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ABSTRACT: The interest in the effect of genotype by environment interaction (GEI) is increasing because animal breeding programs have become geographically broader. Climate changes in the next decades are also expected to challenge the present breeding goals, increasing the importance of environmental sensitivity. The aim of this work was to analyze GEI effect on cattle weight using the environmental sensitivity predicted by random regression reaction norm models, including sex and age effects as additional dimensions in the study. Genetic parameters were estimated for adjusted weights of Brazilian Nelore cattle at different ages (120, 210, 365 and 450 days), using linear polynomials for random regression analysis. The analyses with sex as a fixed effect (total analyses - TA) were compared to those with sex-separated progenies (male and female progeny analyses – MPA and FPA, respectively). (Co)variance components were estimated and breeding values calculated as expected progeny differences (EPDs). The results showed important differences in reaction norm model genetic parameter estimates according to different age and sex analyses. They confirmed the presence of an important genotype by environment by sex by age interaction for Nelore cattle weight. The patterns in these results lead to a revision of the importance of sexual and developmental factors on plasticity and adaptation concepts.

Key-words: cattle, environmental sensitivity, genotype by environment interaction, reaction norm, sex effect, weight

INTRODUCTION

Reaction norm (RN) was defined by Schmalhausen (1949) as the set of phenotypes that can be produced by an individual genotype exposed to different environmental conditions. The introduction of random regression models (RRM) in longitudinal data studies (Kirkpatrick and

Heckman, 1989; Kirkpatrick et al., 1990; Meyer, 1998) opened new perspectives in animal genetic evaluations, including the genotype by environment interaction (GEI) assessment using an RN approach (De Jong and Bijma, 2002; Schaeffer, 2004).

The understanding of this phenomenon requires a complete study of the factors involved. Schlichting and Pigliucci (1998) stated that the time element has been largely neglected in RN studies. They suggested that RN must be positioned in a time vector, where changes in gene expression can be analyzed in a developmental reaction norm (DRN).

When development and environmental vectors are included in the same model, a third factor emerges with potential significance. Hormonal systems that regulate sex-trait expression are highly sensitive to both genetic and environmental variation (West-Eberhard, 2003). But sex has been usually considered as a fixed effect in traditional genetic evaluations (Van Vleck and Cundiff, 1998). Some works have shown that sex, as a fixed effect, can be a source of bias (Rodríguez-Almeida et al., 1995; Yazdi et al., 1998).

The aim of this study was to analyze genetic parameter estimates for beef cattle weight data using a random regression model in a linear reaction norm approach. Sexual and developmental effects were considered in independent models, fitting sex as a fixed effect compared to sex-separated analyses at ages of 120, 210, 365 and 450 days old. Estimates of genetic coefficient matrices, (co)variances and heritabilities as well as expected progeny differences and predicted reaction norm slopes were analyzed to investigate the genetic relationship among genotypes and environments in the face of age and sex effects.

MATERIALS AND METHODS

Data description

The initial dataset had 1,110,662 weights from 408,416 animals. 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 Genetic Improvement Program (Nelore Brasil). Weights were adjusted only for the age of animal: 120, 210, 365 and 450 days (W120, W210, W365 and W450, respectively). The numerator relationship matrix was adapted to a sire model with the complete pedigree of sires and dams (also called sire-dam model (Ferreira et al.,1999)) because the complete animal model would generate less accurate environmental sensitivity estimates for animals without progenies, due to the impossibility of exposing a single animal to different environments during the same developmental phase. This would make correlation analyses less reliable. Moreover, computational and time restrictions had to be considered for the large dataset. In previous analyses, progeny's dam information was considered as an uncorrelated random effect, but it was not significant, probably due to the large number of dams (levels) and to the ignorance of the A matrix for this kind of fit. Thus, the analyses were focused on 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

Adjusted weights were studied using a random regression model. The environmental descriptor was calculated using the method presented by Pegolo et al. (2009): 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. Since management group has an implicit sex factor, the records were separated according to sex. At this point, the datasets were varied: for total analyses (TA: W120T, W210T, W365T and W450T, with 306,694, 245,864, 221,929 and 193,429 progeny weights, respectively), after the definition of the environmental groups as standardized weight averages, the data of the different sex groups were merged by EGs. For the sex-separated analyses, the datasets were maintained separate for the male progeny weight analyses (MPA: W120M, W210M, W365M and W450M, with 154,933, 123,937, 110,739 and 95,143 progeny weights, respectively) and female progeny weight analyses (FPA: W120F, W210F, W365F and W450F, with 151,761, 121,927, 111,190 and 98,286 progeny weights, respectively). An alternative possible procedure to define the environmental descriptors could be the Bayesian approach with unknown covariates from Su et al., (2006). Its choice would be valid if a complete animal model was used, where the dataset to calculate the EGs was the same to estimate the genetic parameters. In the present study, the sire model allowed differing the dataset used to calculate the environmental description (967,916 progeny weights) from the dataset used to estimate the parameters (462,559 progeny weights). Thus, the dependencies between the estimates of the variance components and the control variable (EG) were reduced. 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) and elected by Pegolo et al. (2009) was used in all analyses. Smaller numbers of records in both extremes of environmental gradient are expected when EG averages are used as an environmental descriptor because the weight variable

has a normal distribution. Limits in both extremes were used to concentrate data, with the assumption that beyond them, averages were not necessarily describing important changes in environment and so, genetic correlations between EGs positioned beyond those limits are close to one. 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).

Parameter estimations

The EG averages were defined using the complete dataset, but additional restrictions were added for estimations. In total analyses, sires were excluded if (1) they had less than 100 progeny weights and (2) the progeny weight distribution along the environmental gradient was smaller than 20 EG units, before the first iteration. This practice avoids concentrating information of sires in just one side of environmental gradient, what could generate confounding and inaccuracy to the environmental sensitivity indicator. Connectedness would be affected if the exclusion limit was less than 20 units (a half of the environmental gradient after the second iteration), and this was not the case.

As the databases for sex-separated analyses are smaller, the rules were relaxed and only sires with less than 70 progeny weights and distribution with less than 20 EG units were excluded before the first iteration. After the application of these criteria, CGs with fewer than six records were removed. Exclusion rules altered relationship matrices' composition (Table 1): a sire with a smaller number of progenies can be excluded in one analysis and maintained in other, depending on the environmental distribution of its progeny.

(Co)variances of random regression coefficients were estimated by REML using version 3.0β 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. 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} progeny's W120, W210, W365 or W450 from the i^{th} sire 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 two) and ε_{ij} is the error effect associated with the pre-defined classes p that have homogeneous variances.

In matrix notation:

$$\mathbf{y = Xb + Zs + e}$$

with

$$E\begin{bmatrix} y \\ s \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \end{bmatrix} \quad \text{and} \quad V\begin{bmatrix} s \\ e \end{bmatrix} = \begin{bmatrix} K_s \otimes A & 0 \\ 0 & R \end{bmatrix}$$

where **y** is the vector of observations; **b** is the vector of fixed effect attributable to contemporary groups; **s** is the vector of sire random coefficients; **X** and **Z** are the corresponding incidence matrices; **e** the vector of residuals; $\mathbf{K_s}$ is the matrix of coefficients of the covariance function for sire effect; **A** is the additive numerator relationship matrix; and **R** is the diagonal matrix of residual variances estimated at five levels. The levels of $\hat{\sigma}^2_{e|p}$ with **p**=1,2,3,4,5 were grouped in EGs from -15 to -9, -8 to -3, -2 to +2, +3 to +8, and +9 to +15, respectively, in the first iteration, and -20 to -12, -11 to -4, -3 to +3, +4 to +11, and +12 to +20, respectively, in the subsequent iterations. These groups were accommodated by identity matrices of appropriate order for each level.

Sire genetic variance in a particular environmental group is defined by:

$$\sigma^2_{s_{EG}} = \sigma^2_{s_0} + 2EG\sigma_{s_0 s1} + EG^2\sigma^2_{s_1} = \mathbf{x}_{EG}{}' G_s \mathbf{x}_{EG}$$

with

$$G_s = \begin{bmatrix} \sigma^2_{s_0} & \sigma_{s_0 s_1} \\ \sigma_{s_1 s_0} & \sigma^2_{s_1} \end{bmatrix}$$

where $\sigma^2_{s_{EG}}$ is the sire genetic variance in a particular environment EG, $\sigma^2_{s_0}$ is the sire genetic variance of the level (k=1), $\sigma_{s_0 s1}$ is the covariance between level and slope coefficients and $\sigma^2_{s_1}$ is the sire genetic variance for slope (k=2). In matrix notation, $\mathbf{x}_{EG}$ is a row vector [1,EG] and G_s the sire genetic covariance matrix of the random regression coefficients.

Direct additive genetic variance estimates in the random regression sire model were obtained by multiplying sire variance estimates by four ($\hat{\sigma}^2_{A_{EG}} = 4\hat{\sigma}^2_{S_{EG}}$). The environmental variances were obtained as the difference between phenotypic variance ($\hat{\sigma}^2_{P_{EG}} = \hat{\sigma}^2_{S_{EG}} + \hat{\sigma}^2_{e|p}$) and additive variance estimates ($\hat{\sigma}^2_{E_{EG}} = \hat{\sigma}^2_{P_{EG}} - \hat{\sigma}^2_{A_{EG}}$). It is important to emphasize that the environmental variances in reaction norm models are more related to special environmental effects than to general environmental effects (Lynch and Walsh, 1997), since the latter are reduced along the environmental gradient. Expected breeding values (EBVs) were twice the expected progeny differences (EPDs), the latter being obtained directly from the sire model by the equation:

$$EPD_{i|EG} = \sum_{m=0}^{k_a-1} \alpha_{im}\phi_m(EG)$$

where $EPD_{i|EG}$ is the i^{th} sire's EPD for the environmental group *EG*, $\phi_m(EG)$ is the m^{th} Legendre polynomial on *EG*, α_{im} is the random regression coefficient for a direct genetic effect and k_a denotes the corresponding order of fit.

Reaction norm models are very useful when environmental sensitivity (plasticity or robustness) is considered. Falconer (1990) suggested the reaction norm slope (RNS) as an indicator of environmental sensitivity. In this study, it was calculated as the predicted first grade reaction norm angular coefficient of the ordinary polynomial (PRNS=ΔEPD/ΔEG).

Genetic trends for PRNS were obtained by regression of PRNS average of sires weighted by the number of progenies of each sire on their year of birth.

We used correlation analyses to compare: 1) EPDs between different environments and analyses; 2) PRNS and EPDs in different environments and analyses.

To simplify result description, we separated the ages in two major groups: pre-weaning phase (PreWP), with 120 and 210-day weight analyses, and post-weaning phase (PostWP), with 365 and 450-day weight analyses. This separation can be useful to verify differences related to maternal effects which were not estimated by the sire model.

RESULTS

Data analysis

The data distributions for each analysis, after exclusions, are presented in Table 1. Total analyses (TA) had approximately twice the number of records and intermediate means when compared to male progeny analyses (MPA) and female progeny analyses (FPA), as expected.

The distribution of the records in EGs can be observed in Figure 1. The number of records in each EG ranged from 225 to 6851, 94 to 3374, and 59 to 3178 in TA, MPA and FPA respectively. Extreme EGs showed accumulation of records due to fixed limits, but it was smaller in the extreme negative EG (EG-20) for 120 and 210-day weight analyses. Culling or maternal effects could explain this fact and must be considered for future investigation.

Parameter estimates

The last iteration random regression parameter estimates are shown in Table 2. All Legendre polynomial covariance function coefficient estimates had an increasing trend along the age vector. In PreWP, for sire genetic effect, FPA had a larger sire genetic variance of level ($\hat{\sigma}^2_{s_0}$) and larger covariance estimates ($\hat{\sigma}_{s_0 s_1}$), whereas MPA had smaller ones, with TA estimates in an intermediate level. In PostWP, TA had larger sire genetic variance of the level estimates,

whereas FPA showed smaller and MPA intermediate ones. Sire genetic variance of the slope estimates ($\hat{\sigma}^2_{s_1}$) were larger for TA at all ages. MPA had the smallest ones, except in W210F, where it was practically the same as the FPA. Covariances and correlations between level and slope estimates ($\hat{r}_{s_0,s_1}$) had larger values during PreWP, and smaller values in PostWP in FPA, showing a defined decreasing trend with age. MPA had the opposite tendency, with smaller correlation estimates in earlier weights and increasing to the largest estimate in the oldest weight.

The changes of variance components and heritability (h^2) are shown in Figure 2. They are functions of a two-dimensional variable (EG x age) plane, for each analysis. Although the age variable is discrete, the age axis is shown as continuous to facilitate overall visualization. MPA had a general larger phenotypic and environmental variance than FPA. Each analysis had a different additive genetic variance distribution in the EG x age plane. TA had intermediate values in almost all cases. All additive genetic variance estimates increased in different proportions with the increase of EG values and with the days of age, except the FPA genetic variance estimate, which increased also in extreme negative values in PostWP.

Within FPA, h^2 estimates were higher in positive environments of PreWP and in all environments of PostWP. There was a general trend of higher female h^2 estimates on larger positive EG values, except in PostWP, where h^2 estimates increased also in extreme negative EGs, with minimum values near to the middle of the environmental gradient range. Across sexes, MPA h^2 estimates were smaller than FPA estimates, except in very negative EGs of W120M, where they were similar. In PreWP, the curves were nearly parabolic, with MPA h^2 estimate minimum values in intermediate EGs. These minimum values shifted to more negative EGs in PostWP curves, reaching the extreme negative environment in W450M. TA h^2 estimates were

intermediate between MPA and FPA in PreWP and reached higher values in more positive EGs and lower values in more negative EGs in PostWP.

The h^2 estimates vary differently within each analysis. In TA, they ranged from 0.11 (EG-14) to 0.31 (EG+20), 0.14 (EG-6) to 0.30 (EG+20), 0.17 (EG-11) to 0.42 (EG+20) and 0.20 (EG-11) to 0.39 (EG+20) for 120, 210, 365 and 450-day weights, respectively; in MPA, they ranged from 0.11 (EG-12) to 0.18 (EG+20), 0.12 (EG-7) to 0.22 (EG+20), 0.13 (EG-11) to 0.26 (EG+20) and 0.15 (EG-20) to 0.33 (EG+20); and in FPA, they ranged from 0.08 (EG-20) to 0.35 (EG+20), 0.11 (EG-20) to 0.37 (EG+20), 0.18 (EG-10) to 0.35 (EG+20) and 0.26 (EG-9) to 0.38 (EG+20), respectively.

GEI importance was initially studied by genetic correlations between extreme environments. Robertson (1959) proposed the threshold of 0.8 for these correlations: values above would indicate less important GEI; values below would indicate important GEI and possible re-rankings. Genetic correlations between extreme environments in TA were 0.29, 0.09, 0.21 and 0.24 for 120, 210, 365 and 450 days old, respectively. In MPA, they reached 0.51, 0.34, 0.44 and 0.49 and in FPA, values were 0.74, 0.52, 0.13 and 0.26, respectively.

These results allowed understanding the role of the Legendre polynomial correlation coefficient (Table 2). When correlations between level and slope estimates ($\hat{r}_{s_0,s_1}$) are highly positive, they indicate that reaction norms with more positive levels have more positive slopes, and reaction norms with more negative levels have more negative slopes. As variances in negative environments are smaller than in positive environments, a prominent heteroskedasticity situation occurs because reaction norms will have lower possibilities to cross. They are getting more separated in more positive environments. When correlations between level and slope are close to zero (or negative), reaction norm levels and slopes are almost independent (or have

opposite behaviors), with higher possibilities to cross. This situation favors re-ranking. Even with a larger slope variance in PreWP for FPA, higher $\hat{r}_{s_0,s_1}$ indicated a prominent heteroskedasticity, instead of large genetic value ranking changes. These situations are opposite in MPA, with higher $\hat{r}_{s_0,s_1}$ and lower GEI in PostWP and lower $\hat{r}_{s_0,s_1}$ and higher GEI in PreWP. Very low genetic correlations between extreme EGs in TA at all ages suggest a confounding effect due to an important genotype by environment by sex interaction.

EPD correlation analysis

Correlation analyses between EPDs from TA, MPA and FPA for each age showed positive correlation coefficients (r_{EPD}). The lowest value reached 0.38. The results are shown in Table 3.

The genotype by sex interaction was evaluated by r_{EPD} between MPA and FPA in each extreme environment at each different age. The r_{EPD} values were slightly higher in the extreme negative environment EG-20 (0.66, 0.66, 0.80, 0.82, for W120, W210, W365 and W450, respectively) than in extreme positive environment EG+20 (0.60, 0.60, 0.61, 0.74), with intermediate values for the intermediate environment EG0, except for W450, that was the highest (0.64, 0.64, 0.71, 0.84). The sex effect increased the GEI importance between opposite extreme environments, with lower r_{EPD} values across sexes (0.53, 0.45, 0.44 and 0.55 at 120, 210, 365 and 450 days old, respectively) than within each sex. These results are much lower than those obtained by Van Vleck and Cundiff (1998). Their study did not take into account the environmental gradient and showed genetic correlations between the expression of a sire's genotype in male and female progenies for birth, weaning and yearly weights of 0.85, 1.00 and 0.92, respectively.

Pegolo et al. (2009) showed that intermediate environment EG0 (in the total analysis situation) was the most correlated to the traditional univariate model EPDs in 450-day weight for all environmental descriptors studied. Thus, the total analyses of EG0 EPDs were considered, in this study, as the most correlated with traditional univariate model EPDs, presently used in sire evaluation breeding program in Brazil. EG0 EPDs were more highly related to EG+20 EPDs than to EG-20 EPDs. The differences increased in PostWP female progeny analyses.

Comparisons between different ages are shown in Table 4. Higher r_{EPD}s have darker grey background, whereas lower r_{EPD}s have lighter grey (from 0.30 – white – to 0.90 – dark grey, by 0.10 steps). There is a darker main diagonal, showing a higher correlation between closer ages, similar environments and same sex analyses. The lighter inverse main diagonal shows lower values between further ages, different sexes and extreme opposite environments. There are lower values in the comparisons between PreWP and PostWP ages. The lowest values are in the comparisons between W120F and W365M, even in similar environments. General patterns are not observed when sex and environment are considered concomitantly, which implies an important sex-age-environment-genotype interaction.

Not shown in the table, W120T EG0 EPDs (associated to the one-dimensional analyses in present Brazilian breeding program) were more correlated to W450F EG+20 EPDs (r_{EPD}s = 0.64). In contrast, W450T EG0 EPDs were more correlated to W120M EG+20 EPDs (r_{EPD}s = 0.65).

Environmental sensitivity

The correlation coefficients between EPDs in different environments and PRNS in total and sex-separated analyses ($r_{PRNSxEPD}$) are shown in Table 5. The majority of correlations are positive. This suggests that selecting animals with larger EPDs will also select animals with

positive PRNS. Only EG-20 EPD had negative or near nil $r_{PRNSxEPD}$, depending on sex (male or female) or total analyses. Again, these results suggest that PreWP and PostWP were divergent situations in the male and female analyses. PreWP PRNS had higher $r_{PRNSxEPD}$ on Female EPDs, whereas PostWP PRNS had higher $r_{PRNSxEPD}$ on Male EPDs. EPDs in intermediate and extreme positive environments are positively correlated with PRNS in all analyses, as higher or lower following the rule of sex-phase association. Total EPD showed that present selection based on traditional EPD (highly correlated with EG0 EPD (Pegolo et al., 2009)) can affect the PRNS in total and sex-separated situations.

Genetic trends

Genetic trends for PRNS were obtained by regression of PRNS of sires weighted by the number of progenies of each sire on their year of birth. All genetic trends were positive, confirming the prediction of increasing RNS due to artificial selection based on present breeding program evaluations (Figure 4). The trend angular coefficients were significant for all analyses ($p<0.01$), but they were always larger in FPA than MPA.

DISCUSSION

Ignorance of the RNs can give a completely erroneous picture of the causative relations among genotype, environment and phenotype expressed by heritability, as shown by Lewontin (1974). He pointed out the importance of the environmental sensitivity – the RN slope (RNS) – and the connection between the range of environments and the population distribution for understanding the variance components. These aspects are even more important nowadays because the enlargement of breeding programs and their more international orientation expand

the possible environmental range (Mulder and Bijma, 2005). Also, climate changes are expected to alter the production environments in a shorter time than the usual breeding goals can be achieved (IPCC, 2007), increasing the importance of studying environmental sensitivity.

Random regression reaction norm models were first applied by Kolmodin et al. (2002) and Calus and Veerkamp (2003) using dairy cattle data. In beef cattle, weights at different ages are the main trait for traditional analyses. Pegolo et al. (2009) analyzed 450-day adjusted weights from Brazilian Nelore cattle in an RN approach using RRM and considering different methods to calculate environmental variables. They found important GEI and RNS variability, and showed that the large Brazilian cattle production area can be considered heterogeneous for selection based on 450-day weight. But this analysis considered only one point in the development vector. According to West-Eberhard (2003), genetic changes in the timing of expression of a phenotype trait (heterochrony) can be affected by environmental elements or by correlated selection responses. In cattle production, the time vector corresponds to the animal's age. Some authors have investigated the various genetic parameter estimates for the weight trait at different ages (Koots et al., 1994a,b; Mercadante et al., 1995; Lôbo et al., 2000; Giannotti et al., 2005), but in all of these models, GEI and environmental sensitivity were not taken into account.

Random regression models show difficulties to analyze extremes in the independent variable (Meyer and Kirkpatrick, 2005). This fact is attributed to the oscillations at the extremes due to the finite number of data and a bad definition of effects in test-day model for lactation curve estimates (Bohmanova et al., 2008; Jamrozik et al., 2001; López-Romero et al., 2004). But in the reaction norm approach, using a contemporary group average based gradient, extremes were the most important situation, where environments reach the most reliable aspects, with probable lower correlations and higher heritabilities in important GEI circumstances. So, this is

an opposite situation to lactation curves in test-day models. Therefore, Legendre polynomials, even without asymptotes, appeared to be adequate to this study modeling.

There is a strong assumption in considering linear reaction norms due to the fact that their shape is not necessarily a straight line. Previously, in a doctoral thesis, Pegolo (2009) compared results from linear and cubic Legendre polynomial regressions applied to the same database of the present study. Principal component analysis showed that the sum of eigenvalues corresponding to the first and second order coefficients totalized more than 95% of the sum of all four eigenvalues of the cubic analysis, showing that the first ones are responsible for the great majority of genetic variation. To obey parsimony, linear reaction norms were elected in the present study. Kirkpatrick (2009) analyzed the extent to which genetic correlations limit the ability of populations to respond selection by using several nondimensional statistics to quantify the genetic variation present in a suite of traits. A review of five datasets suggested that the total variation differs substantially between populations. However, in all cases, the effective number of dimensions is less than two: more than half of the total variation is explained by a single combination of traits. Genetic correlations may typically reduce a population's effective number of evolutionary dimensions to something less than two. In this case, the author considered that traits or dimensions can be defined by different order coefficients. Thus, it corroborates that a linear model can really be good enough to reveal true patterns of variance estimates.

The sire model applied to this study has an important restriction to the results because it hides the maternal effects. But the usual maternal effects act as environmental effects to the progeny, whereas it is a genetic effect to the dam. So, challenges are expected to be less important in PreWP because maternal cares, mainly milk production, work as a buffer to environmental changes, whereas in PostWP, environment differences are more accentuated. This

idea is corroborated by the increasing importance of GEI from PreWP to PostWP in TA (Figure 3). However, increasing environmental challenges had different effects in sex-separated analyses: GEI importance increased in MPA but it had minor changes in FPA.

One important challenge to reaction norm model studies has been to define the environmental descriptor. Cluster averages were a first approach and they still seem to be the best one, if the proper care is taken to separate the genetic effects from those averages (Calus and Veerkamp, 2003; Calus et al., 2004; Su et al., 2006; Pegolo et al., 2009). It was verified that increasing the seasonal precision within the cluster definition until reaching herd-year-season-management average level reveals a bimodal distribution of joint records along the environmental gradient, due to the different distributions presented by male and female records (Pegolo, 2009). Therefore, it would be logical to standardize the sex-separated data distributions before defining the environmental gradient, assuming this transformation would compensate the differences between sexes. In fact, the present study showed this is not enough, and analyses must be performed separately because reaction norms are different when weight records come from male or female progenies. Divergent genetic coefficient matrices, with similar intercepts but much smaller slopes in MPA, suggest that environmental sensitivity is better expressed in females and partially lost in males, causing differences also in the variance component estimates and heritabilities. Cartwright (1970) pointed out that the breeding goals for different animal categories within a farm can be antagonistic, or at least, independent, due to the different functions of each one in the production system. Most of the genetic correlations between MPA and FPA were lower than 0.8 in the present study. Other works have already suggested that males and females must be evaluated separately (Lee and Pollak, 1997; Stalhammar and Philipson, 1997; Näsholm, 2004). In a heterogeneous environment, biases can be accentuated by

a sexually antagonistic selection (Brommer et al., 2007). Foerster et al. (2007) verified antagonistic genetic variance between progenies of different sexes in red deer populations. They related the differences in the average fitness to the heterogeneous environment, even without an environmental vector in the analysis. Heritabilities were also higher in females than in males, but authors suggested the lack of more information and high stochasticity of male mating success as explanations to the divergence. But this is not the case in our study with cattle weight trait. Here, the differences in heritabilities and environmental sensitivity need further explanation. Divergences along the developmental axis must be considered too, because our results showed that the age factor can affect those differences. As reference, a Bayesian meta-analysis for growth traits in Brazilian zebu beef cattle (Giannotti et al., 2005) obtained 0.31 (0.29 to 0.33), 0.24 (0.23 to 0.25), 0.28 (0.26 to 0.30) and 0.33 (0.30 and 0.35) as pooled h^2 estimates (with a confidence interval of 95%) for birth weight, weaning weight, 365-day weight and 550-day weight for direct effects. In a random regression animal model, fitting direct and maternal effects for zebu cattle growth, Albuquerque and Meyer (2001) found that h^2 estimates decreased after birth (0.32) until the animals were about 120 to 180 days old (0.14) and increased faster after that, reaching the highest values after 550 days of age (around 0.40).

There are different meanings for decreasing heritability in the reaction norm approach, but the majority of them are not clearly plausible explanations for the sex differences found in this study:

1) A possible reason for low h^2 is the small genetic variance, due to the selection for one character linked to a specific environment and the fixation of genes (selected alleles). This situation would imply in a phenotypic variance reduction in reaction norm models in that environment, since there should be an increase of precision and a decrease of environmental

variance due to the EG axis. In fact, both phenotypic and environmental variances in MPA were larger than in FPA.

2) Another possible reason would be the confounding generated by the intersections between reaction norms, mainly in important GEI situations. If the animal ranking is altered by the environments, intermediate EGs must have similar intermediate EPDs, because the expression of different groups of genes is not distinguished. At this point of the environmental gradient, lower heritability will be found. This is exactly the case where important GEI occurs in the study. But this scenario explains the variation in heritabilities within each analysis, but not the differences between MPA and FPA.

3) A third explanation can be associated to the sex determination system. An animal's 'sex' can be defined at the level of the sex chromosomes (XY or XX), the gonads (testes or ovaries), and the sex phenotype (male or female body form). It is the rule that sexual phenotype (male or female) is correlated with the presence (in males) or the absence (in females) of the Y chromosome, and the presence (in males) or the absence (in females) of testes. Thus, in genetic terms, the male phenotype in mammals can be considered a Y-chromosome linked dominant genetic trait (Silversides et al., 2001). The sire model in this study could generate a lower heritability in MPA if the expression of the weight trait was linked to a gene group in the X chromosome (really expressed or triggered by it). The male progeny received only the Y chromosome from the sire and it would affect additive variances in MPA. But this would cause a proportional lower genetic variance. Indeed, the h^2 is reduced by the increase of environmental variances and not by the decrease of additive genetic variances in MPA.

4) Finally, a last explanation is that the increase of environmental variances can be caused by the impropriety of the model for MPA. The environmental variance should be expected to be smaller

in a reaction norm model due to the increase of precision along the environmental gradient. But this is not always true: single-environment specialist individuals and increasing dominance and epistasis effects are not suitable in this model and they can elevate environmental variance.

Geodakian (1974) predicted that female and male reaction norms could be different and this difference would generate an asynchronous evolution. His evolutionary theory states that the origin of sex can be explained as a strategy to deal with the paradox of keeping genetic information (heredity) and generating adaptive changes (adaptation): sexual differences evolved in response to the challenges of environmental adaptation. Males became specialists and females became generalists, with different RNs. The present results showed that a unique individual can have divergent adaptive reaction norms, if information for its RN comes from male progenies or female progenies. Specialist male progenies, carrying predominant environment-specific (level coefficient) information, and generalist female progenies, carrying predominant environment-ample (slope coefficient) information, can generate distributions for single sires that fit as a perfect explanation for the divergence between heritabilities: amply lower in MPA and higher in extremes in FPA at older ages, when environmental challenges are more important. Maintenance of genetic variances with increasing environmental variances is expected if male progenies present a regular response just in a single extreme environment, with an irregular response in the opposite extreme environment. And maintenance of genetic variance and decreasing environmental variances are expected in female progeny analyses if the plasticity is also heritable, with progenies with regular responses in all environments. This is borne out by the lower slope coefficients in MPA and higher slope coefficients in FPA. It implies that sexual divergent selection can occur within the progeny of a single sire. Male progenies seem to be able to test environments as specialists, keeping information for just one environment, leaving

females as generalists, with the genetic libraries from old times driven slowly by the male environmental information: a proper asynchronous evolution. Joining both data (males and females progenies) in one analysis (TA) seemed to have this synergistic effect and variance estimates are not only averages. Male information increases genetic variance on extremes of environmental gradient, and female information increases genetic variance of linear coefficient (environmental sensitivity). Together, they result in larger intercept and larger slope coefficients than in sex-separated analysis, mainly when the environmental gradient shows important GEI and intersexual conflicts (PostWP situation). The asynchronous evolution appears to be supported by genetic trend results (Figure 4). In the Brazilian Nelore program, selection of males is based on breeding values (EPDs) calculated by traditional models, and cattle shows' results (phenotypic selection), with the increasing weights as the breeding goal. At the same time, commercial herds, located in pasture conditions and with a major female composition, are also selected for fertility (calving rate). Buttram and Willham (1989) showed that small cows are reproductively more efficient in terms of calving rate than larger cows and the differences may be accentuated under less favorable conditions. So, there is a sexual conflict in selection goals for mature weight in unfavorable environments. This situation would explain the restriction of increasing PRNS in FPA for W450. In males, selection is based on information highly correlated to TA EPD in EG0 (as shown in Pegolo et al., 2009). There is also a phenotypic selection in favorable environments. Genetic gain for PRNS is proportional to correlated accuracy of selection (r_{PRNS,TA_EPD_EG0} – Table 5) and genetic variance in TA EG0 for the first strategy, and to the phenotypic variance and heritabilities in EG+20 for the second strategy (Figure 2). In the selection of females, there is a phenotypic selection component based on heritability and phenotypic variance in EG-20 (commercial herds). Heritability in this case is higher, but

r_{PRNS,TA_EPD_EG0} is negative (Table 5), which restricts PRNS increase in females. In TA, this conflict appears to be diluted and PRNS trend is the largest.

The increase of dominance and epistasis effects is more than just another possible reason for the increasing environmental variances in male progenies: it can be a causative explanation for the resulting sexual divergences. Pigliucci (1996) proposed that environmental stimuli need at least three genes without segregation to generate a coordinated genetic response. Thus, environmental sensitivity would depend on an epistasis phenomenon with an additive behavior that can be associated with the proximity of genes and the chromosome architecture. Convergence and divergence of certain regions on sex chromosomes have prompted molecular biologists to further explore the evolutionary concept of mammalian sex chromosomes (Verma, 1996). According to Rice (1996), there are "hot spots" (more probable regions) to position the sexually antagonist genes in the sexual chromosomes. Also, Chippindale and Rice (2001) observed a higher variation due to epistasis in the Y chromosome, reducing the heritable variation in *Droshophila* males. Rice (1996), Gatford et al. (1998) and West-Eberhard (2003) have shown processes that corroborate the idea that Y chromosome evolution favors epistasis. Such discussions are beyond the objectives of this study, but a hypothesis of environmental dependent expression linked to sexual chromosomes is coherent and it suggests a new direction for causality studies, mainly considering different gene expression connected to genotype by environment, sex and development interactions. Mittwoch (1996) asserted that the primary decision of sex-determining mechanisms may not be males versus females, or testis versus ovary, but big versus small or fast versus slow growth in embryonic development. In fact, our results show that genotype, environment, sex and development interact, not only in the embryonic phase, but also after birth and through a big part of the bovine lifetime.

Finally, many hypotheses have been presented to explain the maintenance of variation under selection situations, such as overdominance (Barton, 1990), frequency-dependent selection (Slatkin, 1979; Barton, 1990), genotype by environment interaction (Zhivotovsky and Gavrilets, 1992), epistatic interaction (Gavrilets and De Jong, 1993) and mutation-selection balance (Zhang and Hill, 2005). Environmental variance was shown to be under genetic control (Sorensen and Waagepetersen, 2003; Rowe et al., 2006) and the maintenance of its variation is still an important issue (Hill, 2010). Adding sexual and developmental dimensions in a single analysis opens new comprehension horizons. Explanations for the results in this work included elements of all those previous hypotheses, showing that it is possible to tie them together with a unique sexual line under the developmental reaction norm perspective. This possibility appears to be logical and it should be better evaluated in future works. This study is a step and it is possible to catch a glimpse for the next ones: better parameter comparisons (Houle, 1992), with improvements to the covariance matrix structure (Pegolo et al., 2010) and to the environmental descriptor definition (Su et al., 2006).

CONCLUSION

This study showed an important genotype by environment by sex by age interaction in Brazilian Nelore cattle weights by using reaction norm random regression models.

Sex effects were considered by comparing male and female progeny analyses. Variance component estimates were divergent and there were lower correlations between expected progeny differences from male and female analyses. This fact confirmed environmentally dependent sexually divergent genetic variances in the cattle weight trait.

Developmental aspects were considered by the age effects. Comparisons between weights at different ages showed that environmental sensitivity (measured by reaction norm slopes) in male and female progeny analyses were also divergent along the time axis. Differences were accentuated in the post-weaning phase, when the animals were more exposed to environmental factors. Environmental sensitivity had larger genetic variances in female progeny analyses compared to male ones. This characteristic was more genetically expressed by female progenies at later ages. Comparison between pre and post-weaning phases indicated that maternal effects have influence in GEI expression and sexual divergence, but they were not estimated by the sire model applied in the study.

Genetic correlations between total analysis EPDs in intermediate environments and sex-separated analysis EPDs in extreme environments showed that the present selection probably increases environmental sensitivity, mainly in the female population. This was reinforced by the slope genetic tendency assessment, which reveals the environmental sensitivity increase from 1974 to 2006.

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TABLES

Table 1. Descriptive statistics (mean, standard deviation, minimum and maximum values (*standardized values in parentheses), number of records, number of sires with records, number of contemporary groups (CGs) and number of animals in the relationship matrix) for total[1] and sex-separated[2] analyses, after exclusions.

	Mean, kg	Standard deviation, kg	Minimum, kg (st.value*)	Maximum, kg (st.value*)	Number of records	Number of sires w/records	Number of CG	Relationship matrix
W120T	125.28	19.46	46 (-4.07)	239 (5.84)	150,990	299	6,220	13,977
W120M	129.30	19.68	46 (-4.23)	239 (5.57)	69,517	218	2,897	12,915
W120F	121.12	18.16	50 (-3.91)	222 (5.55)	68,439	220	2,998	13,007
W210T	183.44	28.75	74 (-3.81)	344 (5.58)	118,808	263	5,373	12,887
W210M	190.54	28.94	75 (-3.99)	343 (5.27)	55,790	200	2,499	11,857
W210F	176.61	26.57	78 (-3.71)	328 (5.70)	53,597	194	2,580	11,923
W365T	236.23	41.32	107 (-3.13)	536 (7.25)	102,977	238	4,239	12,870
W365M	249.58	41.11	117 (-3.23)	536 (6.97)	48,054	181	2,016	11,736
W365F	223.47	36.97	107 (-3.15)	508 (7.70)	46,290	170	1,960	11,509
W450T	273.65	48.25	127 (-3.04)	603 (6.83)	89,784	220	3,862	12,348
W450M	291.84	48.28	137 (-3.21)	603 (6.44)	41,344	167	1,850	11,070
W450F	256.42	40.47	127 (-3.19)	577 (7.92)	40,224	153	1,745	10,966

[1] Total analyses (TA) for weights at 120, 210, 365 and 450 days (W120T, W210T, W365T and W450T, respectively)

[2] Sex-separated analyses: male progeny analyses (MPA) and female progeny analyses (FPA) for weights at 120, 210, 365 and 450 days (W120M, W210M, W365M, W450M and W120F, W210F, W365F, W450F, respectively)

Table 2. Random regression sire variance estimates of the Legendre polynomial level ($\hat{\sigma}^2_{s_0}$) and slope ($\hat{\sigma}^2_{s_1}$), covariance ($\hat{\sigma}_{s_0 s_1}$) and correlation (in parentheses) between level and slope, and residual variance estimates for different classes from 1 to 5 ($\hat{\sigma}^2_{e|p=1}$, $\hat{\sigma}^2_{e|p=2}$, $\hat{\sigma}^2_{e|p=3}$, $\hat{\sigma}^2_{e|p=4}$ and $\hat{\sigma}^2_{e|p=5}$) in total[1] and sex-separated[2] analyses. The approximate standard errors are shown below each parameter.

	$\hat{\sigma}^2_{s_0}$	$\hat{\sigma}^2_{s_1}$	$\hat{\sigma}_{s_0 s_1}$	$\hat{\sigma}^2_{e\|p=1}$	$\hat{\sigma}^2_{e\|p=2}$	$\hat{\sigma}^2_{e\|p=3}$	$\hat{\sigma}^2_{e\|p=4}$	$\hat{\sigma}^2_{e\|p=5}$
W120T	16.40	3.30	4.05 (0.55)	205.60	205.12	215.97	211.46	237.22
	0.76	0.46	0.42	3.28	2.15	2.08	2.32	3.31
W120M	14.02	1.59	1.59 (0.34)	225.34	224.60	232.69	229.18	254.96
	1.81	1.01	0.99	4.21	4.54	6.33	9.92	20.80
W120F	19.09	2.00	5.12 (0.83)	188.14	186.11	194.71	187.43	221.52
	2.23	1.07	1.20	3.58	3.84	5.71	8.38	18.59
W210T	30.65	8.66	4.80 (0.30)	368.84	400.22	399.48	413.37	450.51
	3.07	2.08	1.90	5.50	6.20	8.22	12.14	24.06
W210M	29.50	5.01	3.72 (0.31)	402.92	429.82	443.83	451.70	484.31
	3.98	2.38	2.34	8.28	9.61	12.49	18.62	42.56
W210F	35.26	4.94	8.85 (0.67)	334.60	364.57	363.57	366.55	398.87
	4.61	2.56	2.61	7.31	7.96	10.48	17.28	41.13
W365T	67.34	16.13	20.02 (0.61)	452.51	499.94	563.54	602.59	784.25
	6.49	4.32	4.22	8.34	7.32	13.13	22.93	48.64
W365M	54.27	8.31	12.29 (0.58)	522.37	556.87	657.11	653.53	862.23
	7.90	5.19	5.10	13.16	11.41	20.90	35.26	86.37
W365F	50.92	13.40	12.10 (0.46)	381.50	426.29	482.24	515.59	702.47
	7.22	5.62	5.10	10.64	9.12	16.33	31.96	100.37
W450T	77.21	16.64	16.62 (0.46)	476.10	564.59	617.27	681.47	853.99
	6.91	4.61	4.44	9.43	9.21	16.07	29.40	55.59
W450M	76.58	11.26	19.61(0.67)	563.96	654.36	749.48	765.93	989.06
	9.43	5.33	5.41	14.20	12.97	19.43	29.46	71.38
W450F	69.87	14.03	10.56 (0.34)	391.82	454.12	506.76	540.44	712.18
	8.48	5.87	5.45	11.45	11.26	18.56	33.05	77.24

[1] Total analyses (TA) for weights at 120, 210, 365 and 450 days (W120T, W210T, W365T and W450T, respectively)
[2] Sex-separated analyses: male progeny analyses (MPA) and female progeny analyses (FPA) for weights at 120, 210, 365 and 450 days (W120M, W210M, W365M, W450M and W120F, W210F, W365F, W450F, respectively)

Table 3. Correlation coefficients (r_{EPD}) between expected progeny differences (EPDs) predicted by total[1] and sex-separated analyses[2], in extreme negative, intermediate and extreme positive environmental groups (EG-20, EG0 and EG+20, respectively).

		W120T			W120M			W120F		
		EG-20	EG0	EG+20	EG-20	EG0	EG+20	EG-20	EG0	EG+20
W120T	**EG-20**	1.00	0.80	0.57	0.86	0.73	0.56	0.77	0.65	0.58
	EG0		1.00	0.94	0.78	0.84	0.80	0.83	0.85	0.83
	EG+20			1.00	0.61	0.77	0.81	0.73	0.82	0.84
W120M	**EG-20**				1.00	0.92	0.76	0.66	0.58	0.53
	EG0					1.00	0.96	0.67	0.64	0.61
	EG+20						1.00	0.61	0.62	0.60
W120F	**EG-20**							1.00	0.95	0.90
	EG0								1.00	0.99
	EG+20									1.00
		W210T			**W210M**			**W210F**		
		EG-20	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**
W210T	**EG-20**	1.00	0.75	0.38	0.86	0.67	0.42	0.77	0.59	0.47
	EG0		1.00	0.90	0.78	0.87	0.79	0.79	0.86	0.83
	EG+20			1.00	0.51	0.77	0.82	0.58	0.81	0.85
W210M	**EG-20**				1.00	0.86	0.61	0.66	0.58	0.50
	EG0					1.00	0.93	0.60	0.64	0.62
	EG+20						1.00	0.45	0.58	0.60
W210F	**EG-20**							1.00	0.90	0.78
	EG0								1.00	0.98
	EG+20									1.00
		W365T			**W365M**			**W365F**		
		EG-20	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**
W365T	**EG-20**	1.00	0.72	0.41	0.91	0.73	0.56	0.92	0.69	0.39
	EG0		1.00	0.93	0.77	0.88	0.85	0.65	0.87	0.79
	EG+20			1.00	0.52	0.76	0.82	0.36	0.77	0.83
W365M	**EG-20**				1.00	0.89	0.74	0.80	0.67	0.44
	EG0					1.00	0.97	0.64	0.71	0.59
	EG+20						1.00	0.50	0.67	0.61
W365F	**EG-20**							1.00	0.75	0.42
	EG0								1.00	0.92
	EG+20									1.00
		W450T			**W450M**			**W450F**		
		EG-20	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**	**EG-20**	**EG0**	**EG+20**
W450T	**EG-20**	1.00	0.75	0.44	0.88	0.73	0.61	0.90	0.75	0.46
	EG0		1.00	0.92	0.77	0.88	0.87	0.72	0.91	0.85
	EG+20			1.00	0.53	0.77	0.83	0.46	0.81	0.89
W450M	**EG-20**				1.00	0.90	0.79	0.82	0.76	0.55
	EG0					1.00	0.98	0.71	0.82	0.71
	EG+20						1.00	0.62	0.79	0.74
W450F	**EG-20**							1.00	0.83	0.51
	EG0								1.00	0.91
	EG+20									1.00

[1] Total analyses (TA) for weights at 120, 210, 365 and 450 days (W120T, W210T, W365T and W450T, respectively)

[2] Sex-separated analyses: male progeny analyses (MPA) and female progeny analyses (FPA) for weights at 120, 210, 365 and 450 days (W120M, W210M, W365M, W450M and W120F, W210F, W365F, W450F, respectively) $P<0.001$ for all regressions

Table 4. Correlation coefficients (r_{EPD}) between expected progeny differences (EPDs) at different ages predicted by total [1] and sex-separated[2] analyses, in extreme negative and positive environmental groups (EG-20 and EG+20, respectively).

		W210M		W210F		W365M		W365F		W450M		W450F	
	EG	-20	+20	-20	+20	-20	+20	-20	+20	-20	+20	-20	+20
W120M	**-20**	0.81	0.68	0.63	0.52	0.65	0.56	0.59	0.42	0.61	0.39	0.59	0.42
	+20	0.61	0.85	0.52	0.59	0.49	0.67	0.37	0.55	0.52	0.58	0.45	0.62
W120F	**-20**	0.57	0.51	0.85	0.81	0.48	0.43	0.58	0.63	0.57	0.50	0.61	0.58
	+20	0.44	0.52	0.69	0.86	0.31	0.42	0.36	0.73	0.46	0.54	0.44	0.69
W210M	**-20**					0.74	0.53	0.64	0.47	0.66	0.43	0.58	0.41
	+20					0.54	0.78	0.34	0.59	0.54	0.63	0.45	0.63
W210F	**-20**					0.60	0.46	0.75	0.64	0.68	0.53	0.73	0.58
	+20					0.45	0.53	0.47	0.83	0.56	0.62	0.55	0.76
W365M	**-20**									0.87	0.62	0.81	0.42
	+20									0.71	0.82	0.65	0.70
W365F	**-20**									0.74	0.45	0.85	0.33
	+20									0.56	0.69	0.50	0.86

[1] Total analyses (TA) for weights at 120, 210, 365 and 450 days (W120T, W210T, W365T and W450T, respectively)
[2] Sex-separated analyses: male progeny analyses (MPA) and female progeny analyses (FPA) for weights at 120, 210, 365 and 450 days (W120M, W210M, W365M, W450M and W120F, W210F, W365F, W450F, respectively)
P<0.001 for all regressions

Table 5. Correlation coefficients between predicted reaction norm slopes (PRNS) and expected progeny differences (EPD) in extreme negative, intermediate and extreme positive environmental groups (EG-20, EG0 and EG+20, respectively) for total[1] and sex-separated[2] analyses, within each age.

	TA EPD			MPA EPD			FPA EPD		
	EG-20	EG0	EG+20	EG-20	EG0	EG+20	EG-20	EG0	EG+20
PRNS W120T	0.04	0.62	0.84	0.19	0.46	0.62	0.38	0.57	0.63
PRNS W210T	-0.30	0.40	0.77	-0.07	0.33	0.55	0.07	0.42	0.55
PRNS W365T	-0.14	0.59	0.85	0.03	0.39	0.56	-0.15	0.43	0.68
PRNS W450T	-0.17	0.52	0.81	0.01*	0.37	0.51	-0.09	0.40	0.68
PRNS W120M	-0.13	0.35	0.55	0.03	0.41	0.66	0.17	0.28	0.32
PRNS W210M	-0.23	0.30	0.58	-0.12	0.40	0.71	-0.01	0.21	0.30
PRNS W365M	0.09	0.61	0.76	0.27	0.69	0.85	0.08	0.42	0.53
PRNS W450M	0.30	0.74	0.85	0.47	0.81	0.91	0.35	0.63	0.71
PRNS W120F	0.41	0.75	0.82	0.39	0.55	0.54	0.73	0.91	0.96
PRNS W210F	0.17	0.67	0.83	0.29	0.49	0.56	0.46	0.81	0.91
PRNS W365F	-0.18	0.43	0.66	-0.04	0.22	0.34	-0.20	0.51	0.81
PRNS W450F	-0.25	0.34	0.61	-0.08	0.20	0.31	-0.28	0.31	0.69

[1] Total analyses (TA) for weights at 120, 210, 365 and 450 days (W120T, W210T, W365T and W450T, respectively)
[2] Sex-separated analyses: male progeny analyses (MPA) and female progeny analyses (FPA) for weights at 120, 210, 365 and 450 days (W120M, W210M, W365M, W450M and W120F, W210F, W365F, W450F, respectively)
P<0.01 for all regressions, except in *.