due to a much lower estimate of the residual variance. A potential explanation is that large herds based on TMR are grouped and fed according to level of production, with less opportunity to express genetic differences between cows competing for grazing. For clarity, we used a rather trivial lactation model in this study but our conclusions can be extended to more complex genetic or genomic evaluation models, for example based on multivariate random regression models [34].

Conclusions
This study shows that important G×E interactions exist in Holstein cattle in South Africa that could result in large re-rankings of bulls. In absence of a generalized recording of the farms’ feeding systems, these interactions could be taken into consideration in national genetic evaluations by defining a heterogeneous residual variance by region and a genetic term involving a reaction norm on long-term averages of climatic variables for each herd. In local breeding programs, calculating a different breeding value depending on the environment (region or feeding system) should be considered.

Supplementary Information
The online version contains supplementary material available at https://doi.org/10.1186/s12711-022-00735-5.

Acknowledgements
The authors would like to thank the South African Holstein Society for making the data available for the study.

Author contributions
FN, JVW, VD conceived the study. CP, FN and VD prepared the data. AC, VD, CP conducted the study. VD, CP and FN designed the statistical approaches. JD, JVW and FN wrote the manuscript. All authors read and approved the manuscript.

Funding
Not applicable.

Declarations
Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.
Competing interests
The authors declare that there is no competing interest.

Author details
1 Université Paris-Saclay, INRAE, AgroParisTech, GABI, 78350 Jouy-en-Josas, France. 2 Department of Animal Science, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa. 3 ARC-Animal Production Institute, Private Bag X2, Irene 0062, South Africa.

Received: 29 October 2021  Accepted: 24 May 2022
Published online: 11 June 2022

References
1. South Africa Yearbook, 2018/19. Government communication and information system. Republic of South Africa. https://www.gcis.gov.za/south-africa-yearbook-201819/. Accessed 20 Jun 2021.
2. Wikipedia. Climate of South Africa. 2020. https://en.wikipedia.org/wiki/Climate_of_South_Africa/. Accessed 21 Sep 2021.
3. Mesisser HH, Scholtz MM, Palmer AR. Sustainability of the South African livestock sector towards 2050. Part 1: Worth and impact of the sector. S Afr J Anim Sci. 2013;43:282–97.
4. Scholtz MM, Du Toit J, Neser FWC. Antagonism in the carbon foot-print between beef and dairy production systems. S Afr J Anim Sci. 2014;44:517-20.
5. Muller CJ, Scholtz MM. Ways to reduce the environmental impact of dairy farming. Appl Anim Husb Rural Dev. 2014;7:31–7.
6. Interbull. 2021. http://www.interbull.org/. Accessed 15 Sep 2021.
7. Zwalf NR, Weigel KA, Fiske WF, Rekaya R. Characterization of dairy-production systems in countries that participate in the International Bull evaluation service. J Dairy Sci. 2001;84:2530–4.
8. Zwalf NR, Weigel KA, Fiske WF, Rekaya R. Identification of factors that cause genotype by environment interaction between herds of Holstein cattle in seventeen countries. J Dairy Sci. 2003;86:1009–18.
9. Strandberg E, Kolmodin R, Madsen P, Jensen J, Jorjani H. Genotype by environment interaction in Nordic dairy cattle studied by use of reaction norms. In: Proceedings of the 2000 Interbull meeting: 14–15 May 2000, Bled, 2000.
10. Schaeffer LR. Multiple-country comparison of dairy sires. J Dairy Sci. 1994;7:2671–8.
11. Kolmodin R, Strandberg E, Madsen P, Jensen J, Jorjani H. Genotype by environment interaction in Nordic dairy cattle studied using reaction norms. Acta Agric Scand A Anim Sci. 2002;52:11–24.
12. Kearney JF, Schutz MM, Boettcher PJ, Weigel KA. Genotype x environment interaction for grazing vs confinement: I Production traits J Dairy Sci. 2004;87:501–9.
13. Kearney JF, Schutz MM, Boettcher PJ. Genotype x environment interaction for grazing vs confinement. II Health and reproduction traits. J Dairy Sci. 2004;87:510–6.
14. Hammami H, Rekki B, Soyeurt H, Bastin C, Stoll J, Gengler N. Genotype x environment interaction for milk yield in Holsteins using Luxembourg and Tunisian populations. J Dairy Sci. 2008;91:3661–71.
15. Hammami H, Rekki B, Gengler N. Genotype by environment interaction in dairy cattle. Biotechnol Agron Soc Environ. 2009;13:155–64.
16. Madsen P, Jensen J, Mark T. Reduced rank estimation of (co)variance components for international evaluation using AI-REML. Interbull Bull. 2000;25:46–50.
17. Tarres J, Liu Z, Ducrocq V, Reinhardt F, Reents R. Data transformation for rank reduction in multi-trait MACE model for international bull comparison. Genet Sel Evol. 2008;40:295–308.
18. Leclerc H, Fiske WF, Ducrocq V. Principal components and factorial approaches for estimating genetic correlations in international sire evaluation. J Dairy Sci. 2005;88:3306–15.
19. Tyrisva AM, Meyer K, Fiske WF, Ducrocq V, Jakobsen J, Lidauer MH, et al. Principal component approach in variance component estimation for international sire evaluation. Genet Sel Evol. 2011;43:21.
20. Fiske WF, Rekaya R, Weigel KA. Assessment of environmental descriptors for studying genotype by environment interaction. Livest Prod Sci. 2003;82:223–31.
21. Céron-Muñoz MF, Tonhati H, Costa CN, Maldonado-Estrada J, Rojas-Sarmiento D. Genotype x environment interaction for age at first calving in Brazilian and Colombian Holsteins. J Dairy Sci. 2004;87:2455–8.
22. Huquet B, Leclerc H, Ducrocq V. Modelling and estimation of genotype by environment interactions for production traits in French dairy cattle. Genet Sel Evol. 2012;44:35.
23. Mostert BE, Groeneveld E, Kanfer FHJ. Testday models for production traits in dairy cattle. S Afr J Anim Sci. 2004;34:535–7.
24. Haile-Mariam M, Carrick MJ, Goddard ME. Genotype by Environment interaction for fertility, survival, and milk production traits in Australian dairy cattle. J Dairy Sci. 2008;91:4980–53.
25. Meyer K. WOMBAT - A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). http://didgeridoo.une.edu.au/km/wombat.php/. Accessed Jun 2021.
26. Wikipedia. 2021. https://en.wikipedia.org/wiki/Bayesian_information_criterion#References/. Accessed 15 Sep 2021.
27. Allaire FR, Lin CY. Heritability of age at first calving. J Dairy Sci. 1980;63:171–3.
28. Moore RK, Kennedy BW, Schaeffer LR, Moxley JE. Relationships between age and body weight at calving, feed intake, production, days open and selection indexes in Aryshires and Holsteins. J Dairy Sci. 1992;75:294–306.
29. Heise J, Stock KF, Reinhardt F, Ha NT, Simianer H. Phenotypic and genetic relationships between age at first calving, its component traits, and survival of heifers up to second calving. J Dairy Sci. 2018;101:425–32.
30. Interbull. 2021. https://interbull.org/fr/gerforms/. Accessed 15 Sep 2021.
31. Boettcher PJ, Fatehi J, Schutz MM. Genotype x Environment interactions in conventional versus pasture-based dairies in Canada. J Dairy Sci. 2003;86:383–9.
32. Aguilar I, Misztal I, Tsuruta S. Genetic components of heat stress for dairy cattle with multiple lactation. J Dairy Sci. 2009;92:5702–11.
33. Nguyen TT, Bowman PJ, Haile-Mariam M, Price JE, Hayes BJ. Genomic selection for tolerance to heat stress in Australian dairy cattle. J Dairy Sci. 2016;91:2849–62.
34. Van Niekerk M, Neser FWC, Ducrocq V. Fixed and regression models for South African Holstein under two production systems. In: Proceedings of the 69th Annual Meeting of the European Association for Animal Production: 27–30 August 2018; Dubrovnik, 2018.

Publisher’s Note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:
• fast, convenient online submission
• thorough peer review by experienced researchers in your field
• rapid publication on acceptance
• support for research data, including large and complex data types
• gold Open Access which fosters wider collaboration and increased citations
• maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.
Learn more biomedcentral.com/submissions