

Sexually dimorphic environmental sensitivity in beef cattle studied by principal component analyses in a developmental reaction norm model.

N. T. Pegolo*, **R. B. Lôbo[†]** and **H. N. de Oliveira[‡]**

*Federal Institute of Education, Science and Technology of São Paulo, Campus Avaré, Brazil, [†]Ribeirão Preto Medical School, USP, Brazil, [‡]Faculty of Agronomic and Veterinary Sciences of Jaboticabal, UNESP, Brazil.

ABSTRACT: Selection in heterogeneous environments has had increasing importance since production system definition is linked to economic instability and climatic changes. The aim of this work was to compare environmental sensitivity between sexes and along development. Data were collected in 366 Brazilian herds for the Brazilian Nelore Cattle Breeding Program with 1,110,662 body weights from 408,416 animals. Eight different analyses were applied using a principal component analysis of the cubic polynomial random regression coefficients' estimates, with a sex-separated developmental reaction norm approach. Results showed different estimated eigenvalues for coefficients of different orders in different sexes. Eigenvalues of level and slope coefficients explained a great majority of the variation of Nelore beef cattle weight in Brazilian production systems, with a distinguished increase of slope coefficient eigenvalue in female analyses along the age axis when compared to male analyses.

Keywords: environmental sensitivity; principal component analysis; reaction norms; sexual dimorphism

Introduction

Reaction norms (RA) are the set of phenotypes produced by one genotype in different environments (Schmalhausen (1949)). In a provocative work about relationships among genotype, phenotype and environment, Lewontin (1974) outlined the importance of reaction norm to understand the heritability concept and the problems related to its use to consider causes and predict consequences. A possibility to predict genetic values in a reaction norm approach was considered by Kirkpatrick and Heckman (1989) using random regression models. De Jong and Bijma (2002) suggested using this methodology to study genotype by environment interaction and Kolmodin et al. (2002) had the first field results in Nordic dairy cattle. Since then, the number of works with this method have greatly increased and different situations have been analyzed, scrutinizing them using different definitions of environmental gradient and different regression functions to predict the reaction norm shape, and also considering data from dairy and beef cattle, sheep and others species (e.g. Calus et al. (2004); Pollot and Greeff (2004); Su et al. (2006); Pegolo et al. (2009); Corrêa et al. (2009); Cardoso and Tempelman (2012)). One important point was detached in Pegolo et al. (2011): sex, age and environment seem to have a joining effect that leads to a confounding of causes and consequences, restoring Lewontin's worries. Principal

component analysis has been used to facilitate the interpretation of the coefficient matrix resulted from those methods (Kirkpatrick and Heckman (1989); Meyer and Kirkpatrick (2005)). The aim of this work was to compare environmental sensitivity between sexes and along development using a principal component analysis of the estimated coefficients in a cubic polynomial random regression of body weight trait using a sex-separated developmental reaction norm approach.

Materials and Methods

Data. The data were collected from 1974 to 2006 in 366 Brazilian herds by the ANCP (Associação Nacional de Criadores e Pesquisadores, or National Association of Breeders and Researchers) for the Brazilian Nelore Cattle Breeding Program (Nelore Brasil) with 1,110,662 weights from 408,416 animals. Weights were adjusted for 120, 210, 365 and 450 days (W120, W210, W365 and W450, respectively). The numerator relationship matrix was adapted to a sire model because of the constraints of the analysis (computational and time restrictions). Analyses were focused on the direct genetic effects. Contemporary groups (CGs) were defined by using information on sex, year, farm, management group and calving season. CGs with less than six individuals were excluded.

Environmental descriptor. The environmental descriptor was calculated using the method presented by Pegolo et al. (2011): the farm-year-season-management group averages were standardized to a mean of zero and a standard deviation (SD) of one for each age; then, the standardized values were multiplied by ten and the environmental groups (EG) were obtained by considering only the integer part of those values. In this way, several CGs could be joined in a single EG. The integer format is a convenience for the software employed. Datasets were maintained separate for the male progeny weight analyses and female progeny weight analyses. To avoid the bias resulting from the non-random use of sires or low number of animals in some herds, the iterative algorithm described by Calus et al. (2004) was used in all analyses. Initially, the EG values below -15 were considered in EG = -15 (bottom limit) and those above +15, in EG = +15 (upper limit). For the subsequent analysis, the fixed effect (CG) solutions were used to position records on the respective EG. Since the first iteration resulted in a wider data distribution along the environmental gradient, the EG limits were changed to -20 (bottom limit) and +20 (upper limit) from the second to

the final iteration. The process was stopped when the correlation between the EG positions in the previous and present analyses was > 0.999 . This convergence was reached after three iterations, similar to the simulated data used by Calus et al. (2004).

Model. (Co)variances of random regression coefficients were estimated by REML using version 3.0 β of the DFREML package (Meyer (1988)). The DXMRR subroutine in the program allowed estimation of the heterogeneous residual variance and five classes were defined. Estimates were obtained by using the Powell, Simplex and AI-REML algorithms, thereby avoiding problems with “derivative-free” possible local max estimates. Considering eight analyses (four ages and two sexes), the general model was:

$$y_{ij} = F_{ij} + \sum_{m=0}^{k_a-1} \alpha_{im} \phi_m(EG_{ij}) + \varepsilon_{ij}$$

where y_{ij} is the j^{th} male or female progeny’s W120, W210, W365 or W450 from the i^{th} animal and EG_{ij} is the environmental group of the j^{th} progeny of i^{th} sire (from -15 to +15 in non-iterative models and from -20 to +20 in iterative models), $\phi_m(EG_{ij})$ is the m^{th} Legendre polynomial on environmental group, F_{ij} is the CG fixed effect, α_{im} is the random regression coefficient for a direct genetic effect, k_a denotes the corresponding order of fit (defined in all analyses as four) and ε_{ij} is the error effect associated with the pre-defined classes p that have homogeneous variances within.

Principal component analysis (PCA). Eigenfunctions and eigenvalues were calculated using the canonical decomposition of the estimated covariance function (CF) coefficient matrix of each analysis (Kirkpatrick and Heckman (1989)). In matrix notation:

$$\mathbf{K} = \mathbf{E} \mathbf{\Lambda} \mathbf{E}'$$

and

$$\mathbf{E}' = [\mathbf{x}_0 \ \mathbf{x}_1 \ \mathbf{x}_2 \ \mathbf{x}_3]$$

with \mathbf{K} the CF coefficient matrix, \mathbf{E} orthonormal, i.e. $\mathbf{E}'\mathbf{E} = \mathbf{I}$, where \mathbf{x}_m denotes the eigenvectors (in fact, coefficients of the eigenfunctions in a random regression model), and $\mathbf{\Lambda}$ the diagonal matrix of eigenvalues (λ_m) of CF. According to Kirkpatrick et al. (1990), this procedure is equivalent to the principal component analysis of the cubic random regression and it gives an independent evaluation of the importance of each coefficient and its influence in the variance of adaptive reaction norm shapes.

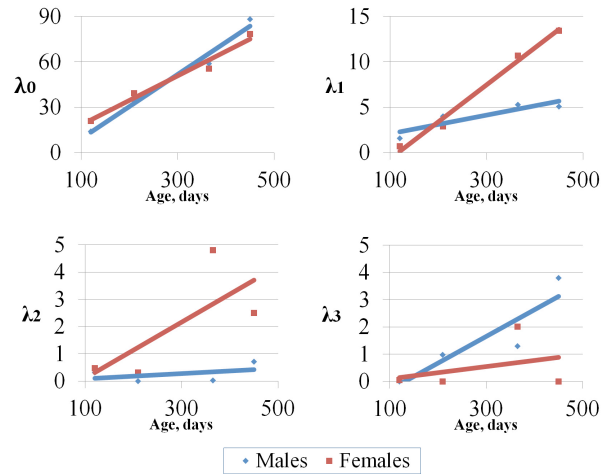


Figure 1: Trends in eigenvalues (λ_m) of level coefficient ($m=0$), slope coefficient ($m=1$), quadratic coefficient ($m=2$) and cubic coefficient ($m=3$) of estimated covariance function of reaction norm model in weights at different ages (120, 210, 365 and 450 days) in separated-sex analysis (progeny weights of Males and Females).

Results and Discussion

Results showed different eigenvalues for estimated coefficients of different orders in different sexes and they were represented by points and trends (with linear regression lines) in Figure 1. For $m=0$ (level coefficient), there was a similar situation in male and female progeny weight analyses: trends showed similar increasing importance along the age axis. For $m=1$ (slope coefficient), trends of eigenvalues showed very different situations: male had a little larger values in pre-weaning weights (W120 and W210) and female had very larger values in post-weaning weights (W365 and W450). The first and second eigenvalues ($m=0$ and $m=1$) represented more than 95% of the sum of eigenvalues in all analyses and indicated that these were the coefficients with more importance in the variance of reaction norms. For $m=2$ (quadratic coefficient), eigenvalues were less important, but numbers were increasing in post-weaning weights for female analysis. For $m=3$ (cubic coefficient), eigenvalues had an increasing trend in post-weaning weights in male analysis. Estimated eigenfunctions were represented by surfaces along age and environmental axes in Figure 2. For the first coefficient ($m=0$) values were always positive (red color). For other coefficients ($m=1, 2$ or 3), values were positive or negative, depending on EG. This indicates that selection on different coefficients can alter reaction norm shape but they can be antagonistic depending on the range of selection environment and on the age when selection is applied. Differences between eigenvalues of male and female progeny weight analyses were expressive when the slope coefficient was considered in post-weaning weights. There were not important differences in eigenvalues of level coefficient either in pre-weaning weights. This indicates that genetic differences between sexes are related to environmental sensitivity. And,

coherently, those differences had increased importance in ages when environmental challenges are more aggressive and maternal effects have less expected importance: the post-weaning phase. According to Cartwright (1970), selection objectives of different categories in the farm are different, and even antagonistic, due to the different functions of each category in the production system. A sexual conflict is expected and confirmed in populations under natural selection (Chapman (2006); Clutton-Brock (2007)), but less studied in domestic herds, where sexual dimorphism does not have an economic value directly associated. However, in harsh environment production systems, these conflicts can be underestimated by traditional evaluations. Divergences of slope coefficient eigenvalues between males and females can meet parallels in the asynchronous evolution theory, proposed by Geodakian (1974), with natural selection generating specialist males and generalist females. An adaptation of this theory is easily changed to a quantitative genetic approach trying to explain the patterns found in this study. Specialist male progenies do not allow highly heritable reaction norm slopes because they have punctual environmental adaptation. In the other hand, generalist female progenies generate heritable reaction norm slopes because they have consistent adaptation to a large range of environmental situations. This is a possible explanation to the eigenvalue sexual differences that can also explain the patterns and the lower levels of male progeny heritability found in all analyses (values not presented in this work) and still, an increasing eigenvalue of the cubic coefficient along the developmental axis.

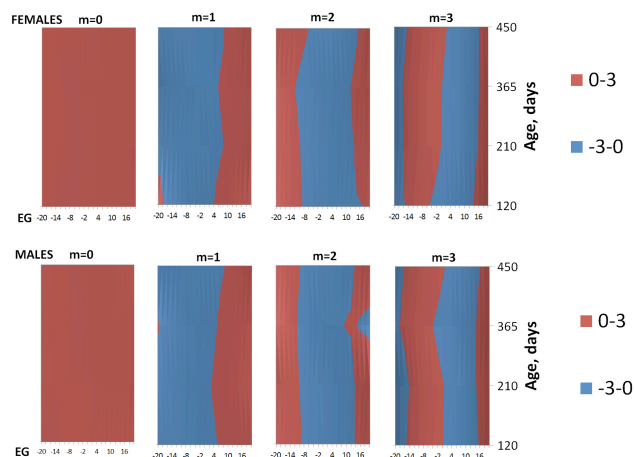


Figure 2: Eigenfunction surfaces calculated for the environmental gradient (EG) of the reaction norm model along the developmental axis (Age, in days). Positive values of the eigenfunctions were represented in red (-3 to 3) and negative values were represented in blue (0 to 3).

Conclusion

Principal component analyses of coefficients' estimates of cubic polynomial random regression in a reaction norm model approach showed that level and slope coefficients were able to explain a great majority of the variation of Nelore beef cattle weight in Brazilian production systems. There were important differences between analyses considering sex and age effects, with distinguished increase of slope coefficient eigenvalue in female analyses along the age axis when compared to male analyses result, what suggests differential genetic strategies across sexes to deal with increasing environmental challenges along individuals' ontogeny.

Literature Cited

- Calus, M. P. L., Bijma, P., and Veerkamp, R. F. (2004). *Genet. Sel. Evol.*, 36:489-507.
- Cardoso, F. F., and Tempelman, R. J. (2012). *J. Anim. Sci.*, 90:2130-2141.
- Cartwright, T. C. (1970). *J. Anim. Sci.*, 30:706-711.
- Chapman, T. (2006). *Curr. Biol.*, 16:R744-R754.
- Clutton-Brock, T. (2007). *Science*, 318:1882-1885.
- Corrêa, M. B. B., Laurino, J. N., and Cardoso, F. F. (2009). *R. Bras. Zootec.*, 38:1460-1467.
- De Jong, G., and Bijma, P. (2002). *Livest. Prod. Sci.*, 78:195-214.
- Geodakian, V. (1974). *Zh. Obshch. Bio.*, 35:376-385.
- Kirkpatrick, M., and Heckman, N. (1989). *J. Math. Biol.*, 27:429-450.
- Kirkpatrick, M., Lofsvold, D., and Bulmer, M. (1990). *Genetics*, 124:979-993.
- Kolmodin, R., Strandberg, E., Madsen, P., et al. (2002). *Acta Agr. Scand. A-An.*, 52:11-24.
- Lewontin, R. C. (1974). *Am. J. Hum. Genet.*, 26:400-11.
- Meyer, K. (1988). *J. Dairy Sci.*, 71:33-34.
- Meyer, K., and Kirkpatrick, M. (2005). *Phil. Trans. R. Soc. B.*, 360:1443-1455.
- Pegolo, N. T., Oliveira, H. N., Albuquerque, L. G., Bezerra, L. A. F., et al. (2009). *Genet. Mol. Biol.*, 32:281-287.
- Pegolo, N. T., Albuquerque, L. G., Lôbo, R. B., et al. (2011). *J. Anim. Sci.*, 89:3410-25.
- Pollot, G. E., and Greeff, J. C. (2004). *J. Anim. Sci.*, 82:2840-2851.
- Schmalhausen, I. I. (1949). *Factors of evolution*. The Blakiston Company, Philadelphia, 327 p.
- Su, G., Madsen, P., Lund, M. S., et al. (2006). *J. Anim. Sci.*, 84:1651-1657.