Genetic Variability On Residual Variance Of Production Traits In Nellore Beef Cattle

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Introduction

The hypothesis that part of residual variance (VE) of some traits is under genetic control was investigated in recent studies, which provided statistical support (e.g. Sorensen & Waagepetersen (2003); Mulder et al. (2009)) and reasonable experimental evidence (e.g. Mackay & Lyman (2005); Garreau et al. (2008)) for this phenomenon.

The increasing interest for uniformity of production in livestock industries has lead to implementation of bonification policies that challenge producers to deliver animals that meet desired standards. Therefore, the existence of genetic heterogeneity on residual variance offers an opportunity to obtain more homogeneous product by selecting for lower residual variance. In order to address this question, structural models enabling simultaneous estimation of genetic effects on the mean and VE has been implemented in a single step, but estimability and computational complexity may hamper the use of this approach in some cases. Previous studies that investigated this subject in chicken, pigs and sheep reported estimates of reasonable magnitude for additive variance on VE (σ^2_{AV}). Although uniformity is an important topic in beef production, there is scarce information about perspectives of using selection to get more uniform product in beef cattle.

Analysis of log squared residuals of observations was employed in other studies as a two-step approach that allows accounting for genetic and environmental effects at the level of each record and could be suitable to analyze beef cattle data. Moreover, Mulder et al. (2009), after testing this approach by simulation, verified that it is able to estimate genetic variance on VE. The objectives of this study were to estimate the additive genetic variance on residual variance based on a two-step approach and to measure the relationship between breeding values for mean and residual variance of beef cattle traits.

Material and methods

Data. Data came from Aliança Nelore database, comprising records from 382 Nellore herds raised in central region of Brazil, collected from 1983 to 2009. Fifteen traits routinely evaluated in this population were analyzed. Traits related to body weight (in kg) were birth weight (BW); weight gain from birth to weaning (W_W) and weight gain from weaning to yearling (W_Y). Rump height was measured both at weaning (H_W, in cm) and at yearling (H_Y, in cm). Scrotal circumference measured at yearling (in cm) was analyzed after adjustment for age (SC_A) and for age and weight (SC_{AW}). Conformation (C), early finishing/precocity (P),

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muscling (M) and sheath (S) were evaluated based on visual scores taken at weaning and yearling. Each score was in a discrete scale, ranging from 1 to 5 (subscripts *W* and *Y* regard to weaning and yearling, respectively). Records were pre-adjusted for known fixed effects relevant to each trait based on adjustment factors previously estimated for the same dataset.

First step. A multivariate animal model was applied to obtain solutions for fixed effect of contemporary group (CG = herd, year, season, sex, date of measurement and management group) and for random effects (direct and maternal additive genetic, maternal permanent environment and residual effects). (Co)variance components used were previously obtained by REML.

Second step. Solutions obtained in the first step were used to estimate the residual ($\hat{e}$) of each observation. For each trait, log transformed squared residuals, $\log(\hat{e}^2)$, were assumed as a measure of the residual variance, following Garreau et al. (2008) and Mulder et al. (2009). To reduce the impact of the departure from normality on estimates of variance components, only $\log(\hat{e}^2)$ records between the mean ± 3*standard deviations were effectively used in the second step. Additional data edition were applied to keep only records of calves sired by bulls with at least 10 sons and raised in CGs with at least 20 individuals. REML estimates of variance components were obtained using MTDFREML package (Boldman et al., 1995), according the following the univariate animal model:

$$\log(\hat{e}_{ij}^2) = \mu + cg_i + a_j + \varepsilon_{ij} \qquad (1)$$

where $log(\hat{e}_{ij}^2)$ is the vector of individual log squared residuals for the trait in analysis, μ is the overall mean, cg_i is the fixed effect of CG i, a_j is the additive random effect of animal j and ε_{ij} is a random residual effect. Assumptions for random effects were $a_j \sim N(0, A\sigma^2_a)$ and $\varepsilon_{ij} \sim N(0, I\sigma^2_\varepsilon)$, where A is the additive genetic relationship matrix and I is an identity matrix.

Calculation of genetic parameters. As estimates of additive variance (σ^2_a) under model 1 were in an exponential scale, they were transformed to scale of the residual variance to give an estimate of σ^2_{AV}, as proposed in Mulder et al. (2007). Estimated breeding values (EBV) for $\log(\hat{e}^2)$ were transformed to the scale of VE, resulting in predicted breeding value for residual variance ($\hat{A}v$). Evolvability of residual variance (Ev) was calculated as an additive coefficient of variation ($Ev = \sigma_{AV} / \sigma^2_{\hat{e}}$, where $\sigma^2_{\hat{e}}$ is the average residual variance, estimated as the variance of raw residuals). Heritability of residual variance (h^2v) and an approximate estimate for accuracy of $\hat{A}v$ were also calculated as in Mulder et al. (2007). Pearson correlation between sire's EBV for the mean and $\hat{A}v$ (r_{mv}) was calculated and is intended to be a rough indicative of the genetic association between these criteria, once direct estimation of this parameter is not feasible under this two-step approach. Because r_{mv} is dependent of EBV's accuracy, only sires with large number of progeny ($N > 50$) were include in calculations in order to reduce this eventual source of bias.

Results and discussion

Estimates of genetic parameters and descriptive statistics related to the data in the second step are presented in Table 1. Large amount of information was available for most traits. For traits measured in both phases, variance of raw residuals ($\sigma^2_{\hat{e}}$) was higher at yearling compared to weaning (Table 1), while estimates of σ^2_a and Ev did not follow this pattern.

Most estimates of evolvability for residual variation were in the range 15-25%, what is slightly lower than reported in previous studies (Mulder et al. (2007); Wolc et al. (2009)) but still indicate some opportunity to improve the uniformity of the traits through selection. Estimate of σ^2_a for birth weight was the highest, implying in a high estimate of Ev for residual variance (almost 70%), which is larger than existing estimates of this parameter for body weight in other species (Mulder et al. (2007)). This result and a relatively high estimate of h^2v for this trait and for S_W should be subject of further studies in order to investigate an eventual overestimation of σ^2_a, possibly related to data distribution and/or confounding of genetic and other environmental sources of heterogeneity in VE.

Table 1: Descriptive statistics[a] and estimates of genetic parameters[b] for residual variance (VE) of Nellore beef cattle traits.

Trait[1]	Nr	Ns	$\sigma^2_{\hat{e}}$	σ^2_a	Ev	h^2v	acc_{50}	r_{mv}
BW	203.336	1540	4,61	0,25898	69,80%	9,94%	0,86	0,49*
C_W	250.272	1577	0,34	0,03505	26,36%	1,90%	0,63	0,21*
C_Y	155.417	1226	0,44	0,01154	15,17%	0,65%	0,44	0,13
H_W	39.027	399	3,34	0,01609	17,90%	0,63%	0,40	0,32
H_Y	44.829	498	5,16	0,02035	20,12%	0,86%	0,48	0,43*
M_W	250.143	1577	0,43	0,02034	20,12%	1,08%	0,53	0,25*
M_Y	154.360	1221	0,60	0,02101	20,45%	1,15%	0,53	0,20*
P_W	248.306	1576	0,44	0,00945	13,73%	0,52%	0,41	0,25*
P_Y	154.907	1221	0,59	0,00765	12,36%	0,42%	0,37	0,19*
SC_A	74.742	1127	2,10	0,03265	25,45%	0,87%	0,48	0,34*
SC_{AW}	74.848	1127	1,87	0,02626	22,84%	0,78%	0,46	0,29
S_W	249.591	1541	0,31	0,13662	51,41%	7,13%	0,83	-0,23*
S_Y	156.611	1197	0,35	0,06148	34,80%	3,35%	0,71	-0,14
W_W	317.444	2382	91,78	0,02712	23,21%	2,02%	0,63	0,00
W_Y	170.568	1685	153,70	0,01663	18,20%	1,17%	0,52	-0,18

[1] BW: birth weight; C: conformation score; M: muscling score; P: early finishing/precocity score; S: sheath score; H: rump height; W_W: weight gain from birth to weaning; W_Y: weight gain from weaning to yearling; SC_A: scrotal circumference adjusted for age; SC_{AW}: scrotal circumference adjusted for age and weight. Subscripts W and Y indicate traits measured at weaning and yearling, respectively. [a] Nr:number of records per trait; Ns: number of sires; $\sigma^2_{\hat{e}}$: variance of raw residuals analyzed in second step. [b] σ^2a: additive variance on VE; Ev: evolvability of VE; h^2v: heritability of residual variance; acc_{50}: average accuracy of predicted breeding value for VE considering sires with 50 or more sons; r_{mv}: Pearson correlation between sire EBVs for mean and residual variance. *: $P<0.05$.

Estimates of h^2v were generally low (1-3%), indicating that large amount of information would be need to predict Av accurately. However, because most sires have large number of progeny, approximate accuracy averaged across sires with at least 50 sons (acc_{50}) achieved meaningful magnitudes, above 60% in the case of BW, S_W, S_Y, C_W and W_W (Table 1). Low to moderate correlations between sire EBVs for mean and VE (r_{mv}), were estimated for C_W, M_W, M_Y, P_W, P_Y, SC_A and S_W (only the last one was negative). Higher positive correlations were found for BW (0.49) and H_Y (0.43). The correlations of the other traits were not statistically different from zero ($P > 0.05$). These values apparently agree with the wide range of estimates previously reported for genetic association between mean and variance, as discussed in Mulder et al. (2009).

Genetic parameters estimated in the second step indicate that it would be possible to achieve considerable reduction in VE by selecting sires with small Âv and large number of progeny (e.g. > 100). Assuming random mating and no selection of dams, selection of top 20% sires for Âv would result in average residual variances 11.8% and 7.6% lower for W_W and W_Y, respectively, after one generation. These calculations are optimistic, once selection intensity for Av is expected to be noticeably lower when selecting simultaneously for other criteria (especially if they were unfavorably correlated), but still show that increasing homogeneity of traits by selection could be feasible in some situations.

A preliminary study carried out with log squared residuals of W_W provided support for fixed (GC) and additive genetic effects acting at the level of residual variance (data not shown) and an animal model including these effects fitted best to the data than a sire model, what motivated analysis of remainder traits by model 1. Otherwise, Yang et al. (2009) pointed out that genetic correlation between mean and variance and also σ^2_{Av} were affected by asymmetry of data distribution when a structural model was implemented, suggesting that statistical support for heteroscedastic models could be an artifact due to scale of measurement. Thus, more investigation is required to assess the reliability of genetic parameters that was estimated at the level of residual variance under model 1.

The straightforward procedure employed in this study indicate existence of useful genetic variability on residual variance of beef cattle traits but further studies are needed to identify more accurate approaches for this data structure. Direct estimation of genetic correlation between mean and residual variance may be subject of future research as well as extension of heteroscedastic models to multivariate approaches, likewise the iterative bivariate REML analysis applied by Mulder et al. (2009), in order to obtain information to optimize selection for both average performance and increased uniformity.

Conclusion

There is evidence of considerable genetic variability for residual variance of most investigated traits. Uniformity of some beef cattle traits can be improved by selecting for lower residual variance, when considering large amount of information to predict genetic merit for this criterion.

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