Genotype-environment interaction for age at first calving in Holstein cows in Brazil

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A B S T R A C T

Dairy cattle production is distributed throughout the Brazilian regions. However, Brazilian producing regions are different in air temperature and humidity, diet, birth season, and other factors that may alter the reproductive performances of cows. The age of the cow at first calving (AFC) is a good indicator of sexual precocity since it shows the beginning of the female reproductive life and has a great influence on cow replacement costs. Researches on genotype-environment interaction (GEI) show the importance of using specific bulls for the different production systems in Brazil since most semen used in the country is imported. The objective of this work was to evaluate GEI for AFC in Holstein cows in Brazil, using reaction norms. The statistical models used were the standard animal model, which disregards the GEI, and hierarchical reaction norm models with homoscedastic (HRNMHO) and heteroscedastic (HRNMHE) residual variance, and one (HRNMHO1S and HRNMHE1S) and two (HRNMHO2S and HRNMHE2S) steps. HRNMHO1S presented better fit to the data, with lower heritability for environments with lower AFC, and higher heritability for environments with higher AFC. The GEI found was complex, with a reclassification of bulls, denoting the importance of considering GEI for evaluation and selection of bulls for different production levels. The reduction of AFC is possible when using breeding bulls adapted to the tropical and subtropical conditions of Brazil.

1. Introduction

Dairy cattle production is distributed throughout the Brazilian regions, where the production systems for Holstein cows are the most technically advanced (Stock et al., 2008), consisting of intensive pasture and intensive feedlot systems (Assis et al., 2005). However, Brazilian producing regions are different in air temperature, relative air humidity, latitude, longitude, diet, birth season, and other factors that may alter the productive and reproductive performances of cows, even within the same state or property.

A milk production system with low reproductive efficiency increases involuntary culling, calving interval, and the number of dry cows, decreasing cow longevity and number of spare animals (Bergamaschi, Machado & Barbosa, 2010). The age of the cow at first calving (AFC) is a good indicator of sexual precocity, since it shows the beginning of the female reproductive life. AFC has a great influence on cow replacement costs (Lemos, Madalena, Teodoro & Monteiro, 1992), lower AFC decrease a generation interval and increase lifespan

(Lira, Rosa & Garnero, 2008) and thus selection of lower AFC is preferable in the most of production systems. This variable is related to the pregnancy, gestation, and calving abilities of the cows (Bormann & Wilson, 2010), however, it presents low to moderate heritability, indicating a dependence high of the environmental factors.

The genotype-environment interaction (GEI) can alter the classification of genotypes in different environments and change relative and absolute magnitudes of genetic, environmental, and phenotypic variances (Corrêa, Dionello & Cardoso, 2009). A genotype does not express a phenotype, but rather a variety of possible phenotypes (Schlichting & Pigliucci, 1998), because the environment does not alter the genetic constitution, but how much of the genome is expressed (Warwick & Legates, 1980). Studies on GEI use the phenotypic expression of a group of individuals, compare to other related ones in different environments, and describe production levels in different environments.

According to Nesser, Van Wyk and Ducrocq (2014), the bull selection is important because selected animals should be adapted to the environmental conditions according to the locations in which their

progeny will be raised. Thus, several studies have been carried out worldwide to identify the presence of GEI in Holstein herds to improve milking period (Ismael et al., 2016a), milk production (Tiezzi, Los Campos, Parker Gaddis & Maltecca, 2017; Tsuruta, Lourenco, Misztal & Lawlort, 2015), fat and protein percentages, and somatic cell counts (Streit, Reinhardt, Thaller & Bennewitz, 2013; Tiezzi et al., 2017).

Researches on GEI show the importance of using specific bulls for the different production systems in Brazil, since most semen used in the country is imported from the United States of America and Canada, considering genetic merits of bulls in their origins (Silva et al., 2016) for selection and recommendation of semen to local breeders. In this context, the objective of this work was to evaluate GEI for AFC in Holstein cows in Brazil, using reaction norms.

2. Material and methods

2.1. Data

The Brazilian Association of Holstein Cattle Breeders (ABCBRH) and its state affiliates provided reproductive and genealogical records of Holstein cows in Brazil, including data on age at first calving, which was collected by technicians of the Milk and Genealogical Control Service of the ABCBRH from 1987 to 2010. The SAS program (SAS Institute Inc., 2017) was used to prepare, format, and describe the data, using routines developed by Cardoso (2007). The AMC program (Roso & Schenkel, 2006) was used to evaluate the connectivity of contemporary groups (CG) using the pedigree and data files, keeping only connected CG (minimum of 20 observations per CG, five progeny per bull, and standard deviation of the trait less than three); maintaining a main archipelago only of animals connected with 18,822 animals in 631 CG. The pedigree has 29,643 animals. Year of birth, birth season, and herd data were used to define the CG; birth seasons were grouped into three classes August to November (1), December to March (2), and April to July (3).

2.2. Data analysis

The Intergen program (Cardoso, 2007) was used with a standard animal model (AM), and with homoscedastic, and heteroscedastic hierarchical reaction norm models (HRNM). The AM estimates the animal´s genetic value and environmental effect based on the CG disregards GEI and thus the AM model was used for comparison with the HRNM. The genetic value of the animal using HRNM is obtained according to the average environmental level, corresponding to the CG solution to which the record belongs.

Kolmodin, Strandberg, Madsen, Jensen and Jorjani (2002) proposed a two-step hierarchical reaction norm model (HRNM$_{2S}$), in which the environmental solutions of the AM are used as covariates in the HRNM, whereas the one-step hierarchical reaction norm model (HRNM$_{1S}$) estimates the environmental effects through the reaction norms of the animals (Su et al., 2006). In addition, the homoscedasticity for AM, HRNM$_{2S}$ (HRNMHO$_{2S}$), and HRNM$_{1S}$ (HRNMHO$_{1S}$), with $e_i \sim N(0, \sigma_e^2)$, and heteroscedasticity for the HRNM$_{2S}$ (HRNMHE$_{2S}$), and HRNM$_{1S}$ (HRNMHE$_{1S}$), with $e_i \sim N(0, \sigma_{eij}^2)$, were used as assumptions for the residual variance.

The AM was calculated as $y_{ij} = x_j' + X_i + a_j + e_{ij}$, wherein y_{ij} is the reproductive record of the animal i in the environment j; x_j' is the incidence vector; X_i is the random environmental effect (contemporary group); a_j is the additive genetic value of the animal j; and e_{ij} is the residual error. HRNM$_{2S}$ was calculated as $y_{ij} = x_j' + \phi \hat{X}_i + a_j + b_j \hat{X}_i + e_{ij}$, and HRNM$_{1S}$ as $y_{ij} = x_j' + X_i + a_j + b_j X_i + e_{ij}$, wherein ϕ is the fixed regression coefficient; a_j is the additive genetic value directly from the intercept or level of the reaction norm of the animal j; b_j is the random regression coefficient or slope of the direct reaction norm in the environment represented by $\hat{X}_i$; $\hat{X}_i$ is the predictor of X_i obtained in the

AM; and e_{ij} is the residual error.

The Bayesian approach, using the Monte Carlo methods via Markov Chains (MCMC), was used to estimate the components of variances, through a pilot sample (55,000 cycles, 5000 burn-in, and 5 thinning) and shows the convergence through the R program (R Development Core Team, 2008) using the Bayesiam Output Analysis package (Smith, 2007) for the diagnosis of Geweke (1992).

Chain convergence analysis (Brooks & Roberts, 1998) is based on an equality test of means of the first samples (10% initial) and the last part of the Markov chain (last 50%) for the different models:

$$Z_i = \frac{(\bar{l}_i^A - \bar{l}_i^B)}{\sqrt{\frac{1}{n_A}\hat{S}_i^A(0) + \frac{1}{n_B}\hat{S}_i^B(0)}} \quad \text{werein} \quad \bar{l}_i^A = \frac{1}{n_A}\sum_{j=1}^{n_A} l_i^{(j)}, \quad \text{and} \quad \bar{l}_i^B =$$

$\frac{1}{n_B}\sum_{j=n^*}^{m} l_i^{(j)}$, with $n_A = 66{,}000$, $n_B = 330{,}000$, $n^* = 330{,}001$, and $\hat{S}_i^A(0)$ and $\hat{S}_i^B(0)$, considering the spectral density estimates at frequency zero obtained by the SAS Spectra Procedure (SAS Institute Inc., 2017), for the first n_A and last n_B cycles of the MCMC of length m. Extreme absolute values of the Z_i score for a two-tailed test indicate rejection of the convergence test. The Raftery and Lewis (1993) test was used to analyze the varcompsam file to determine the new chain size and the thinning; and the Heidelberger and Welch (1983) criteria indicate the burn-in.

The models that best fit the AFC data (AM, HRNMHO$_{1S}$, HRNMHO$_{2S}$, HRNMHE$_{2S}$ and HRNMHE$_{1S}$) were determined by using the deviance information criterion (DIC), deviance based on Bayes factors (DBF), and deviance based on conditional predictive order (DCP).

The bulls were classified according to the slope of the reaction norms robust genotypes presented constant values for slopes (b_j) in the environmental gradient (close to zero), and plastic genotypes presented high values of b_j, presenting significant different performance in the environmental gradient (Falconer, 1990). According to the standard deviation of the slopes for AFC, the bulls were classified as extremely robust ($|b_j| < \sigma_b$), robust ($\sigma_b \leq |b_j| \leq 2\sigma_b$), plastic ($2\sigma_b \leq |b_j| \leq 3\sigma_b$), and extremely plastic genotypes ($|b_j| \geq 3\sigma_b$).

3. Results and discussion

The mean and standard deviation of the age at first calving (AFC) of the Holstein cow population was 790.65 ± 97.08 days which is approximately 26.33 months. In Brazil, AFC varies greatly in Holstein, with means between 24.18 ± 1.59 (Marestone et al., 2013) and 35.63 months (McManus, Teixeira, Dias, Louvadini & Oliveira, 2008).

Holstein cows fed on a mixed feed and pasture in South Africa presented mean AFC of 27.33 and 28.56 months, respectively (Nesser et al., 2014), denoting the sexual precocity of Holstein cows and expressive phenotypic variation of this trait. Although Holstein cows are very sensitive to tropical environmental conditions, pure breed cows in Brazil are almost exclusively raised in advanced production systems, which partially reduce the environmental influence, decreasing AFC.

According to the DIC, DBF, and DCP criteria to evaluate the convergence of the chains, convergence was found only for the models AM ($p > 0.05$) and HRNMHO1S ($p > 0.01$) (Table 1). The models that consider the heterogeneity of residual variances (HRNMHE1S and HRNMHE2S) presented convergence problems, as well as HRNMHO$_{2S}$, which considers homogeneity of residual variance. HRNMHO1S presented the best fit to the data, denoting that the effects of CG, which are unknown covariates in HRNM1S, are more effective than the environmental effects from the estimation of the AM, as in the case of HRNM$_{2S}$, since it eliminates the possibility of biased prediction of the genetic merit of the animals for AFC.

Streit et al. (2013) evaluated protein percentage and somatic cell count in the milk of Holstein cows in Germany using reaction norms and found no presence of residual heterogeneity of variances in the

Table 1
Deviance information criterion (DIC), deviance based on Bayes factors (DBF), and deviance based on conditional predictive order (DCP) of the standard animal model (AM) and homoscedastic hierarchical reaction norm model of one step (HRNMHO$_{1S}$) for age at first calving in Holstein cows.

| Model	DIC	DCP	DBF
AM	262,839[2]	223,056.6[2]	218,023.3[2]
HRNMHO$_{1S}$	261,121.8[1]	220,134.2[1]	211,515.8[1]

[1] and [2] indicates the fit quality classification.

evaluated population. According to Araujo et al. (2009), the homogeneity of variances can be considered when the evaluated bulls present progeny distributed in different herds. Highly parameterized models, such as those that include residual heterogeneity of variances, present problems in estimating variance components due to the covariance structures and the fact that the incidence matrices are denser than those for conventional models (El Faro & Albuquerque, 2003).

The amplitudes of the solutions of the CG (X_i) ranged from -31 to 5.8, representing environments from high to low management levels, with zero representing the medium level environment (Fig. 1). The amplitude of the environmental gradient variation was small, resulting in a small amplitude between means of CG for AFC, which ranged from 648 to 1144 days. The heritability estimated by the AM was 0.07; the heritability estimated by the HRNMHO$_{1S}$ varied throughout the environmental gradient from 0.04 to 0.28, for the lowest to the highest AFC (Fig. 1). The best environments, which had lower AFC, also had lower phenotypic variation, which led to lower estimates of the additive genetic variance and, consequently, lower heritability. Herds that presented medium to high AFC (less favorable environments) had significant phenotypic variation, which generated higher genetic additive variation and higher heritability estimates.

A similar result was found by Scarpati and Lôbo (1999), with lower additive genetic variance generating lower heritability estimates. Ouweltjes, Windig, Van Pelt and Callus (2015) also found a tendency of higher heritability in less favorable environments when evaluating calf mortality rate in first-calving dairy cows in the Netherlands; they found two-fold the heritability for unfavorable environments when compared to favorable environments. Similarly, Ismael et al. (2016b) estimated two-fold lower heritability in the most favorable environments when assessing the fertility of Holstein cows in Denmark.

Nesser et al. (2014) found low heritability (0.06 and 0.05) for AFC in Holstein cows fed on a mixed feed and pasture, respectively. However, higher heritability (0.23) was found for Holstein cows in free-stall systems with fans and sprinklers in tropical climates (Bertipaglia, Silva, Cardoso & Maia, 2007). The use of the same minimum weight for first pregnancy in most herds in Brazil, whether through natural mating or
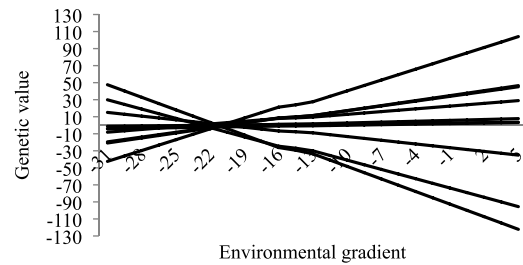

Fig. 2. Reaction norms along the environmental gradient for age at first calving for the 10 Holstein bulls with the highest number of daughters.

artificial insemination, penalizes breeders who produce sexually precocious females, by reducing genetic variability for this trait. Mcmanus, Teixeira, Dias, Louvandini and Oliveira (2008) also pointed out this problem, describing that the use of a minimum weight affects the result and masks reproductive precocity, inhibiting the efficiency of the genetic selection.

The genetic values of the 10 bulls with the highest numbers of daughters along the environmental gradient (Fig. 2) showed small differences between bulls in environments with lower AFC, and greater variations in environments with medium to high AFC. Bulls with potential for decreasing AFC are in the lower values of the environmental gradient, although these environments present lower additive genetic variance. However, the expression of the trait is variable in less favorable environments, with higher values of the environmental gradient, resulting in great differences between bulls. Despite the lower additive genetic variability in environments with lower values, there are significant differences in the genetic values of the bulls, denoting the possibility of choosing suitable bulls according to each environment within the environmental gradient.

The best animals for one environment can be the worst for another (complex interaction type); and even animals with robust genotypes showed inverse classification with variation within the environmental gradient, denoting the importance of using specific bulls for each environment or production system. This type of interaction is one of the most problematic ones, since an inappropriate use of bulls can lead to great genetic losses, and possibly lead to an increase in AFC, since it disregards the presence of GEI.

Selecting bulls with high genetic merit in Brazil requires care; their progenies may not present the same performance when raised in different production systems from which the bull was selected. This is evident in the country where about 80% of the Holstein semen is imported from other countries, and the choice of bull is based on genetic values obtained in temperate countries (Silva et al., 2016), often the USA and Canada.
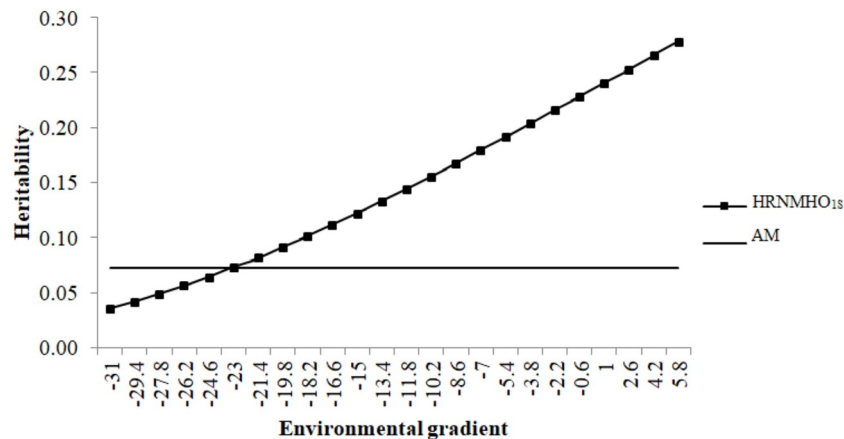
Fig. 1. Heritability for age at first calving of Holstein cows in Brazil estimated by the AM and HRNMHO$_{1S}$ models.
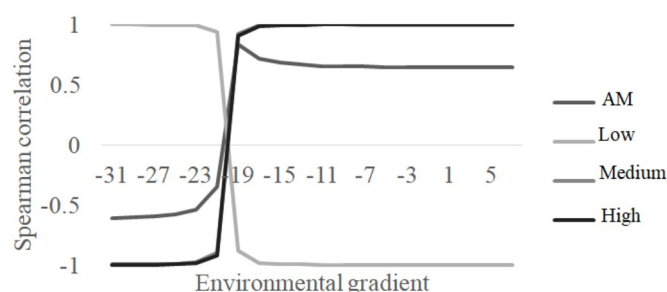
Fig. 3. Spearman correlations between Holstein bulls for age at first calving obtained in the AM and $HRNMHO_{1S}$ for the environmental levels in Brazil.

Chegini, Shadparvar and Hossein-Zadeh (2013) reported a great introduction of genetic material from imported semen in Holstein herds in Iran. The progeny performance of these bulls can be different in tropical and temperate countries, and the objectives and selection criteria are different, requiring the use of bulls that are produced and evaluated in tropical conditions, selected for production, and adapted to the local environment. Ismael et al. (2016b) found no reclassification of Holstein bulls along the environmental gradient in Danish herds and considered GEI to be zero. Tiezzi et al. (2017) performed a genomic prediction for productive traits in dairy herds in the United States of America and found a strong effect of GEI on milk production, moderate effect on somatic cell counts, and a small effect on protein and fat percentages.

Spearman correlations between bull classification obtained in the AM and HRNMHO1S varied throughout the environmental gradient from −0.99 to 0.99 (Fig. 3). Breeding bulls of high genetic value in lower AFC environments are not recommended for environments that provide moderate to high AFC. The Spearman correlations of the classification of bulls obtained in the AM and HRNMHO1S in the environment with lower AFC were moderate and negative, indicating that animals selected for one environment are not recommended for another. The correlations were positive, with medium to high magnitude in environments with moderate to high AFC. Bulls evaluated through the AM can be recommended for environments that provide higher AFC. Animals selected for the environment of moderate AFC can be used in environments with high AFC, although a great variation in the genetic values of these bulls is observed in environments that provide high AFC.

Therefore, inappropriate use of bulls can generate serious economic losses, since the AFC represents the beginning of the productive life of the animal and is directly connected to economic returns. According to Marestone et al. (2013), the higher average daily weight gain of heifers, the lower the AFC and the greater the profitability, not only due to the greater number of calves and milk production, but also due to the possibility of improving the genetic gain throughout the generations. Nesser et al. (2014) emphasized the importance of the careful selection of bulls for breeding, especially regarding their adaptation to the production systems and environments (including the local climate) in which their progenies will be raised.

Tiezzi, Parker Gaddis, Clay & Maltecca (2015) included the effect of GEI on genomic predictions of production traits of Holstein cows in USA and found that climatic variables present the greatest potential to be included in statistical models that consider GEI. Studies involving three regions (Southeast, Northeast, and Southwest) of USA showed moderate genetic correlations between large milk production properties using Holstein cows, with a variation from 0.67 to 0.76; however, the correlations between the regions presented larger variations (0.58 to 0.77) when evaluating small herds. This denotes the occurrence of GEI not only between different regions but also between large and small herds (Tsuruta et al., 2015).

Strandberg, Brotherstone, Wall and Coffey (2009) found high negative Spearman correlations among the genetic values of bulls in the
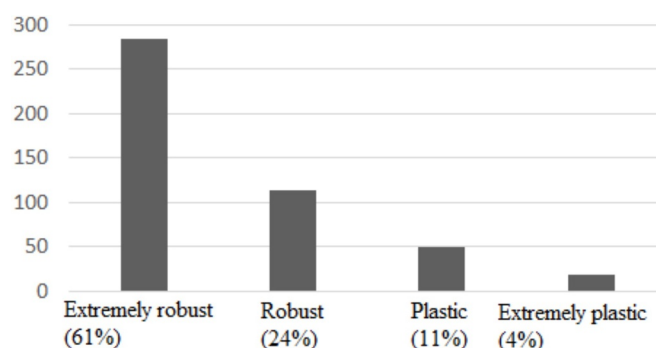

Fig. 4. Percentage of Holstein bulls with extremely robust, robust, plastic, and extremely plastic genotypes for age at first calving.

United Kingdom from low, and medium to high environments for calving interval. Contrastingly, Ouweltjes et al. (2015) found high and positive correlations (above 0.90) among different environmental levels for mortality of calves of first-calf cows in herds in the Netherlands, with a significant improvement in post-partum survival (two-fold higher) with bulls selected in unfavorable environments.

The mean standard deviation of the slope of the reaction norms (*bj*) was 0.142 for bulls that had their progenies evaluated for AFC (Fig. 4). More than 85% of the bulls presented extremely robust, or robust genotypes; and approximately 15% presented plastic, or extremely plastic genotypes (animals that significantly responded to environmental variations). Two of the 10 bulls with the highest number of daughters presented plastic genotypes, three robust, and five extremely robust genotypes (Fig. 2). Extremely plastic, and plastic bulls had the lower average number of daughters (37.5) than robust, and extremely robust bulls (40.4), although plastic bulls presented higher genetic values in the best environment, which resulted in lower AFC. Nesser et al. (2014) emphasized the importance of using specific bulls to each environment or production system to increase the productivity of production systems.

Genetic gains in AFC are possible through the selection of bulls, despite the small heritability in environments that resulted in lower AFC. The complex GEI found showed that bulls with the highest genetic merit for one environment are not recommended for another. Thus, the import of semen of Holstein bulls without genetic evaluations that consider the Brazilian breeding environment requires care, since it can affect the genetic gain of the population for AFC. Thus, it is increasingly necessary to identify and multiply breeding bulls considering the local tropical and subtropical conditions.

4. Conclusion

A genotype-environment interaction of the complex type was found for age at first calving of Holstein cows in Brazil, even for bulls with robust genotype, indicating that the inappropriate use of bulls in environments where their daughters will be raised can decrease genetic gain and cause economic losses for the dairy activity in Brazil.

Although breeders do not perform genetic selection directly for age at first calving, and most bulls used by them are imported, and most of the bulls used in Brazil have robust, or extremely robust genotypes. However, some animals with sensitive genotypes to environmental changes can be identified. This allowing a better direction for mating. Thus, specific animals can be selected for each production system and adapted to local environmental conditions in which their daughters will be raised.

Ethical statement

Not applicable. Database of the Brazilian Agricultural Research Corporation (EMBRAPA) and the Brazilian Association of Holstein

Cattle Breeders.

Conflict of interest

Acknowledgments

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