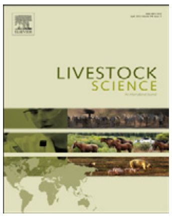
Livestock Science 148 (2012) 189–195

Contents lists available at SciVerse ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci



Short communication

Correlated genetic trend in the environmental variability of weight traits in mice

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ARTICLE INFO

Article history:
Received 31 January 2012
Received in revised form
8 May 2012
Accepted 9 May 2012

Keywords:
Canalisation
Environmental variability
Genetic trend
Weight gain
Mice

ABSTRACT

Genetic trends for weight traits and their environmental variability were analysed in an experimental mice population selected during 17 generations to increase weight gain by comparing three selection methods: classic selection with random mating (Method A), classic weighted selection with random mating (Method B) and classic selection with minimum coancestry mating (Method C). Males were selected based on their own phenotypic records for WG. The analysis involved three traits: weight at 21 days (W21), weight at 42 days (W42) and weight gain between 21 and 42 days (WG). Genetic trends were obtained by averaging, within generations, the breeding values obtained for the traits and their environmental variability under a classical animal model assuming that the environmental variance is homogeneous and an alternative model assuming the heterogeneous environmental variance is partly under genetic control. All the genetic trends were positive for the traits and negative for their environmental variability but the trend in phenotypic variances was steady showing that the model analysing the environmental variability failed to separate correctly the genetic from the systematic effects under an artificial selection scenario. The higher additive genetic variance estimated under the heterogeneity model led to higher genetic trends when this model was used, thus changing the order of the preferred methods of selection moving Method B form intermediate to be the worst. The results also showed that correlated changes in the variability of weight gain and related traits originated as a consequence of selection process in the trait, but these changes do not seem to be unfavourable for the animals since the scale effect tends to compensate the correlated reduction in variability of these traits.

1. Introduction

Growth has been shown to be an economically important trait in livestock species. Nevertheless, in recent years the homogeneity of the body weight is also becoming important. The hypothesis of the existence of a pool of genes controlling the mean of the performance and another pool of genes controlling the homogeneity of the performance (Schneiner and Lyman, 1991) makes it possible to change traits, growth rate and its homogeneity. Additionally, this hypothesis would enable studying the genetic correlation between mean and variability.

Several studies have shown evidence of heterogeneity in the residual variance in different livestock species (Högberg and Rydhmer, 2000; Jaffrezic et al., 2000; See, 1998). There are now also studies fitting a model that assumed additive genes controlling both the mean and variance of a trait (SanCristobal-Gaudy et al., 1998) that

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http://dx.doi.org/10.1016/j.livsci.2012.05.009

have shown statistical evidence of genetic control of the trait homogeneity for farm animals (Hill and Mulder, 2010, for a review).

The mouse is the experimental mammal of choice because conclusions based on these populations can be easily extrapolated to sheep, pigs and rabbits (Hill and Caballero, 2000). Therefore, selection experiments have been conducted in mice (Fernández et al., 1998; Moreno et al., 2011) to quantify the expected success before implementing them in other mammals. Populations under selection, such as the presently analysed, are expected to theoretically reduce their genetic variability (Falconer and Mackay, 1996). Thus, models analysing parameters concerning environmental variability could present difficulties in disentangling the total phenotypic variability and should be carefully checked in these scenarios. Moreno et al. (2011) have shown an important success of artificial selection after 17 generations for weight gain in mice, comparing three different selection methods and concluding that all gave similar responses.

Ibáñez-Escriche et al. (2008a) estimated the genetic parameters for weight at 21 days (W21), weight at 42 days (W42) and weight gain between 21 and 42 days (WG) with this data by fitting a model which assumed the residual variance to be heterogeneous. Results showed a decrease in the heritability of the traits when considering such a model jointly with a negative genetic correlation between the mean and environmental variance. They also found signs of a correlated response in the environmental variability by a reduction of the coefficient of variation across generations. Furthermore, genetic trends have not been assessed under this model with this data. The presence of genetic variation at the level of the residual variance suggests the possibility of being indirectly modified when selecting the trait if there is a genetic correlation between the trait and its environmental variability. Also, the mean and environmental variability of other traits could be affected and, in turn, the profits from livestock production.

The aim of the present study was to analyse and discuss the implications of the correlated genetic trends on W21 and W42 and the environmental variability of the three traits when selecting to increase WG during this period, as well as to study the performance of the SanCristobal-Gaudy et al. (1998) model under a scenario of artificial selection.

2. Material and methods

A highly variable population of mice was split randomly into nine lines, three replicates of each of the three essayed selection methodology: classic selection with random mating (A), choosing animals according to their performance and randomly mating selected individuals, classic weighted selection unbalancing the offspring of each animal according to its genetic superiority (B), and classic selection with minimum coancestry (C), same as (A) but designing mating according to minimum coancestry criterion. The design was conducted in such a way that selection intensities were equivalent across models. The selection was carried out during 17 generations, where 32 males within replicate were evaluated for WG and those eight with the largest phenotypic record for WG were selected. The females were not evaluated nor selected. Other details of the design can be found in Ibáñez-Escriche et al. (2008a) and Moreno et al. (2011).

Genetic parameters were estimated by Ibáñez-Escriche et al. (2008a) using a Bayesian approach (Sorensen and Waagepetersen, 2003) to solve both a classical additive genetic model and the model developed by SanCristobal-Gaudy et al. (1998) to study the genetics of environmental variability. The results of their analysis have been used here to study direct and correlated genetic trends.

Independent univariate analyses were carried out for the three measured traits. The same models were fitted to each of the traits:

- Homogeneity Model (HO), the classical model assuming the environmental variance being homogeneous by fitting the animal effect and litter effect as random effects with the selection-replicate-generation the only systematic effect with 163 levels (18 generations, three selection methods and three replicates by method of selection $=18\cdot 3\cdot 3$) and one level for founder population. This analysis has already been performed to analyse the genetic trend of WG by Moreno et al. (2011) and as they argued, the maternal genetic effect was not explicitly fitted in the model because previous analysis on performances, fitting together both litter and maternal genetic effects, showed that the litter was carrying all the variability explained by the maternal genetic effects.
- The Heterogeneity Model (HE) by SanCristobal-Gaudy et al. (1998), in which it is assumed that the environmental variance was heterogeneous and partly under genetic control, fitted the same effects as in Model HO both for the mean of the trait and for its environmental variability.

Breeding values for each trait and its variability were averaged and plotted within generation and selection method to study the genetic trend of the selected (WG) and the other (W21 and W42) correlated traits, as well as their environmental variability.

The expected phenotypic variances were obtained within the level of systematic effect as: $E(\sigma_i^2)=\sigma_u^2+\sigma_c^2+e^{b_i^*+u_i^*+c_i^*}$, where σ_u^2 and σ_c^2 are the additive genetic and litter variances, b_i^* is the estimation of the i level of the systematic effect, and u_i^* and c_i^* are the average of the additive genetic values and litter effects affecting the corresponding level i of the systematic effect.

In order to discuss the magnitude of the correlated genetic response, a multitrait animal model, as the one described in model HO, was also used to estimate the heritability of the traits as well as their genetic correlations via REML. The VCE v.6.0 program (Neumaier and Groeneveld, 1998) was used for this purpose.

3. Results and discussion

In the present study genetic trends of the selected WG trait as well as the correlated response on W21 and W42 and their environmental variability were analysed using mice as an animal model used as reference for other mammals with longer generation interval, such as pigs.

Table 1 includes heritabilities for WG, W21 and W42 as well as the between-traits genetic correlations, additional random litter and residual by phenotypic variances ratios, and between-traits litter and residual correlations from model HO obtained via REML. They were estimated only for discussion purposes of the trends. Heritabilities and litter ratios were reasonably in agreement with previous estimates under univariate analyses with the same data set (Ibáñez-Escriche et al., 2008a; Moreno et al., 2011). Genetic correlations between the selected trait WG and the correlated W21 and W42 traits were 0.68 and 0.94, respectively.

Genetic trends for WG trait were already drawn under Model HO by Moreno et al. (2011) to report the successes of the different selection methods. They have been addressed here under the Model HE to evaluate whether the same conclusions can be drawn using this model. Fig. 1 shows all of them together by averaging the breeding values (in grams) within fixed effect levels across replicates in the three selection methods after solving both Models HO and HE. The genetic trends of WG trait using model HE were much stronger than those under model HO because of a higher estimated additive genetic variance in the mean of the trait. Ibáñez-Escriche et al. (2008a) found big differences between these models in the estimated genetic additive variance and reported that Model HE would be of choice because of a sensitive lower DIC (Deviance Information Criterion) value (Spiegelhalter et al., 2002) for the three traits. This genetic slope of WG under model HE was positive for the three selection methods although from the fourth generation onwards, selection method (B) reached a lower trend under model HE than those for selection methods (A) and (C), and unlike under model HO according to Moreno et al. (2011) which found selection method (C) to be the worst and the selection method (B) to be intermediate. In this case, selection method (B), the best in terms of minimising the increase in inbreeding and in coancestry (Moreno et al., 2011), becomes the least successful in genetic response. Perhaps the model HE, which estimates a residual variance for each individual, is more sensitive to the difference of information between individuals than HO which assumes that all residual values come from the same distribution.

Table 1

Heritabilities (on diagonal), between-traits genetic correlations (above diagonal) and their corresponding standard errors (in brackets) for weight gain between 21 and 42 days (WG), weight at 42 days (W42) and weight at 21 days (W21) in the top left hand side, litter environmental variances by phenotypic ratio (on diagonal) and between-traits litter environmental correlations (above diagonal) in the top right hand side, and residual variances by phenotypic ratio (on diagonal) and between-traits litter residual correlations (above diagonal) down.

	Heritabilities and genetic correlations			Litter ratio and corresponding correlations		
	WG	W42	W21	WG	W42	W21
WG	0.131 (0.027)	0.941 (0.029)	0.682 (0.132)	0.403 (0.015)	0.772 (0.012)	−0.054 (0.026)
W42		0.208 (0.026)	0.889 (0.055)		0.385 (0.015)	0.593 (0.018)
W21			0.147 (0.025)			0.515 (0.015)
	Residual ratio and residual correlations					
	WG	W42	W21			
WG	0.466 (0.019)	0.865 (0.006)	0.044 (0.024)			
W42		0.407 (0.018)	0.539 (0.018)			
W21			0.338 (0.015)			

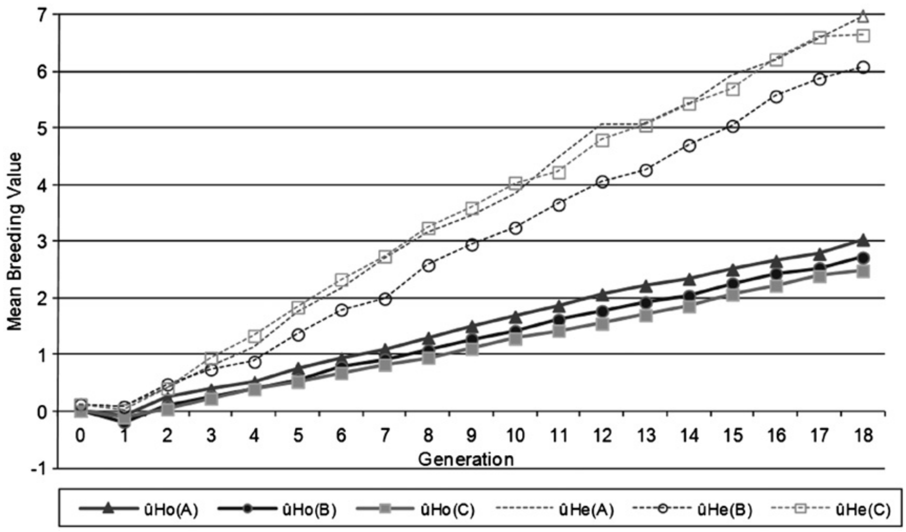

Fig. 1. Average genetic trends across replicates of weight gain between 21 and 42 days (WG) in selection methods A (▲), B (●) and C (■) using heterogeneity (ûHe) and homogeneity models (ûHo).

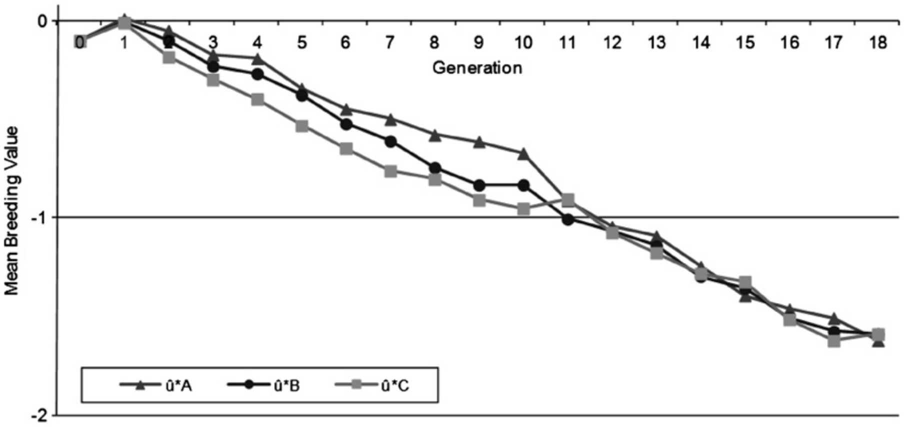

Fig. 2. Average genetic trends across replicates of environmental variance (û*) for weight gain between 21 and 42 days (WG) under model HE plotted by generation of selection. Selection method A (▲), B (●) and C (■).

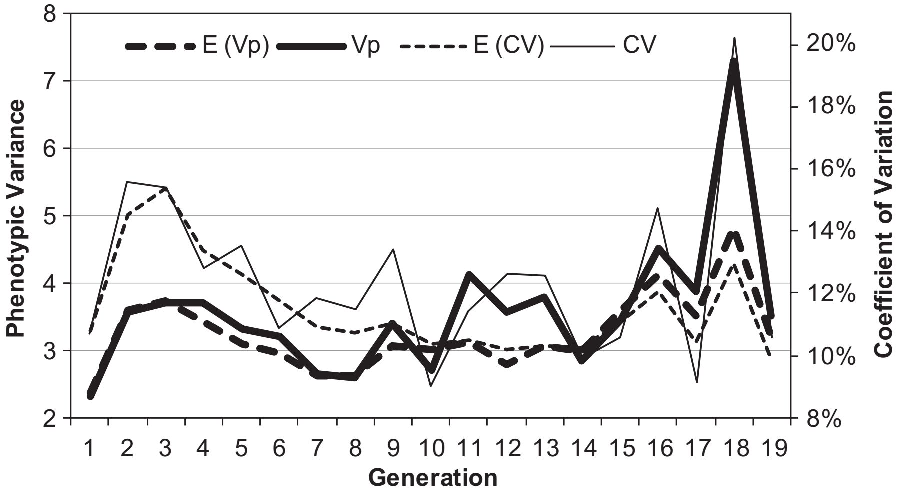

Fig. 3. Average phenotypic trends across all replicates of expected and observed phenotypic variance (E(Vp) and Vp) and expected and observed coefficient of variation (E(CV) and CV) by generation of selection.

The pattern of the correlated genetic trends in the residual variance of WG (Fig. 2), showed a decrease across the selection process as would be expected due to the negative correlation (− 0.19) estimated between the trait and its environmental variability (Ibáñez-Escriche et al., 2008a). Differences between methods of selection in the pattern for the genetic trends of the environmental variability of WG were inappreciable. These results support those reported by Ibáñez-Escriche et al. (2008a) that found signs of a negative trend in the coefficient of variation for this trait. The trend in the expected phenotypic variance of WG was computed by using the mean of the marginal posterior distributions of the systematic effect levels under Model HE and the average of the corresponding posterior means of the additive genetic and litter effects. It was averaged across replicates and methods of selection and is shown jointly with the corresponding average real phenotypic variances by generations in Fig. 3. By also using the real mean values, the mean of the expected and the real coefficient of variations were also computed and their trends are also shown in Fig. 3. The pattern of the trend in the phenotypic variance was rather stable unlike the corresponding genetic trend in the environmental variability, but the one for coefficient of variation was slightly negative. Real and expected variances and coefficients of variation were roughly similar.

Indeed, due to the scale effect linking the mean and the standard deviation, in absence of response on the environmental variability the response achieved on the mean would have lead to an increase of the standard deviation and the coefficient of variation would have remained constant. So it seems that the scale effect has compensated for the negative additive genetic trend in the variability thus achieving a stable trend in the phenotypic variance. Given that the negative additive genetic trend in the variability is roughly constant, the model assigns the irregular evolution of the phenotypic variance to the systematic generation effect.

However, genetic trends of environmental variability in all replicates of all methods of selection were negative and extremely large and should lead to a reduction of the environmental variability of about 80% (Ibáñez-Escriche et al., 2007), which was not observed and remains to studied. Ibáñez-Escriche et al. (2008a) concluded that Model HE was better, but it should be taken with caution given that such an important reduction of the environmental variability was difficult to believe. On the other hand, Yang et al. (2011) commented that the evidences of a genetic component on residual variance could be an artifact due to skewness in the marginal distribution of the data. Anyway, this model seems to present difficulties in correctly separating the influence of the different effects of the model in a data set coming from a highly successful selection experiment. Fortunately, the changes in the variance and/or coefficient of variation were steady across generations while coefficient of variation slightly decreased but not clearly due to selection. This is favourable (Bolet et al., 1996; Baxter et al., 2011; Poignier et al., 2000) if the aim is the canalisation of the trait while increasing its mean.

Correlated genetic response on the mean in the three selection methods using both Models HO and HE are shown in Fig. 4(a) for W21 and in Fig. 4(b) for W42. Their correlated genetic trends in environmental variability are given in Fig. 5. They were conditioned by the genetic correlations of each trait with their environmental variability that was −0.38 for W42 and −0.31 for W21 (Ibáñez-Escriche et al., 2008a). For both traits, trends were much higher when estimated by Model HE than by Model HO. The genetic trends for W42 and its environmental variability are almost identical to those of WG as a consequence of the high genetic correlation between them and not worth further comment. The genetic trend for W21 was much weaker as a consequence of the lower genetic correlation between the selected trait WG and W21. For W21, both genetic values for the trait and its environmental variability did not show important changes across the selective process until the seventh generation. For the subsequent generations, selection methods (A) and (C) showed a similar behaviour and a slight response was observed in selection method (B). However, the genetic trend was lower under Model HE for W21 in which selection Method (B) had a lower trend than all the methods under model HO. As commented before, the unbalanced number of data under method B could affect the estimation of the environmental variability. Observed genetic trends for the environmental variability of correlated traits are not easy to address. Unfortunately, a software such

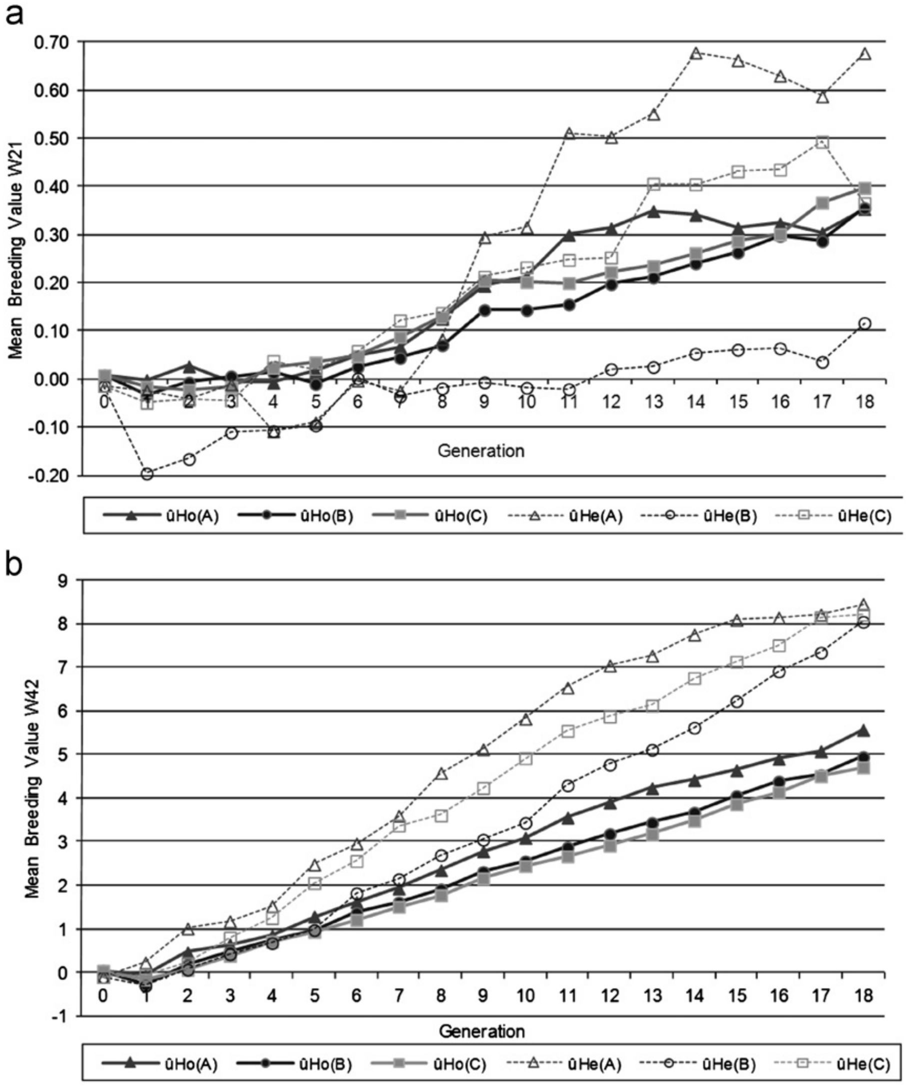

Fig. 4. Average genetic trends across replicates of (a) weight at 21 days (W21) and (b) weight at 42 days (W42) in selection methods A (▲), B (●) and C (■) using heterogeneity (ûHe) and homogeneity models (ûHo).

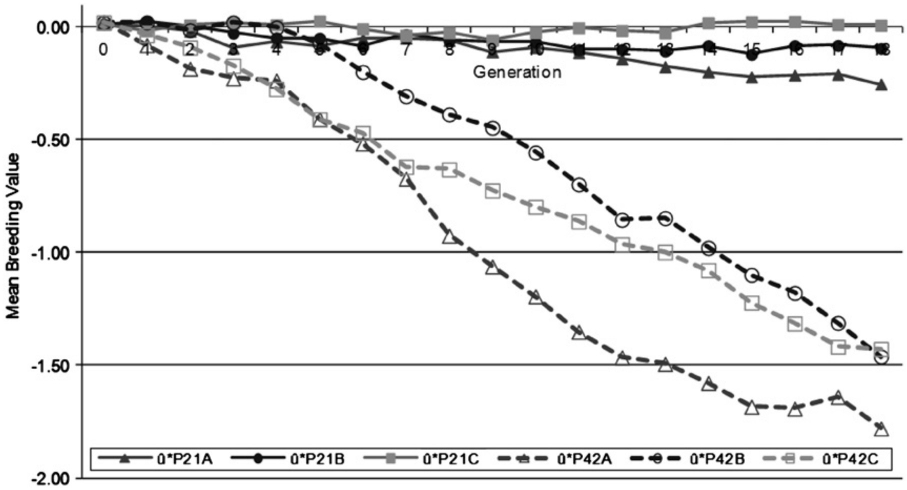

Fig. 5. Average genetic trends across replicates of environmental variance for weight at 21 days (û*P21) and weight at 42 days (û*P42) under model HE plotted by generation of selection. Selection method A (▲), B (●) and C (■).

as GSEVM (Ibáñez-Escriche et al., 2010) is not available to manage model HE under a multitrait context thus making it impractical to estimate a genetic correlation between each trait and the environmental variability of a different one. In practice what is interesting to know is how these genetic trends will affect the variance and the coefficient of variation of the traits. In this context, no trend was found in coefficient of variation of W42 and W21, but signs of a very light positive phenotypic trend in the phenotypic variance was found in W42 (not shown), which is unfavourable but of no concern because the way it is shown it is probably due to scale effect.

Once more, the present study suggests the existence of additive genetic control of the environmental variability, which has been reported by other authors for different weight traits in pigs (Bodin et al., 2002; Damgaard et al., 2001; Högberg and Rydhmer, 2000; Huby et al., 2003; Ibáñez-Escriche et al., 2008b), in rabbits (Bodin et al., 2010; Garreau et al., 2004, 2008), in snails (Ros et al., 2004) or litter size, closely related to fitness, in sheep (SanCristóbal-Gaudy et al., 2001) in mice (Gutiérrez et al., 2006; Ibáñez-Escriche et al., 2008a) in rabbits (Argente et al., 2010), in beef cattle (Neves et al., 2011), in broiler chickens (Mulder et al., 2009) and in alpacas (Cervantes et al., 2010), with a recent revision by Hill and Mulder (2010). The results presented in this study again suggest an additive genetic control of the environmental variability and different estimates of the variance components when using models that assume that environmental variance was heterogeneous. Even when the phenotypic correlated response in the variability of the trait was low, it seems clear that it exists when the selection was carried out on the mean of the trait WG which had a rather low genetic correlation with its environmental variability. Therefore, a significant success should be expected if this variability was directly selected for.

4. Conclusion

The analyses conducted here have enabled us to conclude that correlated changes in the variability of weight gain and related traits originate as a consequence of a selection process in the trait. However, these changes do not seem to be relevant as the scale effect tends to compensate for the reduction in the coefficient of variation to minimally affect the phenotypic variances of these traits. This conclusion was arrived at in this study with an experimental population of mice but we are confident that, to some extent, this may also be applied to other livestock species. The model used to analyse the environmental variability has presented difficulties to correctly separate the genetic from the systematic effects. Finally, once again, the existence of an additive genetic effect controlling the environmental variability seems to be confirmed and opportunities still present themselves for further research in this field.

Conflict of interest statement

There is no conflict of interest for this paper.

Acknowledgements

This paper was partially funded by a Grant from the Spanish Government (AGL2008-00794).

References

Argente, M.J., Garcia, M.L., Muelas, R., Santacreu, M.A., Blasco, A., 2010. Preliminary results in a divergent selection experiment on variance for litter size in rabbits. In: Proceedings of the 9th World Congress on Genetics Applied to Livestock Production. Leipzig, Germany. Communication 0526.

Baxter, E.M., Jarvis, S., Sherwood, L., Farish, M., Roehe, R., Lawrence, A.B., Edwards, S.A., 2011. Genetic and environmental effects on piglet survival and maternal behaviour of the farrowing sow. Appl. Anim. Behav. Sci. 130, 28–41.

Bodin, L., Bolet, G., Garcia, M., Garreau, H., Larzul, C., David, I., 2010. Robustesse et canalisation, vision de généticiens. INRA Prod. Anim. 23, 11–22.

Bodin, L., Robert-Granié, C., Larzul, C., Allain, D., Bollet, G., Elsen, J.M., Garreau, H., Rochambeau, H., Ross, M., SanCristóbal, M., 2002. Twelve remarks on canalization in Livestock Production. In:

Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. Montpellier, France, pp. 413–416.

Bolet, G., Esparbié, J., Falières, J., 1996. Relations entre le nombre de foetus par corne utérine, la taille de portée à la naissance et la croissance pondérale des lapereaux. Ann. Zootechnique 45, 185–200.

Cervantes, I., Pérez-Cabal, M.A., Morante, R., Burgos, A., Salgado, C., Nieto, B., Goyache, F., Gutiérrez, J.P., 2010. Genetic parameters and relationships between fibre and type traits in two breeds of Peruvian alpacas. Small Ruminant Res. 88, 6–11.

Damgaard, L.H., Rydhmer, L., Lovendahl, P., Grandinson, K., 2001. Genetic parameters of within litter variation in piglet weight at birth and at three weeks of age in litters born of Swedish Yorkshire sow. In: EAAP 52nd Annual Meeting. Budapest, pp.54.

Falconer, D.S., Mackay, F.C., 1996. Introduction to Quantitative Genetics. Longman Group Ltd., England.

Fernández, J., Moreno, A., Gutiérrez, J.P., Nieto, B., Piqueras, P., Salgado, C., 1998. Direct and correlated response for litter size and litter weight at birth in the first parity in mice. Livest. Prod. Sci. 53, 217–223.

Garreau, H., Bolet, G., Hurtaud, J., Larzul, C., Robert-Granié, C., Ros, M., Salei, G., SanCristóbal, M., Bodin, L., 2004. Homogeneización genética de un carácter. Resultados preliminares de una selección canalizante sobre el peso al nacimiento de los gazapos. XII Reunión Nacional de Mejora Genética Animal, Las Palmas.

Garreau, H., Bolet, G., Larzul, C., Robert-Granie, C., Saleil, G., SanCristóbal, M., Bodin, L., 2008. Results of four generations of a canalising 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.

Hill, W.G., Caballero, A., 2000. Artificial selection experiments. Ann. Rev. Syst. Ecol. 23, 287–310.

Hill, W.G., Mulder, H.A., 2010. Genetic analysis of environmental variation. Genet. Res. (Camb.) 92, 381–395.

Högberg, A., Rydhmer, L., 2000. A genetic study of piglet growth and survival. Acta Agric. Scand. Sec. A Anim. Sci. 50, 300–303.

Huby, M., Gogué, J., Maignel, L., Bidanel, J.P., 2003. Corrélations génétiques entre les caractéristiques numériques et pondérales de la portée, la variabilité du poids des porcelets et leur survie entre la naissance et le sevrage. J. Recherche Porcine 35, 293–300.

Ibáñez-Escriche, N., Sorensen, D., Waagepetersen, R., 2007. Selection for environmental variation, a statistical analysis and power calculations to detect response. Genetics 180, 2209–2226.

Ibáñez-Escriche, N., Moreno, A., Nieto, B., Piqueras, P., Salgado, C., Gutiérrez, J.P., 2008a. Genetic parameters related to environmental variability of weight traits in a selection experiment for weight gain in mice; signs of correlated canalised response. Genet. Sel. Evol. 40, 279–293.

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

Ibáñez-Escriche, N., Garcia, M., Sorensen, D., 2010. GSEVM v.2, MCMC software to analyze genetically structured environmental variance models. J. Anim. Breed. Genet. 127, 249–251.

Jaffrezic, F., White, I.M.S., Thompson, R., Hill, W.G., 2000. A link function approach to model heterogeneity of residuals variances over time in lactation curve analyses. J. Dairy Sci. 83, 1089–1093.

Moreno, A., Salgado, C., Piqueras, P., Gutiérrez, J.P., Toro, M.A., Ibáñez-Escriche, N., Nieto, B., 2011. Restricting inbreeding while maintaining selection response for weight gain in *Mus musculus*. J. Anim. Breed. Genet. 128, 276–283.

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.

Neumaier, A., Groeneveld, E., 1998. Restricted maximum likelihood estimation of covariances in sparse linear models. Genet. Sel. Evol. 30, 3–26.

Neves, H.H.R., Carvalheiro, R., Roso, V.M., Queiroz, S.A., 2011. Genetic variability of residual variance of production traits in Nellore beef cattle. Livest. Sci. 142, 164–169.

Poignier, J., Szendrö, Z.S., Levai, A., Radnai, I., Biro-Nemeth, E., 2000. Effect of birth weight and litter size on growth and mortality in rabbit. World Rabbit Sci. 8, 103–109.

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

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.

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.

Schneiner, S.M., Lyman, R.F., 1991. The genetics of phenotypic plasticity. II. Response to selection. J. Evol. Biol. 4, 23–50.

See, M.T., 1998. Heterogeneity of (Co)variance among herds for backfat measures of swine. J. Anim. Sci. 76, 2568–2574.

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

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., van derLinde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. Ser. B 64, 583–639.

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