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Genetic variability of residual variance of production traits in Nellore beef cattle

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ABSTRACT

This study was carried out to provide an exploratory analysis of genetic variability of residual variance of fifteen traits in Nellore beef cattle. The possibility of considering, simultaneously, additive and environmental effects on residual variance was investigated by analyzing log squared residuals associated with each observation according to an animal model. There is evidence of genetic variability for residual variance of most investigated traits, such as birth weight, weight gain from birth to weaning, weight gain from weaning to yearling, scrotal circumference and visual scores (specially in the case of scores for conformation, muscling and sheath). Results suggest that uniformity of some beef cattle traits could be improved by selecting for lower residual variance, when considering large amount of information to predict genetic merit for this criterion. Further studies are needed to confirm the results obtained under the exploratory approach of this work.

1. Introduction

The increasing requirements of end product quality and the need for consistent compliance of standards established by industry have made uniformity of production an important topic in livestock systems. Swine and chicken producers of many countries, for instance, receive premiums for delivery of animals that meets desired standards and this policy is expected to be common practice in other livestock chains. In such scenario, breeding schemes should aim not only to change the mean of traits but also to reduce their variability.

In beef cattle, for instance, producers are being challenged to bring a high proportion of their calf crop within specific market windows; otherwise, they would be penalized. These price penalties arose from the need of industries to fit to operational and/or market conditions that imply in an optimum range for many traits.

Some strategies have been proposed to increase homogeneity of livestock products. Hohenboken (1985) reviewed some possibilities of exploring management, mating systems and selection schemes to change the variation of quantitative traits, but as general rule conventional approaches do not seem effective at reducing phenotypic variability, except temporarily, by means of management practices.

The hypothesis that part of the residual variance (σ^2_e) of some traits is under genetic control was investigated in recent studies, which have provided statistical support for this phenomenon in livestock species (e.g. Gutiérrez et al., 2006; Ibáñez-Escriche et al., 2008; Mulder et al., 2007; Ros et al., 2004; SanCristobal-Gaudy et al., 1998, 2001; Sorensen and Waagepetersen, 2003).

Moreover, substantial experimental evidence of this phenomenon was reported by Mackay and Lyman (2005), who found significant variance between isofemale lines of *Drosophila* with respect to within line variation for bristle number.

The first generations of divergent selection experiment in rabbits on variability in birth weight (Garreau et al., 2008) and litter size (Argente et al., 2009), also seem to corroborate previous statistical findings in this matter. Therefore, the presence of genetic heterogeneity of residual variance could

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be exploited to obtain more homogeneous product in livestock by selecting for lower residual variance.

Previous studies that investigated this subject in chicken, pigs and sheep reported estimates of reasonable magnitude for additive variance of residual variance (σ^2_{AV}), offering good prospects to increase product homogeneity by selection. Although uniformity is an important topic in beef production, there is scarce information on perspectives of considering this selection criterion in beef cattle breeding programs.

In order to investigate the strength of genetic heterogeneity on σ^2_e, structural models enabling simultaneous estimation of genetic effects on mean and σ^2_e have been implemented in a single step (Ibáñez-Escriche et al., 2008; Sorensen and Waagepetersen, 2003). However, computational complexity and estimability may hamper using this approach in some cases, as discussed by Mulder et al. (2009).

Analysis of log squared of estimated residuals of observations was employed in some studies as a two-step alternative to investigate this question (Garreau et al., 2008; Gutiérrez et al., 2006; Wolc et al., 2009). Mulder et al. (2009), after testing this approach by simulation, reported that it could be used to estimate genetic variance on σ^2_e. This approach also allows accounting for genetic and environmental effects at the level of each record and can be implemented in standard REML packages, such that it is suitable to analyze data of large beef cattle populations.

The objective of this study was to provide a preliminary assessment of genetic heterogeneity of residual variance in Nellore beef cattle, what was accomplished by employing a two-step approach to estimate the additive genetic variance of residual variance of production traits in a large population of this breed, and also to measure the relationship between breeding values estimated for mean and residual variance.

2. Material and methods

2.1. Data

Data came from Aliança Nelore database, comprising records from 382 Nellore herds raised in pasture systems of Brazil and Paraguay, collected between 1983 and 2009. Fifteen traits routinely evaluated in this population were analyzed. Records were taken at birth, weaning (age about 205 days) and yearling (age about 550 days).

Available information included three traits related to body weight, all of them expressed in kg: 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 (in cm) was measured at yearling and was analyzed after adjustment for age (SC_a) and after adjustment for age and weight (SC_{aw}). Conformation (C), early finishing/precocity (P), 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).

Among the traits included in this study some of them are related with criteria adopted to pay beef producers according to the homogeneity of animals. For instance, price penalties are applied outside optimum ranges for carcass weight (directly related to BW, W_W, W_Y, C_W,C_Y, SCa), fat deposition (P_W, P_Y) and carcass composition (M_W, M_Y). From the perspective of the efficiency of cow–calf producing systems, optimum levels of traits related to birth weight, rump height and sheath score are also established. Adequate levels of BW are desired because of the close association between this trait and dystocia (Paschal et al., 1991), while the consideration of rump height in selection decisions has been proposed to obtain animals of size suitable to the production system (Boligon et al., 2011). Higher scores for sheath predispose to damage in this region and possible reproductive problems (Kriese et al., 1991), such that increasing proportion of animals within the desired range for this trait could be of interest.

Contemporary groups (CG) were defined based on concatenation of herd, year, season, sex, date of measurement and management group. After checking for consistency of the data, CG considered disconnected from the main database (connected groups) were excluded. A minimum of ten direct genetic links was required to include a CG in the set of connected groups. The degree of connectedness among CG was defined on the basis of genetic connections due to each animal and all its common ancestors, such that genetic connections were weighted by additive relationship among animals (Roso et al., 2004).

As recording of some traits started at different times in this breeding program (also due to sequential selection), there is a considerable difference among traits in number of records considered in analysis (Table 1), ranging from 39,027 (for H_W) to 317,444 (for W_W). In the same way, pedigree files for each trait included between 63,364 and 493,824 animals. For each trait, information regarding number of levels of fixed effects (CG), number of herds, number of sires, number of dams and average progeny size of sires is presented in Table 1.

2.2. First step

An animal model was applied to obtain solutions for fixed and random effects relevant to each trait. (Co)variance components used were estimated previously for this population by REML. Fixed effects considered in analyses were animal age, Julian birth date within birth season, age of dam at calving (according calf's sex) and contemporary group (CG). Direct additive genetic random effect and residual effects were fitted as random effects. For BW and the traits measured at weaning, maternal additive genetic effect and maternal permanent environment were also fitted as random effects.

In order to alleviate the effects of sequential selection (from weaning to yearling), bivariate analyses were carried out with measures taken at both phases for each trait. As scrotal circumference is only measured at yearling, it was analyzed in bivariate animal models jointly with WW. Since the major concern was to take into account the culling that occurs after weaning, birth weight was analyzed in a single trait animal model.

2.3. Second step

Solutions obtained in the first step were used to estimate the residual $(\hat{e})$ predicted for each observation. For each trait, log squared of estimated residuals, $ln(\hat{e}^2)$, were employed as a measure of the residual variance, following Garreau et al.

Table 1
Summary statistics[a] of the data pertaining to residual variance of traits.

Trait[b]	N_R	N_S	N_D	N_H	N_{CG}	N_P	$\sigma^2\hat{e}$	Skewness[c]	Kurtosis[c]
BW	203,336	1540	125,530	151	2067	132	5.25	−0.81	0.45
C_W	250,272	1577	172,639	219	7047	159	0.350	−0.96	0.61
C_Y	155,417	1226	113,444	187	3189	127	0.445	−0.96	0.64
H_W	39,027	399	26,336	6	932	98	3.36	−0.78	0.51
H_Y	44,829	498	32,381	21	483	90	5.21	−0.79	0.42
M_W	250,143	1577	172,628	219	7045	159	0.435	−0.96	0.60
M_Y	154,360	1221	112,562	185	3159	126	0.603	−0.97	0.60
P_W	248,306	1576	171,729	219	7020	158	0.445	−0.96	0.60
P_Y	154,907	1221	113,130	187	3175	127	0.593	−0.96	0.60
SCa	74,742	1127	62,406	207	2425	66	2.14	−0.86	0.54
SCaw	74,848	1127	62,523	207	2428	66	1.90	−0.84	0.54
S_W	249,591	1541	172,064	217	6742	162	0.332	−0.88	0.57
S_Y	156,611	1197	114,038	186	3024	131	0.357	−0.89	0.59
W_W	317,444	2382	203,315	259	6304	133	93.0	−0.79	0.53
W_Y	170,568	1685	123,656	224	5577	101	155	−0.79	0.51

[a] N_R: number of records per trait; N_S: number of sires; N_D: number of dams; N_H: number of herds; N_{CG}: number of levels of contemporary groups; N_P: average size of progeny group of sires; $\sigma^2_{\hat{e}}$: variance of raw residuals analyzed in second step.
[b] 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.
[c] Coefficients of skewness and kurtosis for the distribution of log squared of estimated residuals.

(2008), Gutiérrez et al. (2006) and Mulder et al. (2009). Only records of calves sired by bulls with at least 10 progenies and raised in CG with at least 20 individuals were considered.

To reduce the impact of departure from normality on estimates of variance components, only records of $ln(\hat{e}^2)$ in the range of mean ± 3*standard deviations were included in the second step. This procedure is expected to have impact on estimates of genetic variance in σ^2_e (i.e. a downward bias, as reported by Rowe et al., 2006), but was adopted in order to reduce the influence of severe abnormalities on the estimates in the second step.

REML estimates of variance components were obtained using the MTDFREML package (Boldman et al., 1995), according to the following univariate animal model:

$$ln\left(\hat{e}_{ij}{}^2\right) = \mu + cg_i + a_j + \varepsilon_{ij} \quad (1)$$

where $ln(\hat{e}_{ij}{}^2)$ is the vector of individual log squared residuals for the trait in the analysis, μ is the overall mean, cg_i is the fixed effect of contemporary group 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.

To improve convergence in the second step, maternal additive effects and permanent environmental effects were not included in the analysis of BW and of the weaning traits, in contrast to the model employed in the first step.

2.4. Genetic parameters for residual variation

In order to facilitate comparisons among present results and those reported in other studies on genetic heterogeneity of the residual variance in livestock, two genetic parameters were calculated for each trait.

First was an additive coefficient of variation for residual variance (Ev), intended to measure the evolvability of σ^2_e. The original definition of evolvability was proposed by Houle (1992) as the genetic standard deviation relative to the mean of a trait, in order to predict the ability of a population to respond to selection. In the present context, the parameter Ev was calculated as an additive coefficient of variation ($Ev = \sigma_{Av}/\sigma^2_{\hat{e}}$), where σ_{Av} is the additive standard deviation of the residual variance and $\sigma^2_{\hat{e}}$ is the average residual variance (estimated as the overall variance of raw residuals). Thus Ev reflects the opportunity to change the residual variance by selection, being that some studies also referred to this same parameter as 'genetic CV of residual variance' (e.g. Mulder et al., 2007; Wolc et al., 2009).

The second genetic parameter calculated in this study is heritability of residual variance (h^2v), as proposed by Mulder et al. (2007). The heritability of residual variance (h^2v) was derived by Mulder et al. (2007) as a regression coefficient of Av on squared phenotypes and has been used as a central parameter in calculations of accuracy of predicted breeding value for residual variance (Âv). When predicting Âv of sires based on progeny data, these authors suggested an approximate formula for accuracy of prediction ($r_{Av,\hat{A}v}$), derived in the same way as accuracy for breeding values for mean (Cameron, 1997), but replacing h^2 by h^2v. In this work, Âv was obtained after transforming breeding values (EBV) estimated under model 1 to the scale of the residual variance.

Once the estimates of additive variance (σ^2_a) obtained in model 1 were in an exponential scale, they were transformed as proposed by Mulder et al. (2007) to get estimates of additive variance on the scale of the residual variance (i.e. σ^2_{Av}), being these figures employed to compute Ev and h^2v. The heritability of $ln(\hat{e}^2)$ (h^2_{lne2}) and its standard error (SE) were estimated on a log scale and was used to approximate the standard error of h^2v (Mulder et al., 2009).

2.5. Relationship between estimated breeding values for mean and residual variance

For each trait, the Pearson's correlation between estimated breeding values of sires for mean and for residual variance (r_{mv})

was calculated and is intended to be a rough indicative of the genetic association between these criteria, as direct estimation of this parameter is not feasible under this two-step approach. Because r_{mv} is dependent of EBV's accuracy, this parameter was calculated also for the set of sires with large number of progeny (N>50), in order to evaluate this eventual source of bias.

3. Results

Results for descriptive statistics and data distribution in the second step (after trimming outliers) are presented in Table 1. Large amount of information was available for most traits, in general comprising large sire families (average progeny size above 100, except in the case of scrotal circumference and rump height).

For traits measured in both phases, variance of raw residuals ($\sigma^2_{\hat{e}}$) was higher at yearling compared to weaning (Table 1), what could be indicative of a scale effect. Conversely, estimates of σ^2_a and Ev did not follow this pattern (Table 2).

For all traits analyzed, despite log transformation and elimination of outliers, the data effectively considered in the second step presented some departure from normality, with negative coefficients of skewness (between −0.75 and −1.00) and positive kurtosis (about 0.50 to 0.60 in most cases), as shown in Table 1.

Most estimates of evolvability for residual variation were in the range 15–25% (Table 2). The estimate of σ^2_a for birth weight was the highest, implying in a high estimate of Ev for residual variance (almost 70%). Relatively large values of Ev were also obtained for sheath score both at weaning and yearling.

Estimates of h^2v were generally low (1–3%), but significantly different from zero based on a 95% confidence interval, considering the approximate SE, except in the case of rump height, probably due to the lower number of records for this trait. (Table 2).

Low values estimated for h^2v indicate that large amount of information would be needed to predict Av accurately. The approximate accuracy averaged across all sires ($r_{Av,\hat{A}v}$) fell below 0.40 for ten of the studied traits, although their respective average progeny size was above 100 in most cases.

A more detailed inspection about the size of sire families, indicates that a large proportion of sires (between 50% and 80%) had progeny size lower than 50, what contributed to obtain relatively small values for accuracy for most traits when averaging across all sires. However, in the case of sires with large number of progeny, the expected accuracy of prediction of *Av* achieved meaningful magnitude for most traits. For example, values of accuracy averaged across all sires with at least 100 sons ($r_{Av,\hat{A}v100}$) was about 50% or higher for all traits (Table 2).

Weak correlations between sire's estimated breeding values for mean and for residual variance (r_{mv}) were estimated for C_W, M_W, M_Y, P_W, S_W and S_Y (only the last two were negative) (Table 2). Moderate positive correlations were found for BW (0.42) and scrotal circumference (about 0.40). The correlations for the other traits were not statistically different from zero (P>0.05).

When considering only sires with progeny size>50 (r_{mv50}), we found similar correlations, but of higher strength (except in the case of SC traits). In addition, significant positive correlations were also observed in the case H_Y (0.43) and P_Y (0.19). The higher absolute values observed for r_{mv50} when compared to r_{mv} could be partly explained by the fact that sires with limited number of progeny, whose EBV's are more regressed toward zero, did not contribute to computations of r_{mv50}.

For all traits in this study, it was verified a positive correlation between breeding value of sires for $ln(\hat{e}^2)$ and

Table 2
Genetic parameters[a] estimated for log residual variance and statistics[b] related to selection for residual variance (σ^2_e).

Trait[c]	σ^2_a	σ^2_{Av}	Ev(%)	$h^2v \pm$ SE (%)	$r_{Av,\hat{A}v}$	$r_{Av,\hat{A}v100}$	Δ_{VE}(%)	r_{mv}	r_{mv50}
BW	0.259	13.4	69.80	9.94 ± 0.61	0.707	0.913	−44.6	0.42*	0.49*
C_W	0.0351	0.00849	26.40	1.90 ± 0.41	0.453	0.724	−13.4	0.17*	0.21*
C_Y	0.0115	0.00456	15.20	0.65 ± 0.20	0.285	0.541	−5.7	0.06	0.13
H_W	0.0161	0.363	17.90	0.63 ± 0.47	0.297	0.495	−6.2	0.07	0.32
H_Y	0.0204	1.1	20.10	0.86 ± 0.49	0.301	0.587	−8.3	0.19	0.43*
M_W	0.0203	0.00764	20.10	1.08 ± 0.20	0.370	0.631	−8.9	0.14*	0.25*
M_Y	0.021	0.0152	20.40	1.15 ± 0.40	0.357	0.642	−9.2	0.18*	0.20*
P_W	0.00945	0.00373	13.70	0.52 ± 0.20	0.277	0.506	−4.9	0.12*	0.25*
P_Y	0.00765	0.00537	12.40	0.42 ± 0.19	0.237	0.468	−4.1	0.09	0.19*
SC_a	0.0327	0.296	25.50	0.87 ± 0.31	0.262	0.594	−10.6	0.40*	0.34*
SC_{aw}	0.0263	0.187	22.80	0.78 ± 0.34	0.250	0.578	−9.3	0.35*	0.29
S_W	0.137	0.0292	51.40	7.13 ± 0.57	0.667	0.891	−32.1	−0.21*	−0.23*
S_Y	0.0615	0.0154	34.80	3.35 ± 0.60	0.525	0.807	−19.7	−0.13*	−0.14
W_W	0.0271	466	23.20	2.02 ± 0.30	0.445	0.727	−11.8	−0.02	0.00
W_Y	0.0166	796	18.20	1.17 ± 0.28	0.339	0.642	−8.2	−0.09	−0.18

[a] σ^2_a: estimated additive genetic variance for log squared of estimated residuals, $\ln(\hat{e}^2)$; σ^2_{Av}: estimates of additive genetic variance on the scale of the residual variance, assuming the quantitative model for genetic heterogeneity of residual variance (Mulder et al., 2007); Ev: evolvability of σ^2_e; h^2v: heritability of residual variance; SE: standard error.

[b] $r_{Av,\hat{A}v}$: expected accuracy of breeding value for σ^2_e (*Av*) averaged across all sires. $r_{Av,\hat{A}v100}$: expected accuracy of *Av* averaged across sires with 100 sons or more. Δ_{VE}: expected change in residual variance, after one generation of selection. r_{mv}: Pearson correlation between sire's EBV for mean and for residual variance. r_{mv50}: r_{mv} considering only sires with progeny size>50.

[c] 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.

* P<0.05.

residual variation in their progeny, but the values were in general weak (below 0.40), what agrees with the low values expected for accuracy of breeding values for residual variance when averaged across all sires ($r_{Av,\hat{A}v}$) (Table 2).

A simulation study was performed to access further consequences of the two-step approach, by using the same structure of the population in this study (data not shown). Briefly, we found that the two-step approach has lead to some underestimation of genetic parameters for residual variance. Although, a null genetic correlation between mean and residual variance was simulated, the same pattern of skewness for log transformed squared residuals was observed in the second step. In this case, correlation estimated between sire's estimated breeding values for mean and for residual variance was very close to zero (as expected).

4. Discussion

Although squared residuals were log transformed and outliers were removed before second step, the data for all traits still presented negative skewness and positive kurtosis. When residuals are normally distributed, the distribution for their squares $(\hat{e}^2)$ approaches a chi-square distribution. Under these assumptions, a considerable departure from normality is expected for distribution of $ln(\hat{e}^2)$ (skewness about −1.50 and kurtosis about 4.0). Trimming of outliers reduced this departure from normality, while not completely, what was also reported by Mulder et al. (2009) and Rowe et al. (2006) when analyzing body weight of broiler chickens.

Estimates of evolvability for residual variance of the most of traits analyzed were slightly lower than reported previously (i.e. Ev in the range 25–60%) (Mulder et al., 2007; Wolc et al., 2009) but still indicate some opportunity to improve the uniformity of the traits through selection. On the other hand, the estimate of Ev for birth weight was larger than previous estimates of this parameter for body weight in other species (Mulder et al., 2007, 2009; Wolc et al., 2009). 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 for these traits.

Simulations showed a trend of the two-step approach to underestimate σ^2_{Av} when fixed effect of CG and additive effects were simulated on residual variance. Conversely, an overestimation of this parameter may arise from data distribution or confounding of genetic and other environmental sources of heterogeneity in residual variance (e.g. maternal influence, especially in the case of BW), but there is no strong evidence that data distributions of birth weight and sheath score differ markedly from those of other traits (based on coefficients of skewness and kurtosis).

The consideration of maternal additive effects and maternal permanent environmental effects in the second step has lead to poor convergence, what could be related to some confounding between these effects and environmental variability itself, since both of them are based on repeated measurements, as suggested by Gutiérrez et al. (2006).

Because h^2v was low for all traits (below 3% in most situations), accurate estimation of breeding values for residual variance would be feasible only for animals (mostly sires) with large amount of information, as discussed in Mulder et al. (2007). All other studies related to genetic heterogeneity of σ^2_e also reported low figures for h^2v (typically below 5%).

In order to illustrate the potential for reduction of the residual variance by selection in this population, we present in Table 2 the expected change in σ^2_e after one generation of selection (relative to current value). It was assumed selection of top 20% sires (i.e. the 20% sires with smaller $\hat{A}v$), no selection of dams and the value of $r_{Av,\hat{A}v100}$ as average accuracy of prediction. These figures indicate that considerable reduction in σ^2e would be achieved by selection, i.e. about 5 to 15% of the mean σ^2e for most traits. In case of birth weight and sheath score, whose estimates for Ev and h^2v were larger, the expected response would be higher. On the other hand, these predictions deserve some caution, as bias in estimation of σ^2_{Av} would lead to biased estimates of Ev and h^2v, resulting in spurious prediction of response to selection.

The results of this exploratory analysis suggest good prospects to obtain considerable reduction in σ^2_e by selecting sires with small $\hat{A}v$ and large number of progeny (e.g. >100). However, calculations of Δ_{VE} were quite optimistic, since 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.

Results from other studies also indicate that would be possible to improve uniformity through selection. It was argued that reductions up to 20–30% of the mean residual variance of body weight in broilers could be achieved after one generation when selecting solely on this criterion (Mulder et al., 2009). As well, the divergent selection experiment reported by Garreau et al. (2008) evidenced a slower but still significant reduction in residual variance. In this case, there was a difference between lines of 27.3% in within litter variance of birth weight, after four generations of selection.

The values of Pearson correlation between sire's EBV for mean and residual variance apparently agree with the wide range of estimates previously reported for this type of genetic association. For traits related to body weight, some studies had reported negative correlations between mean and residual variance (Gutiérrez et al., 2006; Mulder et al., 2009; Rowe et al., 2006; Wolc et al., 2009), but other authors had obtained positive values for this type of correlation (Gutiérrez et al., 2006; Ros et al., 2004). For traits in discrete scale, there is limited information about this type of parameter, except in the case of conformation, for which Wolc et al. (2009) reported a positive genetic association between mean and residual variance in broilers.

A true positive genetic correlation between mean and residual variance is not favorable when the goal is to improve simultaneously mean of trait and increase homogeneity of final product. Further perspectives of simultaneous selection to change the mean and variance of a trait could be assessed using index selection theory, e.g. by treating mean and residual variance as two separated traits, as in Mulder et al. (2008) and Ros et al. (2004). For example, for traits whose mean is near their optimum, a restricted index could be employed to keep the mean unchanged and simultaneously reduce the residual variance.

A positive mean–variance relationship would induce a positive correlation between mean and residual variance. As

most of significant estimates of correlation in this study were positive, the hypothesis that a scale effect has influenced such correlations should be considered. In addition, it must be taken in account that an incorrect choice of functional relationship could give the wrong results for the genetic correlation between mean and log environmental variance (Ros et al., 2004).

Given the departure from normality for the distribution of $ln(\hat{e}^2)$, the reliability of estimates from the second step could be questioned. It is known that REML estimators are relatively robust to small deviations from normality (Banks et al., 1985; Harville, 1977), what is expected to provide some support for evidences of additive variance on residual variation of most of beef cattle traits in this study. On the other hand, the examination of results presented by Gutiérrez et al. (2006) disclosed important differences between REML estimates obtained under the two-step approach and those obtained with a structural model, being that depending on the model and trait analyzed, the estimates of additive variance on residual variance under the two-step approach were between 2-fold and 9-fold lower than the those obtained using a structural model.

Yang et al. (2011) pointed out that genetic correlation between mean and variance (as well the estimates of 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. For all these reasons, more investigation is required to assess the reliability of genetic parameters that was estimated at the level of the residual variance under model 1.

The straightforward procedure employed in this study indicates existence of useful genetic variability of residual variance of beef cattle traits but further studies are needed to identify more accurate approaches for this data structure. Also, the direct estimation of genetic correlation between mean and residual variance may be subject of future research for beef cattle traits, as well as the extension of heteroscedastic models to deal with multiple traits, in order to obtain information to optimize selection for both average performance and increased uniformity.

5. Conclusion

Results of this study suggest action of genetic additive effects on residual variance of most traits considered, and also that uniformity of these traits could be improved by selecting for lower residual variance, when considering large amount of information to predict genetic merit for this criterion. Further studies are needed to confirm the results obtained under the exploratory approach of this work.

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References

Argente, M.J., Garcia, M.L., Muelas, R., Santacreu, M.A., Blasco, A., 2009. Selección divergente por variabilidad en el tamaño de camada en conejo: resultados de las dos primeras generaciones. XIII Jornadas sobre Producción Animal, AIDA, Zaragoza, Spain, pp. 114–116.

Banks, B.D., Mao, I.L., Walter, J.P., 1985. Robustness of the restricted maximum likelihood estimator derived under normality as applied to data with skewed distributions. J. Dairy Sci. 68, 1785–1792.

Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassel, C.P., Kachman, S.D., 1995. A manual for use for MTDFREML— a set of programs to obtain of variance and covariances. Lincoln, Department of Agriculture/ARS.

Boligon, A.A., Baldi, F., Albuquerque, L.G., 2011. Genetic parameters and relationships between growth traits and scrotal circumference measured at different ages in Nellore cattle. Genet. Mol. Biol. 34, 225–230.

Cameron, N.D., 1997. Selection Indices and Prediction of Genetic Merit in Animal Breeding. CAB International, Wallingford, UK.

Garreau, H., Bolet, G., Larzul, C., Robert-Granie, C., Saleil, G., SanCristobal, M., Bodin, L., 2008. Results of four generations of a canalizing selection for rabbit birth weight. Livest. Sci. 119, 55–62.

Gutiérrez, J.P., Nieto, B., Piqueras, P., Ibáñez, N., Salgado, C., 2006. Genetic parameters for canalisation analysis of litter size and litter weight traits at birth in mice. Genet. Sel. Evol. 38, 445–462.

Harville, D.A., 1977. Maximum likelihood approaches to variance component estimation and to related problems. J. Am. Stat. Assoc. 358, 320–338.

Hohenboken, W.D., 1985. The manipulation of variation in quantitative traits: a review of possible genetic strategies. J. Anim. Sci. 60, 101–110.

Houle, D., 1992. Comparing evolvability and variability of quantitative traits. Genetics 130, 195–204.

Ibáñez-Escriche, N., Varona, L., Sorensen, D., Noguera, J.L., 2008. A study of heterogeneity of environmental variance for slaughter weight in pigs. Animal 2, 19–26.

Kriese, L.A., Bertrand, J.K., Benyshek, L.L., 1991. Genetic and environmental growth trait parameter estimates for Brahman and Brahman-derivative cattle. J. Anim. Sci. 69, 2362–2370.

Mackay, T.F.C., Lyman, R.F., 2005. Drosophila bristles and the nature of quantitative genetic variation. Philos. Trans. R. Soc. B. 360, 1513–1527.

Mulder, H.A., Hill, W.G., Vereijken, A., Veerkamp, R.F., 2009. Estimation of genetic variation in residual variance in female and male broiler chickens. Animal 3, 1673–1680.

Mulder, H.A., Bijma, P., Hill, W.G., 2007. Prediction of breeding values and selection responses with genetic heterogeneity of environmental variance. Genetics 175, 1895–1910.

Mulder, H.A., Bijma, P., Hill, W.G., 2008. Selection for uniformity in livestock by exploiting genetic heterogeneity of residual variance. Genet. Sel. Evol. 40, 37–59.

Paschal, J.C., Sanders, J.O., Kerr, J.L., 1991. Calving and weaning characteristics of Angus-, Gray Brahman-, Gir-, Indu-Brazil-, Nellore-, and Red Brahman-sired F1 calves. J. Anim. Sci. 69, 2395–2402.

Ros, M., Sorensen, D., Waagepetersen, R., Dupont-Nivet, M., SanCristobal, M., Bonnett, J.C., Mallard, J., 2004. Evidence for genetic control of adult weight plasticity in the snail *Helix aspersa*. Genetics 168, 2089–2097.

Roso, V.M., Schenkel, F.S., Miller, S.P., 2004. Degree of connectedness among groups of centrally tested beef bulls. Can. J. Anim. Sci. 84, 37–47.

Rowe, S.J., White, I.M.S., Avendaño, S., Hill, W.G., 2006. Genetic heterogeneity of residual variance in broiler chickens. Genet. Sel. Evol. 38, 617–635.

SanCristobal-Gaudy, M., Bodin, L., Elsen, J.M., Chevalet, C., 2001. Genetic components of litter size variability in sheep. Genet. Sel. Evol. 33, 249–271.

SanCristobal-Gaudy, M., Elsen, J.M., Bodin, L., Chevalet, C., 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. Genet. Sel. Evol. 30, 423–451.

Sorensen, D., Waagepetersen, R., 2003. Normal linear models with genetically structured residual variance heterogeneity: a case study. Genet. Res. 82, 207–222.

Wolc, A., White, I.M.S., Avendano, S., Hill, W.G., 2009. Genetic variability in residual variation of body weight and conformation scores in broiler chickens. Poult. Sci. 88, 1156–1161.

Yang, Y., Christensen, O.F., Sorensen, D., 2011. Analysis of genetically structured variance heterogeneity model using the Box–Cox transformation. Genet. Res. 93, 33–46.