

Genotype-environment interaction for age at first calving in Limousine and Charolais cattle raised in Italy, employing reaction norm model

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Abstract

The genotypes express differentiated responses depending on the environmental conditions and this can cause a re-ordering of the genotype in the environmental gradient. Therefore, our objective was to evaluate the genotype-environment interaction (GxE) for age at first calving (AFC) in Limousine and Charolais cattle raised in Italy, using reaction norm model (RNM). The data comprises information from 35,255 Limousine and 7,339 Charolais animals, born between 1999 and 2017. The standard animal model (AM), which ignores the G x E interaction, and the hierarchical models of reaction norms with homogeneous and heterogeneous residual variances with one and two steps (MHNRRHO1P, MHNRRHO2P, MHNRRHE1P, and MHNRRHE2P) were used for the analysis. In both breeds, the MHNRRHOP1 model presented the best fit. In favorable environments (lower AFC), there was less phenotypic variation; the AFC expression of the animals was close, and this may have caused lower estimates of additive genetic effects (σ_A^2) and consequently lower heritabilities (h^2). In Charolais, the h^2 for the animal model (AM) was 0.13, whereas for MHNRRHOP1 the value varied throughout the environmental gradient from 0.06 to 0.13, for low and high AFC environments, respectively. In Limousine breed, a lower h^2 (0.06) was observed in the animal model (AM), while in the MHNRRHOP1 model it varied from 0.00 to 0.15. In both breeds, bulls with higher genetic merits for one environment were not for another, demonstrating the existence of the GxE. In Charolais and Limousine breeds, more than 93.75% and 87.72% of the bulls presented extremely robust or robust genotypes, respectively. Although most bulls are robust, there are bulls reactive to the environment, which can lead to incorrect selection of breeders. The results suggest that the genotype-

environment interaction should be considered in the selection for AFC in both breeds raised in Italy.

Keywords: genetic evaluation, age at first calving, genetic correlation, reproductive efficiency, phenotypic plasticity, environmental sensitivity.

Introduction

Reproductive performance is one of the determining factors in the economic viability of cattle production (Berry et al., 2014). Indeed, age at first calving relates to birth rates, ability to conceive, precocity and productive longevity of cows (Bormann and Wilson, 2010), as well as favorable genetic correlations with the physical and morphological characteristics of semen (Dias et al. 2008). Females with higher reproductive efficiency spend less idle time in the herd (Laureano et al., 2011), producing more calves for a period of time (Aby et al., 2012) and shortening the generation interval (Lira et al. 2008), making it possible to intensify selection (Azevedo et al., 2006). Therefore, herds with high sexual precocity and fertility present greater genetic progress (Marestone et al., 2013). This justifies the need to consider reproductive aspects as selection objectives in breeding programs.

Genotypes have responses that may vary according to different environmental conditions, whose gradient may eventually affect their performance (Falconer and Mackay, 1996). Thus, the evaluation of the interaction between genotypes and environments (G×E) is one of the efficient approaches to cope with these problems. The effect of G×E interaction for reproductive traits has already been identified, suggesting that the selection of bulls should consider the environments in which their progenies will be reared (Nesser et al., 2014; Montaldo et al., 2017). However, cattle breeding programs in Italy do not take into account G×E interaction, which justifies the importance of the present work in the dissemination of technologies capable of accurately identifying genetically superior individuals for reproductive traits of females.

Reaction norm models (RNM) are among the techniques used to evaluate genotype-environment interaction. The G×E evaluation is based on the complete set of multivariate ontogenetic trajectories produced by a genotype when exposed to different environments (Schlichting & Pigliucci, 1998). This allows describing the gradual and continuous variation of the genotypes, in economically important traits, along with an

environmental gradient (De Jong, 1995). The most stable genotypes tend to be indicated as superior, even if they might not be necessarily the best in all environments (Ambrosini et al., 2016). In general, the use of RNMs for the identification of superior animals may impose a paradigm shift in selection strategies, since for each environment a different genetic value may be obtained from the selected candidate (Mattar et al., 2011).

The Limousine and Charolais breeds are French beef breeds, commonly exported to several countries around the world, where they are used as pure breed or in local crossbreeding systems. (Bouquet et al., 2011). In general, these animals have a robust and muscular body, and a good rate of feed conversion and calving ease (Giorgetti et al., 1992). In Italy, approximately 5,500 Charolais and 19,000 Limousine females are currently registered in the National Herd Book (ANACLI, 2017). The objective of the present study was to evaluate the genotype-environment interaction (G x E) for age at first calving (AFC) in Limousine and Charolais cattle reared in Italy, using reaction norm models.

Material and methods

Data

Data was provided by the Italian Association of Charolais and Limousine Breeders (ANACLI) and included information of animals born between 1999 and 2017. A total of 18,500 females were used for the Limousine breed and 4,330 females for Charolais, respectively (Table 1). The Pedigree contained 293,018 Limousine and 91,419 Charolais individuals.

Table 1. Descriptive statistics.

Breed	Mean	Minimum	Maximum
Charolais	1193.97±310.30	720	2000
Limousine	1101.84±236.21	720	2000

G x E Interaction

In both breeds, contemporary groups (CG) were created, considering farm, year and season of calving. The degree of connectivity between CGs was based on the total number of direct genetic links between one CG and another. For this, the AMC program (Roso and Schenkel, 2006) was used with at least 10 genetic links of connectivity among CG, under an animal model. The G x E assessment was performed applying a hierarchical reaction norm model, in which the genetic value of the animal was obtained by a linear function of the environmental value through random regression. In order to obtain the norms of reaction through random regression, the INTERGEN program (Cardoso, 2007) was used.

First, a standard animal model (AM) was used, ignoring G x E (model 1). Subsequently it was used as a covariate in the reaction pattern models. AM was as following: $y_{ij} = x_i'\beta + X_j + a_i + m_i + ep_i + e_{ij}$ (1), where; y_{ij} is AFC of animal i in environment j ; β , a vector of fixed effects (linear and quadratic for the age of the cow); x_i' corresponds to the incidence vector; X_j , random environmental effect (contemporary group); a_i , additive genetic value of animal i ; m_i , maternal genetic value of animal i ; ep_i , maternal permanent environment effect and, e_{ij} ; residual error.

The G x E was tested by fitting two hierarchical reaction norm models; the hierarchical two-step reaction standard model (MHNR2P) and the hierarchical one-step reaction standard model of a MHNR2P (Kolmodini et al., 2002), which uses the AM environmental solutions as covariates according to the following equation: $y_{ij} = x_i'\beta + \phi\hat{X}_j + a_i + m_i + ep_i + b_{1i}\hat{X}_j + b_{2i}\hat{X}_j + e_{ij}$ (2), where: ϕ = fixed regression coefficient; a_i = genetic additive value directly from the intercept or level of the reaction norm of animal i ; m_i = maternal genetic value of the intercept or level of the reaction norm of animal i ; ep_i , permanent maternal environment effect; b_{1i} = random regression coefficient or slope of the direct reaction norm; b_{2i} = random regression coefficient or slope of the maternal reaction norm; i in the environment represented by \hat{X}_j ; \hat{X}_j = predictor of X_j obtido in (1) e e_{ij} = o the residual error.

MHNR1P (SU et al., 2006) estimates the environmental effects in conjunction with the animal reaction standard, according to the following model: $y_{ij} = x_i'\beta + X_j + a_i + m_i + ep_i + b_{1i}X_j + b_{2i}X_j + e_{ij}$ (3). Two different assumptions were used for the residual variance : (a) homoscedasticity for AM, MHNR_{2P} (MHNRHO_{1P}) and MHNR_{1P}

(MHNRRHO_{2P}), with $\mathbf{e}_i \sim N(\mathbf{0}, \sigma_e^2)$; e (b) heteroscedasticity for the MHNRR_{2P} (MHNRRHE_{2P}) e MHNRR_{1P} (MHNRRHE_{1P}) models, with $\mathbf{e}_i \sim N(\mathbf{0}, \sigma_{eij}^2)$.

The genetic, direct additive and maternal variances in the environment X, $\sigma_A^2|X$ e $\sigma_m^2|X$, were obtained by:

$$\sigma_A^2|X = \text{var}(\mathbf{a}_i + b_{1i}X_j) = \sigma_a^2 + \sigma_b^2x^2 + 2\sigma_{a,b}x$$

$$\sigma_m^2|X = \text{var}(a_i + b_{2i}X_j) = \sigma_m^2 + \sigma_b^2x^2 + 2\sigma_{a,b}x$$

The heritabilities were estimated by the genetic variance ratio with the phenotypic variance (genetic + environmental), based on the following formula:

$$\sigma_a^2|X = \frac{\sigma_A^2|X}{\sigma_A^2|X + \sigma_m^2|X + \sigma_{pe}^2 + \sigma_e^2|X}$$

$$\sigma_m^2|X = \frac{\sigma_m^2|X}{\sigma_A^2|X + \sigma_m^2|X + \sigma_{pe}^2 + \sigma_e^2|X}$$

Where: $\sigma_e^2|X$ = residual variance in the environment X, obtained by $\sigma_e^2|X = \sigma_e^2\hat{\eta}^X$, in the simplified heteroscedastic model and σ_e^2 in the homoscedastic model, where η = variance of the parameter of heterogeneity of residual variance in the environmental gradient (X), following the model structure proposed by Cardoso et al. (2005).

Using a Bayesian approach, the estimates of the variance components were obtained using Monte Carlo methods via Markov Chains (MCMC), adopting the procedure: a) A pilot sample was run (100,000 cycles, 10,000 burn-in and 10 for the thinning interval); b) using the varcompsam response file, and the R program (R DEVELOPMENT CORE TEAM, 2008) - Bayesian Output Analysis - BOA (Smith, 2007), the Raftery and Lewis test (1992) was applied to determine the new chain size and the thinning period; and c) the burn-in period was evaluated by applying the Heidelberger and Welch (1983) method. Averages, standard deviations and percentiles (0.025 and 0.975) of the parameters were obtained from their marginal posterior densities obtained by the SAS KDE Procedure (SAS INSTITUTE INC., 2018). The fit of the models (MA, MHNRRHO_{1P}, MHNRRHO_{2P}, MHNRRHE_{2P} and MHNRRHE_{1P}) were evaluated based on the three criteria: Deviance Information Criterion (DIC), Deviance Based on Bayes Factors (DBF) and Deviance based on Predictive Order Conditional - (POC).

The convergence analysis of the chains for the different models was tested through Geweke diagnosis (1992), based on a Z test of equality of means of the

logarithm of the conditional distribution of the data, denoted by $l_i^{(j)} = \log p(\mathbf{y} | \boldsymbol{\theta}^{(j)}, M_i)$, of the first samples (10% initial), and the last part of the Markov chain (last 50%) (Brooks and Roberts, 1998), according to the following formula:

$$Z_i = \frac{(\bar{l}_i^A - \bar{l}_i^B)}{\sqrt{\frac{1}{n_A} \hat{S}_i^A(0) + \frac{1}{n_B} \hat{S}_i^B(0)}},$$

where $\bar{l}_i^A = \frac{1}{n_A} \sum_{j=1}^{n_A} l_i^{(j)}$, $\bar{l}_i^B = \frac{1}{n_B} \sum_{j=n^*}^m l_i^{(j)}$, $n_A = 66.000$, $n_B = 330.000$, $n^* = 330.001$, and

$\hat{S}_i^A(0)$ e $\hat{S}_i^B(0)$, and their respective estimates of spectral density at zero frequency obtained by the SAS SPECTRA Procedure (SAS INSTITUTE INC., 2018), for the first n_A and last n_B cycles of the MCMC chain of length m . Extreme absolute values of the Z_i score for a two-tailed test indicate rejection of the convergence test.

Results

The Geweke (Z) test suggests that all models converged at 5% ($P < 0.05$) for the Charolais breed, while only models AM, MHNRRHO2P and MHNRRHO1P converged for Limousine. Using three criteria for models' comparison (DIC, PCO and DBF), MHNRRHO1P presented the best fit in both breeds (Table 1).

Table 1. Deviance information criterion (DIC), deviance based on predictive conditional order (PCO) and deviance based on Bayes factors (DBF) for comparison between the standard animal model and the hierarchical models of reaction norms with residual variance homogeneous and heterogeneous with one and two steps in the Charolais and Limousine breeds.

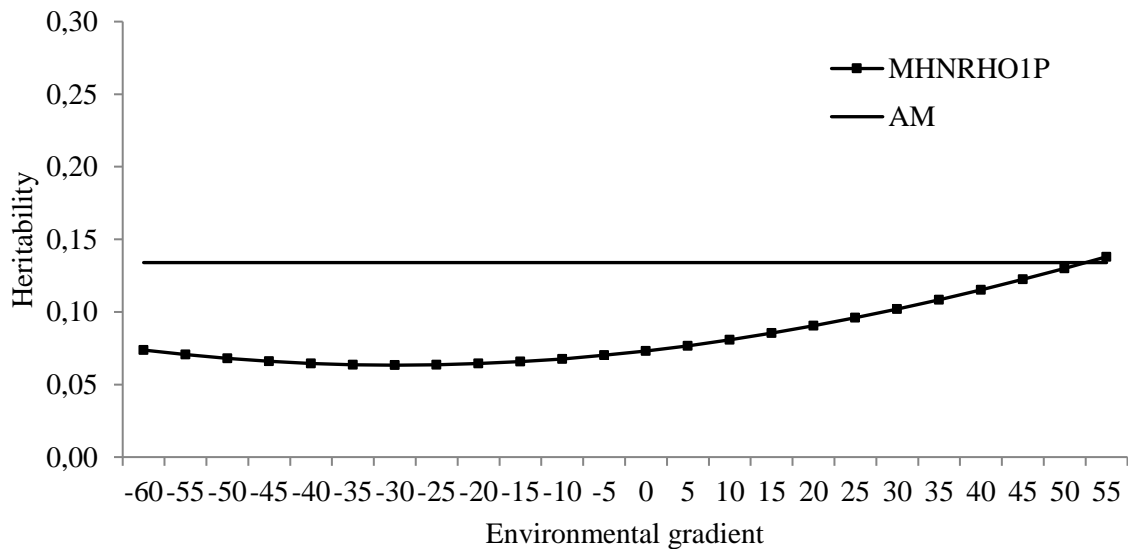
Model	Charolais			Limousin		
	DIC	PCO	DBF	DIC	PCO	DBF
AM	16525.78 ₍₄₎	14099.64 ₍₁₎	13676.83 ₍₃₎	99422.12 ₍₃₎	84677.06 ₍₃₎	81868.33 ₍₃₎
MHNRRHO2P		14099.94 ₍₂₎	13674.78 ₍₂₎	97349.04 ₍₁₎	84645.37 ₍₂₎	81358.03 ₍₂₎
MHNRRHO1P	16248.4 ₍₂₎	14105.14 ₍₂₎	13667.89 ₍₁₎	97353.38 ₍₁₎	84643.61 ₍₂₎	81334.29 ₍₂₎

P	1)	3)	1)	2)	1)	1)
MHNRHE2	16488.88 ₍	14138.63 ₍		nc	nc	nc
P	3)	4)	13727.8 ₍₄₎			
MHNRHE1	16610.36 ₍	14304.23 ₍		nc	nc	nc
P	5)	5)	13976.1 ₍₅₎			

The numbers in parentheses indicate the best fit rating. nc: did not converge. * Number in bold: lower values. AM: animal model; MHNRHO2P: homoscedasticity two-step; MHNRHO1P: homoscedasticity one-step; MHNRHE2P: heteroscedasticity two-step; MHNRHE1P: heteroscedasticity one-step.

According to figure 1, it can be observed that in better environments (<AFC), there were less phenotypic variation, and consequently, lower estimates of additive genetic variance and heritabilities. In the less favoured environments for AFC (medium and high AFC), large variations in phenotypic values were observed, which may influence the greater additive genetic variation and heritability. In the Charolais breed, the heritability for the AM was 0.13, whereas for MHNRHO1P the value varied throughout the environmental gradient from 0.06 to 0.13 (Figure 1-A).

A



B

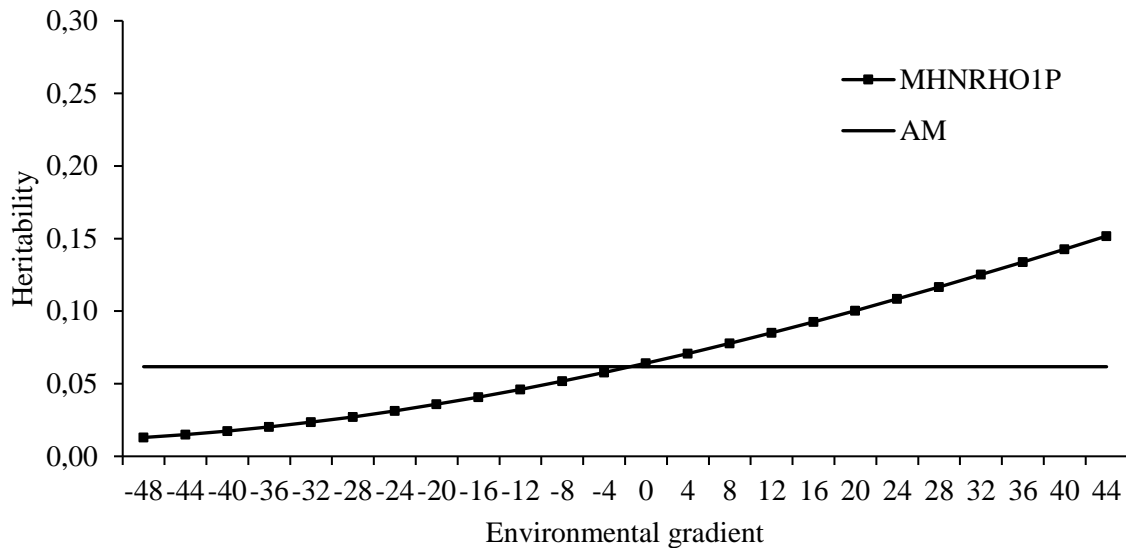


Figure 1. Heritabilities for age at first calving in AM and MHNRRHO1P for Charolais (A) and Limousine (B) breeds.

In the Limousine breed, the lowest AM heritability value was observed (0.06), however the values obtained in MHNRRHO1P ranged from 0.00 to 0.15. In the Charolais cattle, the amplitude of variation throughout the environmental gradient was smaller than in the Limousine. It is also important to point out that there is a biological limit that establishes the phenotypic variability of the AFC. Thus, in good environments, it is not easy to significantly reduce the AFC. However, in unfavorable environments, AFC depends mainly on the management of the farm rather than on the biological limits of AFC. This well explains the greater variation of AFC observed in unfavourable environments.

In figure 2, it is observed that the decrease of AFC is possible through the proper selection of bulls in both breeds. However, it is worth noting that reproductive traits are highly influenced by environmental factors. For the figure interpretation, it is emphasized that the best bulls for poor environments are those that have lower genetic value in favorable environments. In general, we can observe less variation among bulls in low AFC environments and greater variations in medium and high AFC environments, especially for the Limousine breed.

A

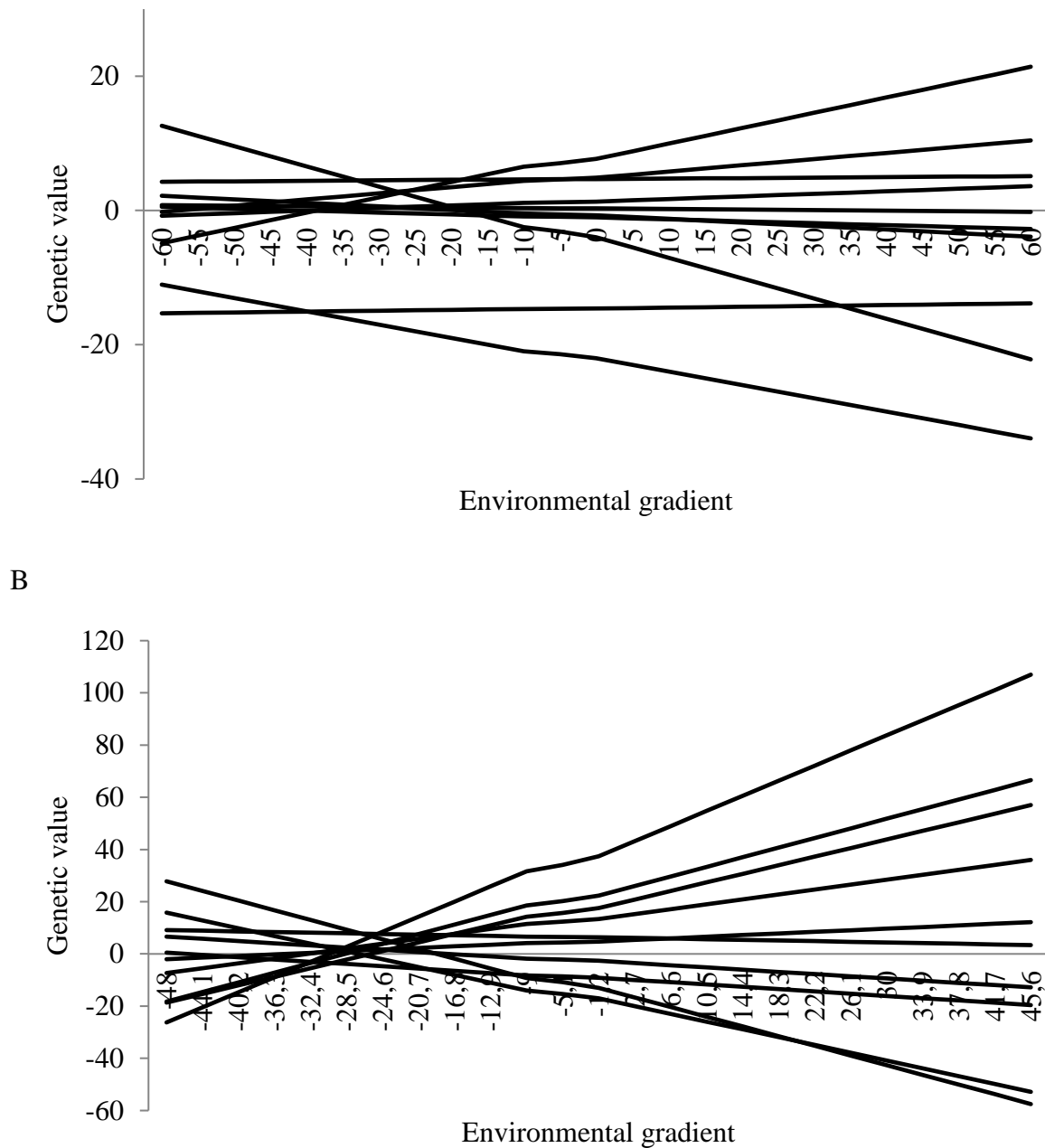
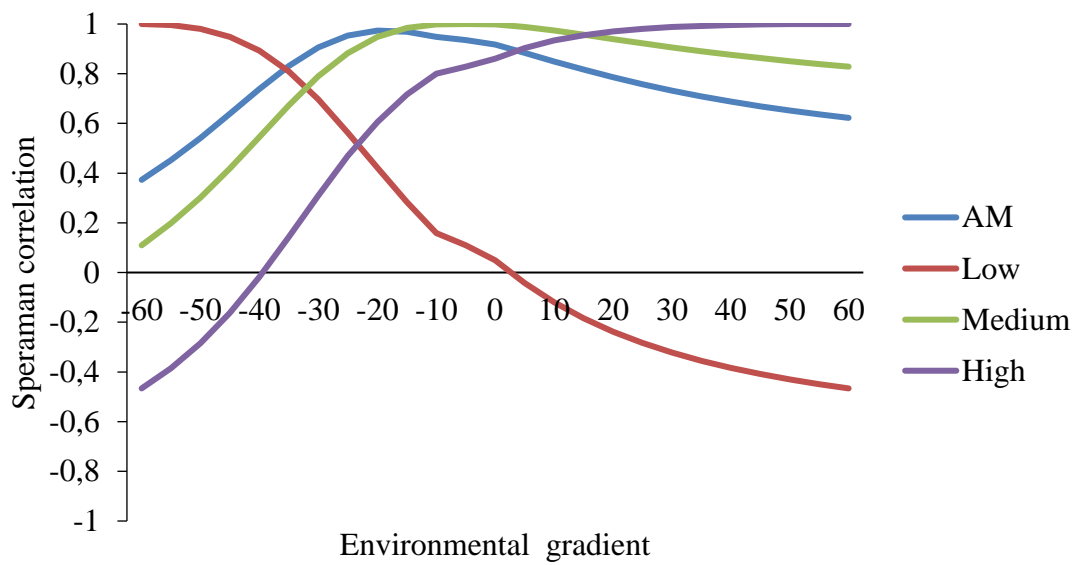


Figure 2. Response norms along the environmental gradient for the first calving obtained for the 10 Charolais (A) and Limousine (B) bulls with the largest number of daughters in Italy.

In the lower values of the environmental gradient (favorable) are the bulls with potential for improvement in other environments, despite their smaller values of additive genetic variance. However, in environments with higher environmental gradient values (less favorable), the expression of the characteristic is quite variable, which reflects the great differences among bulls.

Spearman correlations between bull ranks in AM and MHNRRHO1P varied throughout the environmental gradient (Figure 3), showing that bull breeding in low-AFC environments is not recommended for use in medium- and high-AFC environments, especially in the Limousine breed. In general, the correlations between the AM and MHNRRHO1P in the lower AFC environment were moderate and negative, indicating that animals selected for one environment are not recommended for the others.

A



B

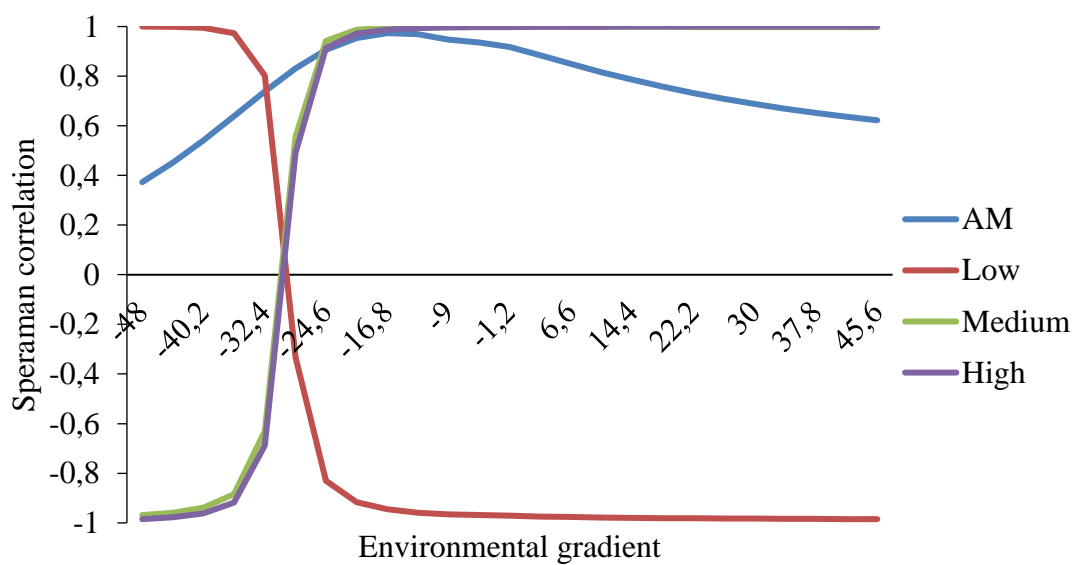
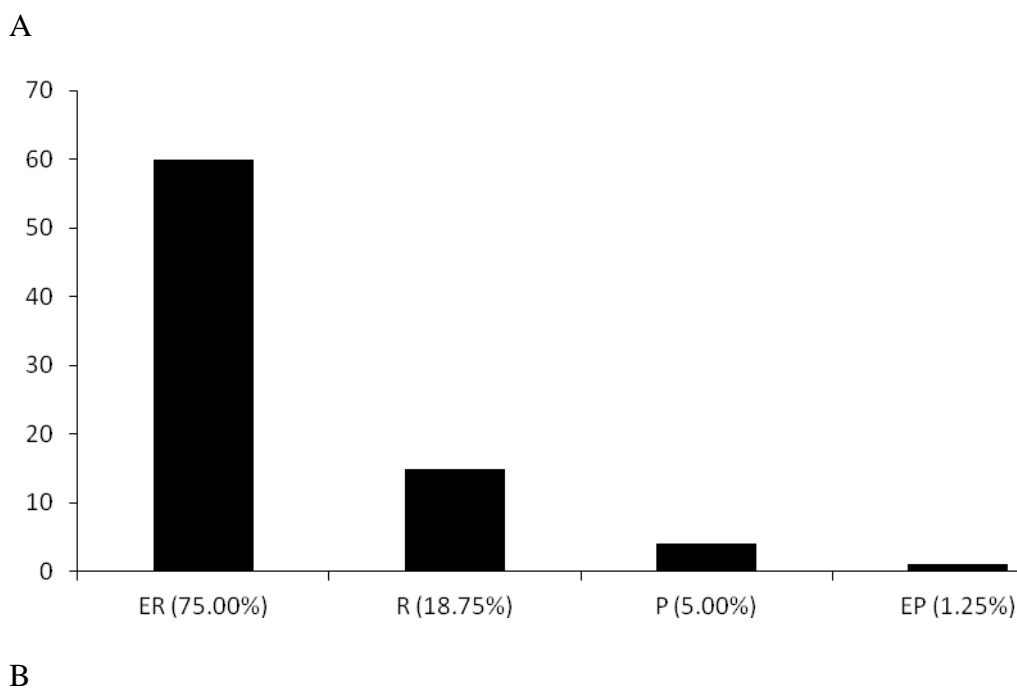


Figure 3. Spearman correlations between Charolais (A) and Limousine (B) bulls for age at first calving obtained by AM and MHNRRHO1P for different environmental levels in Italy.

Breeding values estimated in medium and high AFC environments were medium to high positively correlated, as well as EBV via AM with EBV of medium and high AFC environments. As a general rule, bulls of high genetic value in low AFC environments are not recommended for use in medium and high AFC environments, as well as those evaluated by the standard animal model. Animals selected in the medium AFC environment will have responses similar to those selected in the high AFC environment, although a great variation in the genetic values of bulls is observed in the environments that provide the worst AFC.

In the Charolais breed (Figure 4-A), more than 93.75% of the bulls presented extremely robust or robust genotypes, and slightly more than 6% showed sensitive or extremely sensitive genotypes, that is, those that respond to environmental variations for AFC. It was verified that of the 10 bulls (Figure 2-A), with the largest number of progenies, one is robust, 8 extremely robust and one sensitive. A lower average number of daughters was detected, for extremely sensitive and sensitive bulls (12.40) compared to robust and extremely robust bulls (16.08).



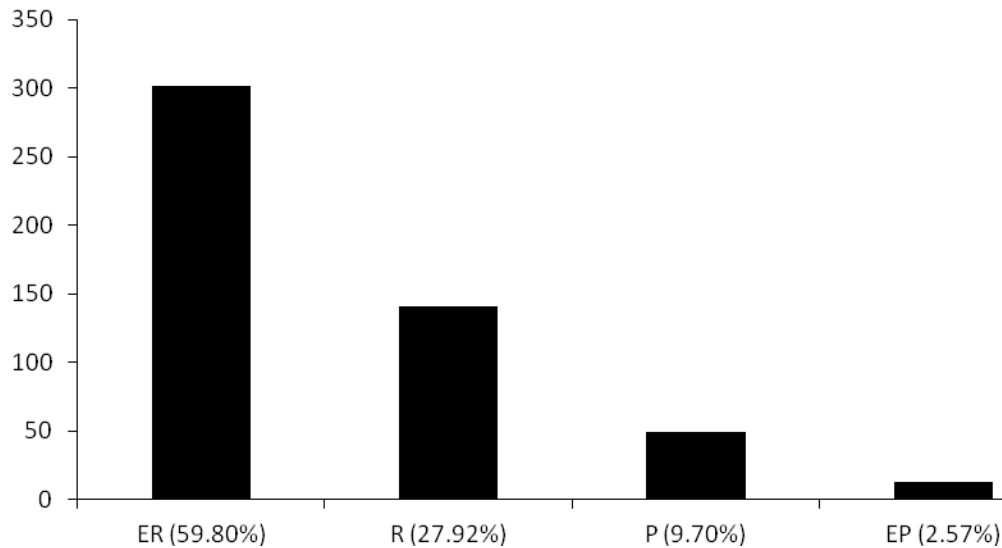


Figure 4. Inclination of the reaction standards with the percentage of Charolais (A) and Limousine (B) bulls evaluated with extremely robust (ER), robust (R), sensitive (P) and extremely sensitive (EP) genotypes for age at first calving in Italy.

The mean values of EPDs for bulls with robust and extremely robust genotypes in the favourable (lower AFC), medium and unfavourable (high AFC) gradients were -0.19, -0.17 and -0.16, respectively. For bulls with extremely sensitive and sensitive genotypes, the values ranged from -2.84 (favourable / lower AFC), -11.06 (medium) and -20.96 (unfavourable / higher AFC). It should be noticed that negative EPDs are used here, that is, reduction of days for AFC.

In the Limousine breed (Figure 4-B), 87.72% of the bulls presented extremely robust or robust genotypes. In general, of the top ten bulls (Figure 2-B), 4 are robust, 5 extremely robust and 1 sensitive. As for the Limousine breed, it is observed that the lowest average number of daughters per bull was found in the group of robust and extremely robust genotypes (15.19) compared to the group of extremely sensitive and sensitive (16.74) genotypes. The mean values of EPDs for bulls with robust and extremely robust genotypes in the favourable (lower AFC), medium and unfavourable (high AFC) gradients were -0.28, 0.30 and 1.02, respectively. For bulls with extremely sensitive and sensitive genotypes, the EPDs were -6.42 (favourable / lower AFC), 7.95 (medium) and 25.31 (unfavorable / high AFC).

Discussion

The results suggest that contemporary group effects considered as unknown co-variates in MHNRIIP are more effective than using environmental effects from the estimation of AM, since it eliminates the possibility of biased prediction of the genetic merit of the animals. The use of the reaction norm model made it possible to describe how genetic merit gradually and continuously changes in an environmental amplitude, a fact also reported by Ambrosini et al. (2012).

This allowed to identify the variation of environmental sensitivity of the Limousine and Charolais bulls used in the selection. The results of this study have shown a reclassification of genetic merit in different environments, which characterizes the G x E interaction. Therefore, the advantage of these models is that the selection response can be predicted, not only the phenotypic expression in the environment, but also the sensitivity of environmental changes (De Jong and Bijima, 2002).

There is a growing demand for technologies capable of finding and quantifying, from a genetic point of view, this adaptation to adverse environmental conditions, especially for low heritability characteristics such as CFA, since it is generally difficult to discard apparently superior animals

As it could be observed, the G x E caused changes in the relative and the absolute magnitude of the additive and phenotypic genetic variance, as already reported by Corrêa et al. (2009). It is emphasized that the environment does not alter the genetic constitution of an individual, but rather the expression of the genome, since the best genotype in one environment may not be in another (Warwick and Legates, 1980).

In this study for both breeds, there was less variance of additive genetics and heritability in a favorable environment. This is an indication that in favorable environments, where the maximum capacity of all animals is expressed, the females will give birth at an early age, mainly because it is possible that they have already reached an ideal minimum weight or other important physiological aspects have been fulfilled, to achieve the service at younger age..

Another possibility is the indirect result of the selection of breeding for generations by breeders through reproductive management, since animals that do not breed, often are discarded. These factors may be a justification for the standardization of phenotypic expression in a favourable environment. Therefore, in this scenario heifers tend to be very close to the physiological minimum AFC, explaining the lower phenotypic variation. However, in unfavourable environments, there are heifers calving

at young and older ages, which causes greater phenotypic variation and consequently greater estimation of heritability.

It is worth noting that despite the lower additive genetic variability in favourable environments, there are differences in the genetic values of the bulls, which shows the possibility of selecting the best bull for specific gradients within each breed, indicating that the influence of the environment acts differently on the estimates of the genetic values of the animals, as already reported by Toral et al. (2004).

In general, it is observed that the animals most suitable for one environment are the worst for the other, which characterizes a complex interaction. With respect to the variation of the h^2 in the environmental gradient for Charolais, it can be said that the less amplitude is due to the reflection of the smaller oscillation between the means of the contemporary groups for AFC. Additionally, the high value observed in the Limousine shows possible differences in the production system of the breeders.

In both breeds, most bulls presented a robust genotype, however, there is a smaller proportion of bulls that could be used in specific environments. In Charolais, these animals sensitive to the environment have a larger number of offspring, which is characterized as a complex G x E interaction, that is the most problematic due to the rearrange of the ranking. It would be interesting to select robust animals, that is, those that perform well regardless of the environmental gradient, however, it is difficult for an animal to have high EPDs in different gradients.

In specific situations, it is recommended to use sensitive bulls, that is, those that respond to the variation of the environmental gradient. These bulls can be used in particular environments, for correcting and/or enhancing the productive and reproductive indices of the herds. As a support for this idea, it was observed that the sensitive Charolais bulls have greater EPDs, compared to the robust ones, in all gradients. In Limousine sensitive bulls are recommended for favourable environments. Considering both breeds, robust bulls performed constantly across gradients, tending to be better in higher gradients (higher AFC).

Interestingly, even when animals have robust genotypes, they suffer a modification in the classification as a product of the environmental variation. This increases the importance of using bulls specific to each environment, as the use of inappropriate bulls will lead to genetic losses and to an increase in the AFC; mainly because the progeny of the bulls may not present the expected performance because they were raised in production systems other than the bull that was selected.

The proportion of sensitive Limousine bulls doubled the sensitive Charolais. The average number of sensitive bulls in the Limousine breed was greater than the robust bulls, which shows the use of locally raised bulls. This environmental sensitivity or phenotypic plasticity constitutes the phenotypic changes observed in different environments. The most sensitive individuals are called the hypersensitive genotypes and the less sensitive ones are the robust ones (Falconer, 1990).

According to Correa (2018), the use of bulls with robust genotypes is often indicated as the most used or at more affordable prices; however, their progeny will have a lower performance compared to other individuals of the herd, especially in the best environment of production. According to this study, the robust genotypes for AFC were intuitively the most used for breeding in both breeds, probably because their genetic merits were destined for weight gain, since these breeds are intended for beef, these sires had lower genetic values at best environment (lower AFC). This fact evidences the emphasis given by breeders to the selection of animals for further growth or other characteristics of economic interest.

Reproductive traits are economically important in beef cattle production systems since cows consume a large proportion of food resources (Malhado et al., 2013). Therefore, the production efficiency of the herd will be improved, even if small changes were made in the genetic structure of the population, which can lead to greater profitability. Finally, the use of EBVs for specific environments to make the selection is highly recommended to improve the genetic gain and profitability of the herd.

Conclusion

In the Italian Limousine and Charolais breeds, bulls with higher genetic merits in one environment are not recommended for others. The environmental associations provide convincing evidence, that the values of genetic parameters depend on the environment in which animals are raised. It is thus demonstrated that also in rather similar environment conditions, as usually are considered the Italian ones, the interaction between genotype and environment is strong and it can affect the results of the classical genetic evaluations for reproductive parameters. Selection of bulls based on EBV derived from standard animal model procedures could thus lead to erroneous choices. Future breeding objectives for these traits in Italian Limousine and Charolais

beef cattle breeds need to take into account this important results. These factors characterized the existence of genotype interaction with the environment.

References

B.A. Aby, L. Aass, E. Sehested. **Effects of changes in external production conditions on economic values of traits in Continental and British beef cattle breeds.** *Livest. Sci.*, 150: 80-93, 2012.

D.P., Ambrosini, C.H.M., Malhado, R., Martins Filho, F.F., Cardoso, P.L.S., Carneiro. **Genotype- \times -environment interactions in reproductive traits of Nelore cattle in northeastern Brazil.** *Trop. Anim. Health. Prod.*, 1: 1-7, 2016.

D.P., Ambrosini, P.L.S., Carneiro, J. Braccini Neto, C.H.M., Malhado, R., Martins Filho, F.F., Cardoso. **Interação genótipo \times ambiente para peso ao ano em bovinos Nelore Mocho no Nordeste do Brasil.** *Pesq. Agropec. Bras.*, 47: 1489-1495, 2012.

ANACLI. <http://www.anacli.it/WEBSITE/index.php?&pagid=2455&sessione=>

D.M.M.R. Azevêdo, R.M. Filho, R.N.B. Lôbo, C.H.M. Malhado, R.B. Lôbo, A.A.A. Moura, E.C.P. Filho. **Reproductive performance of Nelore cows in the North and Northeast Regions of Brazil.** *Rev. Bras. Zootec.*, 35: 988-996, 2006.

D.P. Berry, E. Wall, J. E. Pryce, **Genetics and genomics of reproductive performance in dairy and beef cattle.** *Animal*. 8:105–121, 2014.

J.M. Bormann, D.E. Wilson, **Calving day and age at first calving in Angus heifers.** *J. Anim. Sci.*, 88: 1947-1956, 2010.

A. Bouquet, E. Venot, D. Laloë, F. Forabosco, A. Fogh, T. Pabiou, K. Moore, J.A. Eriksson, G. Renand, F. Phocas. **Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses.** *J. Anim. Sci.* 89:1719–1730, 2011.

S.P. Brooks, G.O. Roberts. **Convergence assessment techniques for Markov chain Monte Carlo.** Stat. Comput., 8:319-335, 1998.

F.F., Cardoso, G.J.M., Rosa, R.J. Tempelman. **Multiple-breed genetic inference using heavy-tailed structural models for heterogeneous residual variances.** J. Anim. Sci., 38: 1766-1779, 2005.

F.F. Cardoso, F.F. **Manual de utilização do programa INTERGEN - Versão 1.0 em estudos de genética quantitativa animal.** Bagé: Embrapa Pecuária Sul, 2008. p.74.

M.B.B. Corrêa, N.J.L. Dionello, F.F. Cardoso. **Caracterização da interação genótipo-ambiente e comparação entre modelos para ajuste do ganho pós-desmama de bovinos Devon via normas de reação.** Rev. Bras. Zootec., 38: 1468-1477, 2009.

G. De Jong. **Phenotypic plasticity as a product of selection in a variable environment.** Am. Nat., 145:493-512, 1995.

G. De Jong, P. Bijma. **Selection and phenotypic plasticity in evolutionary biology and animal breeding.** Livest. Sci., 78:195-214, 2002.

J.C., Dias, V.J., Andrade, J.A.M., Martins, L.L., Emerick, V.R., Vale Filho. **Correlações genéticas e fenotípicas entre características reprodutivas e produtivas de touros da raça Nelore.** Pesq. Agropec. Bras, 43: 53-59, 2008.

D. S. Falconer. **Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance.** Genet Res, 56: 57- 70, 1990.

D. S. Falconer, T.F.C. Mackay. **Introduction to Quantitative Genetics.** Longman Group. 4a ed. Essex, UK. 1996.

J. Geweke. **Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments.** In: Bayesian statisti. JM Bernardo, JO Berger, AP Dawid, AFM Smit, (Eds.) pp:1-21. Oxford University, New York, 1992.

A. Giorgetti, M. Lucifero, A. Acciaioli, C. Sargentini, A. Martini. **Caratteristiche**

produttive di vitelloni Chianini, Charolais e Limousins. Rilievi alla sezionatura commerciale. *Zootec. Nutr. Anim.*, 18:84-85, 1992.

P. Heidelberger, P. Welch. **Simulation run length control in the presence of an initial transient.** *Oper. Res.*, 31:1109-1144, 1983.

R. Kolmodin, E. Strandberg, P. Madsen, J. Jensen, H. Jorjani. **Genotype by environment interaction in Nordic dairy cattle studied using reaction norms.** *Acta. Agric. Scand. A. Anim. Sci.*, 52:11-24, 2002.

M.M.M. Laureano, A.A Boligon, R.B. Costa, S. Forni, J. L. P. Severo, L.G. Albuquerque. **Estimativas de herdabilidade e tendências genéticas para características de crescimento e reprodutivas em bovinos da raça Nelore.** *Arq. Bras. Med. Vet. Zootec.*, 63: 143-152, 2011.

T. LIRA, E.M. ROSA, A.V.GARNERO. **Parâmetros genéticos de características produtivas e reprodutivas em zebuínos de corte (revisão).** *Cien. Anim. Bras.*, 487: 1-22, 2008.

C. H. M. Malhado, A. C. M. Malhado, R. M. Filho, P. L. S. Carneiro, A. Pala, J. A. Carrillo. **Age at first calving of Nelore cattle in the semi-arid region of northeastern Brazil using linear, threshold, censored and penalty models.** *Livest. Sci.*, 154:28–33, 2013

B.S. Marestone, E.R. Santos, G.B.S. Serra, C.A.S.D. Muniz, C.P. Marques, K.B. Alves, R.C.M. Alves. **Reproduction traits, growth traits and age at first calving in Holstein heifers.** *Semin. Cienc. Agrar.*, 34: 4105-4112, 2013.

M., Mattar, L.O.C., Silva, M.M., Alencar, M.M., F.F. Cardoso. **Genotype × environment interaction for long-yearling weight in Canchim cattle quantified by reaction norm analysis.** *J. Anim. Sci.*, 89: 2349-2355, 2011.

H.H. Montaldo, A.Pelcastra-Cruz, H. Castillo-Juáres, F.J. Ruiz López, F. Miglior. **Genotype x environment interaction for fertility and milk yield traits in Canadian, Mexican and US Holstein cattle.** Span. J. Agric. Res., 15: 1-9, 2017.

F.W.C. Nesser, J. B. Van Wyk, V. A. Ducrocq. **Preliminar investigation into genotype x environment interaction in South African Holstein cattle for reproduction and production traits.** S. Afr. J. Anim. Sci., 44: 75-79, 2014.

R Development Core Team, 2008. **R: A language and environment for estatistical computing.** Viena, Áustria: R foundation for statistical computing: [<http://www.R-project.org>].

A. E. Raftery, S.M. Lewis. **One long run with diagnostics: implementation strategies for markov chain Monte Carlo.** Stat. Sci., 7:493-497, 1993.

V. M. Roso, F. S. Schenkel. **AMC, 2006: a computer program to assess the degree of connectedness among contemporary groups.** In: World Congress on Genetics Applied to Livestock Production. p.26-27, Belo Horizonte, 2006.

SAS INSTITUTE. **SAS/STAT user's guide.** Version 9.4. Cary: SAS Institute, 2018.

J.C. Santos, Interação genótipos ambientes em características produtivas e reprodutivas de vacas Holandesas via normas de reação. Disponível em <http://www2.uesb.br/ppg/ppz/wp-content/uploads/2018/09/Tese-Final-JARBAS.pdf>
Acesso: 04 de fevereiro de 2019.

C. D. Schlichting, M. Pigliucci. **Phenotypic Evolution: A Reaction Norm Perspective.** Sinauer Associates, Sunderland, MA. 1998.

B.J. Smith. **Bayesian output analysis program (BOA) version 1.1.7.2 user's manual.** Iowa: University Of Iowa. 2007

G. Su, P. Madsen, M.S. Lund, D. Sorensen, I.R. Korsgaard, J. Jensen. **Bayesian analysis of the linear reaction norm model with unknown covariates.** J. Anim. Sci., 84:1651-1657, 2006.

F.L.B. Toral, L.O.C. Silva, E.N. Martins, A. Gondo, S.M. Simonelli. **Interação genótipo x ambiente em características de crescimento de bovinos da raça Nelore no Mato Grosso do Sul.** Rev. Bras. Zootec., 33: 1445-1455, 2004.

E. J. Warwick, J. Legates. **Cría y mejoramiento del ganado.** 3 ed. México: McGraw-Hill, 623p. 1980.