

DIVERGENT SELECTION FOR RESIDUAL VARIANCE OF LITTER SIZE

Blasco A.¹, García M.L.², Muelas R.², Argente M.J.²

¹Departamento de Tecnología Agroalimentaria. Universidad Miguel Hernández de Elche, Ctra de Beniel Km 3.2, 03312 Orihuela, Spain

²Instituto de Ciencia y Tecnología Animal. Universitat Politècnica de València, P.O. Box 22012. 46071 Valencia, Spain

ABSTRACT

A divergent selection experiment for residual variance of litter size was carried out in rabbits. The selection criterion V_e was the residual variance of litter size, estimated as the phenotypic variance of litter size within female after correcting litter size for the effects of year-season and lactation status (nuliparous, lactating and nonlactating females). Selection pressure on females was approximately 30% in each line. Males were chosen within sire families in order to avoid inbreeding. Each divergent line had approximately 125 females and 25 males per generation. The traits analyzed were V_e and the same trait without any pre-correction (V_r). Results of five generations of selection were analyzed using Bayesian methods. The high and low lines showed a difference (D) of 0.65 for V_e in the first generation, with a probability of being positive $P(D > 0) = 97\%$. This difference remained constant for two generations and increased from the fourth generation of selection. The difference for V_e was 1.12 ($P(D > 0) = 100\%$) in the fifth generation. Selection for V_e displayed a high and positive correlated response in V_r . Besides, selection for reducing V_e had a positive correlated response in litter size.

Key words: Canalization, environmental variance, homogeneity, litter size

INTRODUCTION

Environmental variance of litter size is produced by systematic effects like year season or lactation status, plus permanent effects associated with the doe and residual random effects. Variance of the residual effects can be under genetic control (SanCristobal-Gaudy et al., 2001, sheep; Sorensen and Waagepetersen, 2003, pigs; Gutiérrez et al., 2006, mice). Selection to reduce residual variance can increase heritability of litter size, a trait difficult to select due to the low value of its heritability. Besides, the industry prefers dams with more uniform litters to help management (adoptions, for example) and increase litter viability. Selection for residual variance has been proposed under several models. These models are not robust and their effectiveness has been recently questioned (Sorensen, 2010). It is possible to perform a direct selection for residual variance by selecting for phenotypic variance of litter size within female. Genetic and permanent effects are common for all records of each doe, thus correcting litter size for systematic effects leaves only the residual random effect within doe, and phenotypic variance within doe is, therefore, a direct estimate of the residual variance of litter size. Direct selection on residual variance has the advantage of being less model dependent than the selection methods proposed hitherto.

The objective of this study is to estimate the response to selection for residual variance of litter size in a divergent selection experiment, directly selecting for this trait.

MATERIALS AND METHODS

Animals

Animals came from a divergent selection experiment for residual variance of litter size for five generations. The animals of the base generation came from a line originally selected for litter size, in which selection was relaxed for three generations. Reproduction was organized in discrete generations. Each divergent line had approximately 125 females and 25 males per generation. All animals were bred at the farm of the University Miguel Hernández of Elche. They were kept under a constant photoperiod of 16 h continuous lights: 8 h continuous darkness and controlled ventilation. The females were mated first at 18 wk of age and at d 10 after parturition thereafter, producing an average of 4.5 parities.

Selection criterion

Selection was based on phenotypic variance of litter size within female after correcting litter size for the effects of year-season and lactation status, which we refer to as residual variance of litter size (V_e). The effects were estimated by least squares. The effect of year-season included twenty-three levels and the effect of lactation status included three levels (nuliparous, lactating and nonlactating females). Residual variance without correction for year-season and lactation status was also calculated (V_r). Both V_e and V_r were calculated using the minimum quadratic risk estimator:

$$\frac{1}{n+1} \sum_{i=1}^{n_i} (x_i - \bar{x})^2$$

where x is litter size after correcting for year-season and lactation status and n is the number of parities of each female (n varying from 2 to 9). No Bayesian estimators of the variance were used in order to avoid the influence of prior information, since each variance is estimated with a small number of data. Selection pressure on females was approximately 30% in each line. Males were chosen within sire families to avoid inbreeding. Five generations of selection were performed. Table 1 shows the number of females, number of records of litter size and average number of parities per female for each generation and selected line.

Statistical Analysis

All analyses were performed using Bayesian methodology. The traits analysed were V_e , V_r and litter size (LS). Both V_e and V_r were analyzed using a model having only the effect of line-generation (with eleven levels: base generation, High and Low lines of first, second, third, fourth and fifth generation).

The model used to analyze LS included the effects of line-generation, year-season, lactation status, and doe effect. Bounded uniform priors were used for all unknowns with the exception of the doe effect, which was considered normally distributed with mean $\mathbf{0}$ and variance $\mathbf{I}\sigma_d^2$, where \mathbf{I} is a unity matrix, and σ_d^2 is the variance of the doe. Residuals were normally distributed with mean $\mathbf{0}$ and variance $\mathbf{I}\sigma_e^2$. The priors for the variances were also bounded uniform.

Features of the marginal posterior distribution of differences between lines were estimated using Gibbs sampling. After some exploratory analyses, we used a chain of 200,000 samples, with a burn-in period of 20,000. Only one of every 50 samples was saved for inferences. Convergence was tested using the Z criterion of Geweke (Sorensen and Gianola, 2002) and Monte Carlo sampling errors were computed using time-series procedures described in Geyer (1992).

Table 1. Number of females (N), number of records of litter size (NR) and average number of parities per female (NP) per generation and line.

	Base	G1		G2		G3		G4		G5	
		H	L	H	L	H	L	H	L	H	L
N	268	136	160	137	123	115	121	124	136	141	130
NR	1011	626	706	614	521	617	588	617	6915	664	554
NP	3.8	4.6	4.4	4.5	4.2	5.4	4.9	4.9	4.9	4.7	4.3

Base: base generation. G1 to G5: generations 1 to 5. H: High line for residual variance of litter size. L: Low line for residual variance of litter size.

RESULTS AND DISCUSSION

Table 2 presents the features of the estimated marginal posterior distributions of the differences (D) between the high (H) and low (L) lines. All Monte Carlo standard errors were very small and lack of convergence was not detected by the Geweke test. Marginal posterior distributions were approximately normal, thus mode, mean and median were similar, and only the posterior median of the difference is showed.

The H and L lines showed a difference of 0.65 for V_e in the first generation, with a probability of being positive $P(D > 0) = 97\%$. This difference remained constant for two more generation and increased from the fourth generation. The difference between lines for V_e is 1.12 ($P(D > 0) = 100\%$) in the fifth generation. The response obtained was not coherent with the selection pressure applied (Table 3), thus the point estimates of the differences between H and L lines by generation should be largely due to sampling error. Nevertheless the probability of these differences being positive is high (100% in the last generation of selection), thus a response to selection was obtained, although we cannot state now whether this response is symmetric or not. A control population of frozen embryos of the Base generation has been kept and it will be thawed to examine the possible asymmetries in response.

The variance of corrected data V_e was used as selection criterion instead of V_r because some females could have different litter sizes in some seasons or stage of lactation, increasing the variance of litter size only by environmental reasons. This selection criterion is somewhat model-dependent, but fortunately selection for V_e displays a high and positive correlated response in V_r , thus the effect of precorrecting the data is small.

Selection for reducing V_e seems to increase litter size. This could look surprising since we may expect to have higher V_e for higher LS by a scale effect. Figure 1 shows the evolution of V_e and V_r with the LS average of all parities of each female. At the beginning, when the females have a small litter size, V_e and V_r increase with the increase of litter size due to a scale effect, but when the females have higher litter sizes, V_e and V_r decrease. This happens because does with a high average LS should have all parities with high LS, and consequently they should have a small V_e and V_r .

The negative correlation between V_e and LS can be due to a higher sensitivity to stress and a lower disease resistance of does with higher litter size variability.

CONCLUSION

Selection for residual variance of litter size has been successful and it has shown a negative correlated response in litter size.

Table 2. Features of the estimated marginal posterior distributions of the differences (D) between the high and low lines for residual variance of litter size corrected for year-season and lactation status (Ve), residual variance of litter size without correction (Vr) and litter size at birth (LS) in each generation (G1 to G5).

		D	HPD _{95%}		P (%)
G1	Ve	0.65	-0.02	1.40	97
	Vr	0.55	-0.14	1.33	94
	LS	-0.36	-0.79	0.05	95
G2	Ve	0.43	-0.44	1.11	86
	Vr	0.31	-0.59	1.01	78
	LS	-0.36	-0.80	0.12	93
G3	Ve	0.59	-0.20	1.35	92
	Vr	0.59	-0.23	1.37	92
	LS	-0.96	-1.41	-0.48	100
G4	Ve	0.91	0.20	1.75	99
	Vr	0.99	0.26	1.86	99
	LS	-0.65	-1.09	-0.20	100
G5	Ve	1.21	0.47	2.02	100
	Vr	1.27	0.51	2.10	100
	LS	-0.63	-1.07	-0.17	100

HPD_{95%}: highest posterior density region at 95%. P: P(D>0) when D>0 and P(D<0) when D<0.

Table 3. Selection differential for residual variance of litter size (corrected for year-season and lactation status)

	High line	Low line
Base	2.5	1.6
G1	1.5	0.3
G2	1.6	0.3
G3	2.2	0.5
G4	1.8	0.3

Base: base generation. G1 to G5: Generations 1 to 5

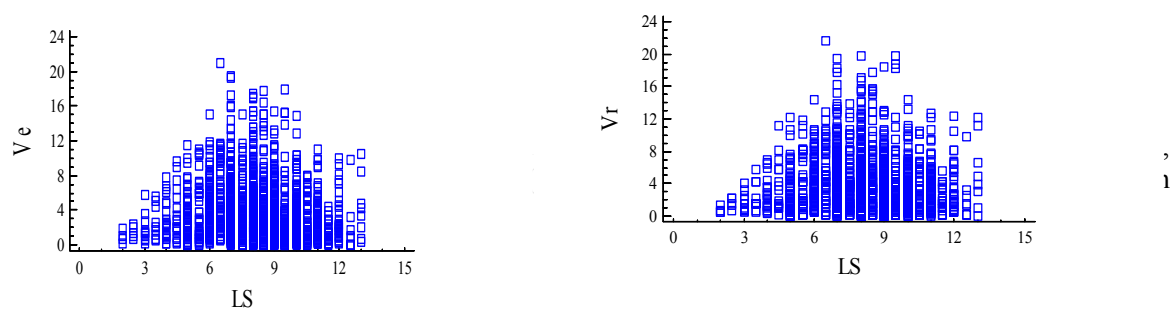


Figure 1. Evolution of residual variance of litter size corrected for year-season and lactation status (Ve) and without correction (Vr), with mean litter size of all parities of each female (LS).

ACKNOWLEDGEMENTS

This study was funded by projects of the Plan Nacional de Investigación AGL2008-05514-C02-02 and AGL2011-29831-C03-02. The authors are grateful for the software provided by Dr. W. Mekkawi

REFERENCES

- García M.L., Argente M.J., Muelas R., Birlanga V., Blasco A. 2012. Effect of divergent selection for residual variance of litter size on animal welfare. *In Proc. 10th World Rabbit Congress, 2012, September, Sharm El-Sheikh, Egypt.*
- Geyer, C. M., 1992. Practical Markov chain Monte Carlo (with discussion). *Stat. Sci.*, 7, 467–511.
- Gutiérrez J.P., Nieto B., Piqueras P., Ibáñez N., Salgado C. 2006. Genetic parameters for components analysis of litter size and litter weight traits at birth in mice. *Genet. Sel. Evol.*, 38, 445-62.
- 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.
- Sorensen D. 2010. The Genetics of Environmental Variation. *In: Proc. 9th World Congress on Genetics Applied to Livestock Production, 2010 August, Leipzig Germany.*
- Sorensen D., Waagepetersen R. 2003 Normal linear models with genetically structured residual variance heterogeneity: a case study. *Genet. Res.*, 82, 207–222.
- Sorensen, D. and D. Gianola, 2002. Likelihood, Bayesian, and MCMC Methods in Quantitative Genetics. *First Edition. Springer-Verlag, New York.*