RESPONSE TO SELECTION FOR GROWTH RATE IN RABBITS ESTIMATED BY USING A CONTROL CRYOPRESERVED POPULATION

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Abstract: An experiment of selection for growth rate in rabbits was carried out. Response to selection was estimated by analyzing a mixed model and estimating the genetic effects of the animals in each generation, and also by comparing the last generation of selection with a control population. Animals originated from a synthetic rabbit line. Embryos from generations 3 and 4 were frozen and thawed in order to be contemporaries of rabbits born in generation 10. Group C was the offspring of generations 3 and 4, and group S was the contemporary offspring of generation 10. Random samples of the posterior distributions of the growth genetic parameters were drawn by using Markov Chain Monte Carlo methods. The heritability of daily gain was 0.11 (with an s.d. of the marginal posterior density equal to 0.02). At commercial slaughtering age (9 wks old), selected animals had a higher growth rate (49.8 g/d, s.d. 0.75 *vs.* 45.9 g/d , s.d. 0.76) and slaughter weight (2350 g, s.d. 34 *vs* 2180 g, s.d. 40). Both methods of estimating the selection response yielded similar results.

Key words: selection, rabbits, Bayesian analysis, growth rate.

INTRODUCTION

Current commercial rabbit selection programs normally include a terminal sire line selected for growth rate. Several experiments on selection for growth rate have been conducted, but only two of them (Rochambeau *et al.*, 1989 and Lukefahr *et al.*, 1996) had a control population. Moura *et al.*, (1997) and Larzul *et al.*,(2000) have performed experiments of divergent selection for growth rate. The standard method of estimating the response to selection is based on the linear function of

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genetic predictions provided by BLUP, conditional on REML estimates of variance components. (See, for example, SORENSEN and KENNEDY, 1986.) More recently, SORENSEN et al. (1994) provided a Bayesian way of estimating the response to selection that has the advantage of taking into account the uncertainty in the estimation of variance components. However, both methods are dependent on the genetic parameters, and their reliability lies in how accurately these parameters are estimated. The need for a control population has been emphasized by Sorensen and JOHANSON (1992) and SORENSEN et al. (2002). A control population has the advantage of providing information independent of the genetic parameters. The main problem for medium or long term experiments is that genetic drift acts on control populations (usually of small size) and the estimate of the response to selection may be biased. With the exception of one generation, frozen control populations are not affected by genetic drift. Thus they can be a good alternative to medium-large size experiments of selection. They also allow for the concentration of all the facilities in the selection line. The objective of this paper is to estimate the response to selection for growth rate of a rabbit population, using a frozen control population, and to compare this result with a Bayesian approach that does not use a control population.

MATERIAL AND METHODS

Animals

The rabbits were from a synthetic line selected for increased growth rate. This line was originated by crossing a Californian line with a synthetic line created by mating rabbits from commercial male lines. Two generations were not selected in order to reduce gametic disequilibrium. Generations were not overlapping as matings between animals of different generations were precluded. Selection of parents was based on daily body weight gain between 4 and 9 weeks of age. Individual phenotypic selection was practiced, but sires were selected within sire families in order to reduce inbreeding. Mating was random, with the avoidance of mating between animals having common grandparents. The offspring of each selection generation were from matings between 16-27 sires and 62-95 dams (Table 1). Dams produced between

one and eight litters each, the average being 2.25. Average litter size at birth was 7.8 rabbits. The number of animals measured and the intensity of selection from weighted selection differentials for all generations of selection are given in Table 1.

Table 1: Intensity of selection (i) per generation.

Generation	N	NSM	NSF	i-males	i-females
2	1111	25	88	1.05	0.85
3	1192	27	95	0.25	0.17
4	1508	23	81	1.28	0.90
5	1191	18	66	0.54	0.11
6	861	23	68	1.08	0.58
7	999	24	80	0.78	0.54
8	1245	23	74	0.80	0.32
9	802	22	44	1.09	0.19
10	400	16	62	0.42	0.20

N: Number of rabbits, NSM: Number of selected males, NSF: Number of selected females.

Animals were reared in the farm of the Universidad Politécnica de Valencia. This farm has insulated roof and walls, controlled lightening and ventilation, and a cooling-system to avoid high temperatures in summer. Weaning took place at 4 weeks of age. After weaning, rabbits were housed in flat-deck cages, 8 rabbits per cage, until they were 9 weeks old, and they were fed ad libitum on a commercial diet (16.0% crude protein, 15.5% fiber, 3.4% fat).

Embryos from generations 3 and 4 were frozen and thawed to be contemporaries of rabbits born in generation 10. The procedure has been described by VICENTE and GARCÍA-XIMÉNEZ (1993a and b). The offspring from these thawed embryos constituted the control group (C), and were contemporaries of offspring from parents born in the 10th generation of selection (selected group, S). Four males and two females

from generation 3 and one male and three females from generation 4, all unrelated, were recovered. They were the parents used to produce group C, whereas 6 males and 15 females produced group S. All the rabbits were born between October 1994 and June 1995. Response to selection for increased growth rate was estimated from the 127 rabbits in group C and the 141 rabits in group S.

Models

Response to the selection for increased growth rate was estimated in three ways (Table 2). First, we compared groups S and C in a model without genetic effects (Model 1). Second, we compared groups S and C with a model that also included the breeding values of the animals (Model 2). Third, we estimated the genetic values of all the animals involved in the selection process, and we estimated the response to the selection as the average of the estimated genetic values of each generation (Model 3). We used Bayesian inference as described by SORENSEN *et al.* (1994).The models can be written as:

$$y = Xb + Zu + Wp + e$$

where **b** is a random vector containing the group (S,C), parity (first, second and third or more), litter size (with eight levels: less than 6, six levels from 6 to 11, and more than 11) and year-season effect, **u** is a random vector containig the genetic effects and **p** a random vector containing the common litter effects.

Table 2: Models.

	Model 1	Model 2	Model 3
b	Group (two levels)	Group (two levels)	Year-Season
	Parity (three levels)	Parity (three levels)	Parity (three levels)
	Litter size (8 levels)	Litter size (8 levels)	Litter size (8 levels)
u	-----------	Only animals from groups (S,C) and parents	All animals and all relationships
p	Common litter effect	Common litter effect	Common litter effect

We used flat priors within limits for **b** and for variance components. The prior distribution for **u**, **p** and **e** were

$$\mathbf{u} \sim N(\mathbf{0}, \mathbf{A}\sigma_u^2) \qquad \mathbf{p} \sim N(\mathbf{0}, \mathbf{I}\sigma_p^2) \qquad \mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$$

where **A** is the relationship matrix between individuals, with the information of groups C and S and their parents only, i.e., with sibs and parental relationships (Model 2), or with the full relationship matrix, including information on all the generations (Model 3). Model 1 has less information than models 2 and 3, but it does not depend on the genetic estimation of the variance components. Model 1 ignores that data are correlated because it does not take into account the genetic relationships between individuals. This produces an underestimation of the standard deviation of the posterior densities. Model 2 takes into account the main pedigree relationships, but does not use all available information. In addition, it depends on the assumptions about the genetic determination of the traits, as does also Model 3. Model 3 offers an estimate of the response to selection using all the information, but it does not use the control population. Thus it depends on the variances of the random effects and, as does Model 2, on how well the model describes the data.

Bayesian inference

Univariate marginal posterior distributions were derived by using Gibbs sampling. An introductory description of Bayesian inference and Gibbs sampling can be found in BLASCO (2001). We used JOHNSON's (1996) method of coupling chains, as implemented by GARCÍA-CORTÉS *et al.* (1998). After several trials, the length of each chain was fixed at 500,000. The burn-in period was 100,000 iterations, higher than the minimum burn-in required, in accordance with JOHNSON's (1996) method. Sampling interval was 10, so that a total of 40,000 samples were kept from each chain. All these samples were used to estimate features of posterior distributions. Convergence was tested separately for each chain using GEWEKE's (1992) criterion. For each variable the chain is divided into two "windows" containing the first 10% and the last 50% of the samples. If the whole chain is stationary, the means of the values in both groups should be the same. The Z-score is the difference between

these two means divided by the asymptotic standard error of the difference. As the chain length approaches infinity, the sampling distribution of Z tends to be N(0,1). Hence, the values of Z which fall in the extreme tails of a standard normal distribution suggest that the chain did not reach convergence in the early states.

Statistical inferences are derived from the samples of the marginal posterior distributions obtained using Gibbs' sampler. A histogram of a sample gives the approximate distribution of the function. When the marginal posterior distribution is approximate to normal, the average and standard deviation of the sample are enough for inferences. The sampling variance of these chains was obtained computing Monte Carlo standard errors.

Table 3: Means of the posterior distribution of weight at 4 wk (WW) and 9 wk (SW) of age and daily gain (DG) for group C, S and their difference

		Model 1			Model 2		
		S	C	S-C	S	C	S-C
WW(g)	Mean	607	576	31	609	579	31
	s.d.	18	21	26	29	36	46
	MCse	0.10	0.13	0.16	0.43	0.69	0.84
	Z	0.94	-0.37	0.85	0.56	0.62	-0.19
SW (g)	Mean	2350	2180	168	2350	2180	162
	s.d.	34	40	50	49	59	75
	MCse	0.19	0.23	0.28	0.60	0.90	1.10
	Z	0.89	-0.36	0.82	0.57	0.15	0.20
DG (g/d)	Mean	49.8	45.9	3.92	49.6	45.9	3.72
	s.d.	0.65	0.76	0.95	1.07	1.33	1.69
	MCse	0.003	0.004	0.005	0.015	0.024	0.029
	Z	0.91	-0.30	0.78	0.59	0.36	0.03

s.d.: Standard deviation of the posterior distribution. MCse: Monte Carlo standard error Z: Z-score of the Geweke test.
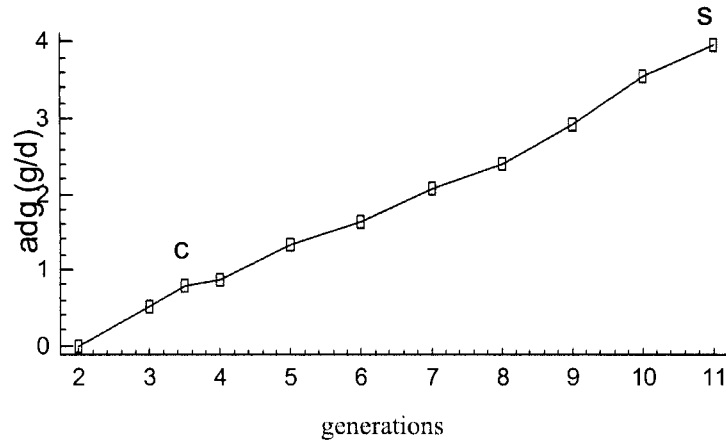
Figure 1. Genetic trend of average daily gain (adg). C: Control group. S: Selected group.

RESULTS

Table 3 shows the estimates of the correlated response to the selection for live weight at 4 and 9 wk of age and the response on daily gain for the control and selected groups, using models 1 and 2. Figure 1 shows the estimates of the genetic averages of each generation (model 3). The Z-score did not detect lack of convergence and trace plots of samples from the chains suggested acceptable mixing. Monte-Carlo standard errors were low. Estimates of the response to selection given by models 1, 2 and 3 were in general agreement. As expected, standard deviations were higher in model 2 since model 1 did not account for the genetic relationships between data. Growth rate increased 7% overall among the selected animals compared to that of the animals in group C, this implies an approximate improvement rate of 2% per year (the generation interval was approximately 6 months). Slaughter weight was higher in the selected group, but weaning weight remained practically the same. Heritability of daily gain was 0.11 (with a s.d. of the posterior density 0.02). Parity effect was low, the maximum difference between levels being 0.76 g/d (with s.d. 0.25 g/d), a 1.5% of the mean. Litter size also had a small effect (the maximum difference between levels was 2.90 g/d with s.d. of 0.37 g/d, a 5.8 % of the mean). Seasonal effects were more important showing a cycle in which summer had an

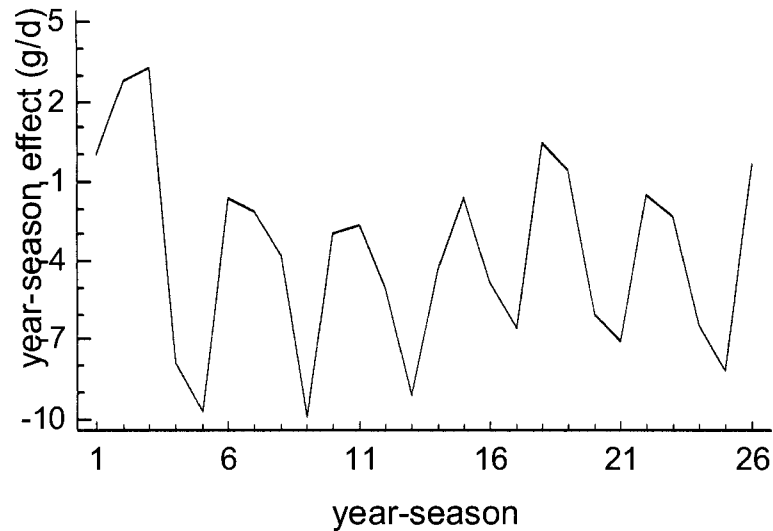unfavorable effect and winter a favorable effect on growth rate (Figure 2).

Figure 2: Environmental trend for average daily gain.

DISCUSSION

Although rarely used in selection experiments, frozen control populations offer the advantages of optimizing the experimental facilities and a reducing the genetic drift. All the models used, with the exception of Model 3, tend to underestimate the s.d. of the posterior distributions resulting from genetic drift. Thus it is advisable to reduce this by using frozen control populations. Moreover, frozen control populations avoid the unadvertised selection of related traits that often occurs, and they also reduce the effect of natural selection. Due to technical problems when thawing the embryos, only four males and two females from generation 3 and one male and three females from generation 4, all unrelated, were recovered. This is reflected in the higher s.d. of the marginal posterior distributions of the group C.

Using a different set of data of the same C and S populations, PILES *et al.* (2000)

also showed, in a different context, that selection for growth rate was successful in this experiment. Selecting for growth rate has been also successful in other experiments on rabbits. ESTANY *et al.*, (1992) give a progress of 0.6 and 0.7 g/day per generation in two lines selected for growth rate between 4 and 11 weeks of age. ROCHAMBEAU *et al.*, (1989) show a progress of 0.83 g/d per generation for selection between 4 and 11 weeks of age. The results of all of them were higher than ours; however, they had been given one week more for fattening. LUKEFAHR *et al.*(1996) and ROCHAMBEAU *et al.* (1994) were also successful in selecting rabbits for weight at 10 weeks of age. In our, experiment we found that growth rate selection was successful. The consequence of this progress is a reduction of the age of slaughter, because the slaughter weight is fixed by the market.

Response to selection calculated from the model separating environmental and genetic effects or with a control population was the same. The latter is dependent on the parameters used in the model, and obtaining higher or lower genetic trends depends on the genetic parameters estimated (SORENSEN and JOHANSON, 1992). Genetic trends can also change if the model used for the analysis changes. Thus, it is important to obtain independent proofs corroborating the same results in order to show that the model used to estimate the response to selection is appropriate. A control population gives this independent proof, although the accuracy of the estimation of the response to the control population selection is lower, mainly in frozen populations because fewer animals are used. In our case, as the response to selection is coincident in both cases, we consider the model to be validated and confide in the results of the Bayesian analysis.

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