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DIVERGENT SELECTION FOR RESIDUAL VARIANCE OF LITTER SIZE

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ABSTRACT

A divergent selection experiment for residual variance (Ve) of litter size was carried out in rabbits. The selection criterion Ve 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: residual variance of litter size within female with (Ve) and without (Vr) correction for year-season and lactation status effects (Vr) and litter size at birth. Results of five generations of selection were analyzed using Bayesian methods. The high and low lines showed a difference (D) of 0.65 for Ve 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 Ve was 1.12 (P (D > 0) = 100 %) in the fifth generation. Selection for Ve displayed a high and positive correlated response in Vr. Besides, selection for reducing Ve seemed to increase litter size. In conclusion, there has been response to selection for Ve, and selection for Ve showed a negative 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, 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 then a direct estimate of the residual variance of litter size. Therefore 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.

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 (Ve). 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 (Vr). Both Ve and Vr were calculated using the minimum quadratic risk estimator:

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

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). Selection pressure on females was approximately 30% in each line. Males were chosen within sire families in order 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 Ve, Vr and litter size (LS). Both Ve and Vr were analyzed using a model with 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 **0** and variance $\mathbf{I}\sigma_d^2$, where **I** is a unity matrix, and σ_d^2 is the variance of the doe. Residuals were normally distributed with mean **0** and variance $\mathbf{I}\sigma_e^2$. The priors for the

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.

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).

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 Ve 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 Ve 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 due largely 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 Ve was used as selection criterion instead of Vr 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 Ve displays a high and positive correlated response in Vr, thus the effect of precorrecting the data is small.

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.

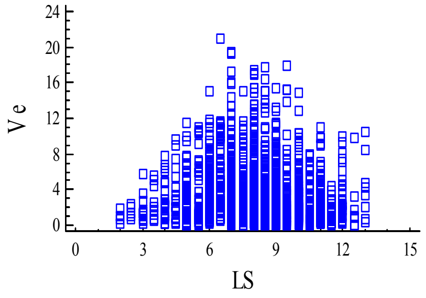
Table 3. Selection differential for residual variance of litter size (corrected for year-season and lactation status)

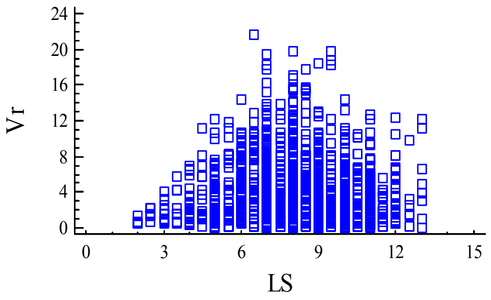
	High line	Low line
Base	2.5	1.6
G1	1.5	0.3
G2	1.6	0.3
G3	2.2	0.5
G4	1.8	0.3

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

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

The negative correlation between Ve and LS can be due to a higher sensitivity to stress and a lower disease resistance of does with higher litter size variability. In a companion paper, Garcia et al. (2012) analyze the effect of selection for residual variance on health status and stress of the does.





CONCLUSION

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

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