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Livestock Production Science 78 (2002) 91–98

**LIVESTOCK
PRODUCTION
SCIENCE**

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Estimation of correlated response on growth traits to selection in litter size of rabbits using a cryopreserved control population and genetic trends

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Received 12 September 2001; received in revised form 3 May 2002; accepted 3 May 2002

Abstract

An experiment is performed to contemporaneously compare young rabbits six generations apart in order to evaluate the correlated response to selection on growth traits in a line selected on litter size at weaning for 21 generations. The selection method was based on a BLUP procedure using a repeatability animal model. The contemporary comparison was possible because techniques of embryo cryopreservation and transfer were used in generation 15. The direct response to selection between both generations has been studied by García and Baselga [Livest. Prod. Sci. 44 (2002) 45–53] and was 0.51 ± 0.25 rabbits weaned/litter (0.085 per generation). In this paper, growth traits have been studied and the results show that non-significant differences between both generations were found, using as covariate total litter size at birth. Also, heritability, genetic correlations between growth traits and litter size at weaning, and genetic trends have been estimated using mixed model methodology with all the data of the selection process (12 651 parities and 93 085 growth records across 21 generations of selection). The genetic correlations were close to zero and the estimated genetic trend for weaning weight and post-weaning daily gain were positive and significant but small, less than 0.3% of the means per generation.

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Keywords: Correlated response; Growth; Litter size; Frozen embryos; Control population; Rabbit

1. Introduction

Genetic improvement of prolificacy traits in species such as pigs or rabbits has considerable importance for total productivity. Statistical methods using mixed models have dominated the analysis of

data from livestock production improvement schemes, for the prediction of breeding values and the estimation of genetic parameters and genetic trends. Specialised dam lines in rabbits are selected for litter size by BLUP methodology (Estany et al., 1989; Gómez et al., 1996; de Rochambeau et al., 1998).

Long-term selection for litter size has been successful. Significant responses have been estimated using, for comparison, a cryopreserved control popu-

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lation (García and Baselga, 2002), or a standard control population (non-cryopreserved unselected population; de Rochambeau et al., 1998).

Traits related to growth are important in meat rabbit production. The survival of the young rabbit or the efficiency of production itself are affected by them. The most important traits are weight at weaning and at the end of the fattening period, post-weaning daily gain, feed intake and the conversion index of feed in live weight.

Estimates of genetic correlation between litter size and growth traits in rabbits are very limited and contradictory. Whereas positive genetic correlations have been reported by Mgheni and Christensen (1985) and Camacho and Baselga (1990), opposite results have been shown by de Rochambeau et al. (1989) and Camacho and Baselga (1990), since the magnitude and the sign of the correlations depend on the population or strain under study.

In pigs, Hermesch et al. (2000) showed that the genetic correlation between daily gain and number born alive was negative or close to zero, according to parity order. Crump et al. (1997) found that the number of piglets born was weakly correlated with growth traits, like feed intake or conversion index.

García and Baselga (2002) have reported a significant direct response to selection for litter size at weaning in rabbits. The response was 0.085 rabbits weaned/litter per generation, significantly improving ovulation rate but without significant changes in prenatal survival. The aim of this paper is to analyse growth data from a long-term selection experiment proven as successful in improving litter size at weaning. The analyses intend to show if significant correlated responses on different growth traits have been produced when the objective of selection was litter size. Two different approaches were used, one comparing the last generation with a generation previously cryopreserved, and the other applying mixed model methodology to compute genetic trends.

2. Material and methods

2.1. Animals

Line V is a maternal rabbit line selected during 21 generations for number of young weaned per litter by

BLUP methodology using a repeatability animal model (Estany et al., 1989). García and Baselga (2002) have previously described the population structure and the selection procedure in detail.

The animals were kept at the experimental farm of the Universidad Politécnica de Valencia (Spain). Young rabbits were weaned at 28 days of age and the fattening period lasted 5 weeks. During the fattening period, the rabbits were fed with a commercial pelleted feed supplied ad libitum (16% crude protein, 15.5% crude fibre and 3.4% ether extract).

2.2. Estimation of response with control group

The results reported by Cifre et al. (1999) concerning the effects of recovery, cryopreservation and transferring techniques on growth characteristic suggested that it was better to work with the offspring of the animals cryopreserved than directly with these animals. Thus, a control group (CG) consisted of the offspring of 73 does and 31 bucks. These parents come from embryos of generation 15 that were vitrified in 1992 and transferred after thawing 5 years later. Young rabbits, pertaining to generation 21, the current generation at the time, and contemporaneous to the rabbits of the control group were the selected group (SG). Generation 21 had 340 does and 25 bucks. The number of rabbits in the CG and SG was balanced and a total of 1854 rabbits were used for comparing the groups.

Rabbits were weaned 28 days after birth and then placed in collective cages housing nine young in each cage. The mortality between weaning and slaughter during the experiment was 7%: this value is unusual and was due to digestive troubles in the fattening period so only cages with at least seven young alive at the end of the 5 weeks of fattening were considered in the experiment (206 cages) as a compromise between the number of observations and the eventual distortion caused by the digestive troubles. Recorded characters included individual weaning weight at 28 days of age (WW, in grams), individual weight at the end of the fattening period at 63 days of age (WS, in grams), and individual average daily gain during the fattening period (DG, in grams per day). Daily feed consumption between weaning and slaughter (FC, in grams) and the conversion index of feed in live weight during the fattening period (CI, in grams per grams) were also

controlled, but these traits were computed as one average for each cage. The model takes into account the proportion of animals in a cage for each random and fixed effects and the averages of the covariates.

The data were analysed solving a mixed model (Henderson, 1984) that for all traits had the same fixed and random effects and, also, the covariate total litter size at birth. The only difference between traits was that the model for the conversion index included as second covariate the weight at the end of the fattening period.

The fixed factors were: parity order (1, 2 and ≥ 3); year-season (1–5) and group (CG, SG). The random factors were: the animals, related to each other through their parents; and the maternal and residual effects. Because the data analysed for feed consumption and conversion index were averages within cages, the model took into account that in a cage there were seven to nine different rabbits of several fixed and random effects.

The parameters used for random factors were in the range accepted in the literature (Estany et al., 1992) and are shown in Table 1. The significance of the regression coefficients of the covariates and the contrasts between effects of the same factor was determined by the corresponding *F*-test. The α used for the statistical tests was 0.05.

2.3. Genetic trends

Data from 21 generations of line V were used in the analysis. As selection was applied for litter size at weaning, this trait was included in every analysis in order to obtain parameter estimates unbiased by selection (Sorensen and Johansson, 1992). A total of 12 651 parities and 93 085 growth records from 1982

to 1999 were analysed. The pedigree file included 93 380 individuals.

The traits studied were individual weaning weight at 28 days of age (WW, in grams), individual weight at the end of the fattening period at 63 days of age (WS, in grams) and individual average daily gain during the fattening period (DG, in grams per day).

Variance and covariance components were estimated using the derivative-free multiple trait restricted maximum likelihood (REML) procedure (Neumaier and Groeneveld, 1998). A bivariate animal model was used with growth traits and litter size at weaning. The averages of the individual genetic predictors in each generation were regressed on generation number to estimate the genetic trend.

The mixed model used for growth traits was:

$$y_{ijklmn} = \mu + b*LS + YS_i + PO_j + a_k + p_l + c_m + e_{ijklmn}$$

where y_{ijklmn} is the growth trait, μ is the general mean, LS is the covariate litter size at birth, YS_i is the fixed effect of year-season in which the animal was weaned with 73 levels, PO_j is the fixed effect of parity order in which the animal was born (1, 2, >2 parities), a_k is the additive genetic value of the animal, p_l is the permanent environmental and genetic non-additive effect over all the parities of the dam of the animal k , c_m is the random effect of the litter in which the animal k was born, and e_{ijklmn} is the residual.

It was necessary to consider, in the dam, the permanent environmental effect and the litter effect in order to distinguish the non-additive effects of a dam on all her progeny from the specific environmental effects of the dam on the progeny of a particular litter. Additionally, this partition allows a better connection with the model of litter size at weaning in the sense that the correlation between the dam environmental effects in both models (r_p) and the correlation between litter effects in the growth trait model and the residuals in the litter size model (r_e) can be computed.

The litter size at weaning was analysed with the following mixed linear model:

$$y_{ijkl} = \mu + YSR_i + RS_j + a_k + p_k + e_{ijkl}$$

where y_{ijkl} is the litter size at weaning, μ is the

Table 1
Estimation of response with control group

	Traits ^a				
	WW	WS	DG	FC	CI
h^2	0.13	0.20	0.25	0.20	0.20
m^2	0.17	0.10	0.05	0.10	0.10

Heritability (h^2) and non-genetic maternal component (m^2) are used for the solution of the mixed models for the different traits.

^a CI, conversion index; DG, average daily gain; FC, daily feed consumption; WS, weight at slaughter; WW, weight at weaning.

general mean, YSR_i is the fixed effect of year-season of parity, with 78 levels, RS_j is the fixed effect that considers the reproductive state of the doe at conception (nulliparous doe, lactating doe or non-nulliparous non-lactating doe), a_k is the additive genetic value of the doe, p_k is the permanent environmental and non-additive genetic effect of the doe over all its parities, and e_{ijkl} is the residual.

3. Results

3.1. Fixed effects and covariates

The parity order or the year-season are some effects factored into the models, but they are not fully reported. The first parity had a negative influence in the growth traits studied. This result agrees with those found in the literature.

The main results concerning seasonal effects on growth, feed intake and feed conversion could be explained by the effects of temperature on these traits. For instance, Ozimba and Lukefahr (1991), Torres et al. (1992) and Feki et al. (1996) reported the depressing effect of high temperature on these traits.

Line V had response to selection in litter size at birth (0.103 born/generation; García and Baselga, 2002), so this covariate has been included into the model in order to separate the differences between the groups due to the differences in litter size from the other differences. The effect of the covariate litter size at birth was always significant and negative, except for conversion index (Table 2). These results agree with the results of Feki et al. (1996). However, there is some variability in the reported

results, so, some of them are non-significant (Torres et al., 1992). Camacho and Baselga (1991) indicated that post-weaning daily gains were insignificantly affected by maternal and litter effects.

The comparison between groups for conversion index has been done at a constant total litter size (10.9 young) and a constant weight at slaughter (1904 g). These covariates have not been significant for this trait.

3.2. Estimation of response with control group

The generalised least-square means for growth traits, concerning group effect (CG, SG), estimated at a constant total litter size at birth of 10.9 young/litter are shown in Table 2.

The comparison between control and selected group was not significant for any growth traits between weaning and 5 weeks post-weaning, meaning that selection for litter size at weaning has not modified these traits when they are compared at the same litter size. This is equivalent to saying that the total modification of the growth traits achieved by selecting litter size at weaning has been due to the strict modification of litter size. In this sense, given the significant and negative coefficient of the covariates for weaning weight, weight at slaughter, daily gain and feed consumption, the difference between the selected and control group is significant and negative for those traits if the correction for litter size is not considered.

de Rochambeau et al. (1994) found a correlated negative genetic trend in weaning weight when they analysed data of two lines selected for litter size for 18 generations, but they did not include total litter size as a covariate in the models, although they

Table 2

Generalised least-square means and covariate regression coefficient and their standard errors for selected group (SG) and control group (CG) on growth characters

	Traits ^a				
	WW	WS	DG	FC	CI
CG	492±12	1879±25	39.2±0.6	106.8±2.0	2.72±0.05
SG	488±11	1831±23	37.9±0.6	103.5±1.9	2.73±0.04
Covariate ^b	-20.8*±2.1	-39.3*±4.3	-0.54*±0.11	-1.22*±0.36	0.004±0.010

* $P < 0.05$, covariate effect is significant.

^a CI, conversion index; DG, average daily gain; FC, daily feed consumption; WS, weight at slaughter; WW, weight at weaning.

^b Average covariate: 10.9 litter size at birth.

found direct response to selection for litter size. When they use a standard control population, the estimated response was 0.081 rabbits weaned per generation (Poujardieu et al., 1994) and 0.075 rabbits weaned per generation if the genetic trend is estimated with a mixed model approach (de Rochambeau et al., 1998).

3.3. Genetic trends

Estimated variance components for growth traits are shown in Table 3. Estimates of heritability were 0.224 ± 0.009 for weaning weight, 0.302 ± 0.013 for weight at slaughter, and 0.198 ± 0.009 for daily gain.

The non-additive plus permanent environmental effects of the doe over all their parities had lower estimates, which varied between 0.183 and 0.258.

The common environmental effect of litter explained a greater part of phenotypic variance and their values were 0.415 ± 0.005 for weaning weight, 0.284 ± 0.006 for weight at slaughter, and 0.288 ± 0.004 for daily gain. These estimates were

Table 3

Estimates of heritabilities (h^2), the ratio between the variance of non-additive plus permanent environmental effects and the phenotypic variance (p^2) and the ratio of litter variance to phenotypic variance (c^2) with their standard errors

	Traits ^a		
	WW	WS	DG
h^2	0.224 (0.009)	0.302 (0.013)	0.198 (0.009)
p^2	0.183 (0.004)	0.207 (0.007)	0.258 (0.005)
c^2	0.415 (0.005)	0.284 (0.006)	0.288 (0.004)

^a DG, average daily gain; WS, weight at slaughter; WW, weight at weaning.

Table 4

Estimates of genetic (r_g), non-additive plus permanent environmental (r_p) and environmental (r_e) correlations between growth traits and litter size at weaning with their standard errors

	Traits ^a		
	WW	WS	DG
r_g	0.049 (0.068)	-0.025 (0.077)	0.059 (0.059)
r_p	-0.161 (0.049)	0.043 (0.066)	0.094 (0.056)
r_e	-0.599 (0.018)	-1.000 (0.001)	-0.879 (0.184)

^a DG, average daily gain; WS, weight at slaughter; WW, weight at weaning.

higher than their additive variances, and this tendency agrees with the results reported by Lukefahr et al. (1996), McNitt and Lukefahr (1996) and Su et al. (1999).

There is evidence that the common litter effect decreases over time, so the estimates are higher for growth at weaning than at slaughter (Camacho and Baselga, 1990; Lukefahr et al., 1996; McNitt and Lukefahr, 1996; Su et al., 1999).

Estimates of genetic, non-additive plus permanent environmental, and environmental correlations between growth traits and litter size at weaning are given in Table 4. Results for bivariate analyses including data for objective to selection did not vary for all traits, so the genetic correlation between growth traits and number of weaned did not differ from zero. The non-additive plus permanent environmental correlations were close to zero when the traits were controlled at the end of the fattening period, but this correlation was significant and negative for weight at weaning (-0.161 ± 0.049). Estimates of the residual environmental were negative and they increased over time.

When the selection response was studied in terms of genetic trend, the correlated responses for weight at weaning and daily gain were significant, so their regression coefficients were 1.4 ± 0.153 and 0.11 ± 0.012 , respectively (Figs. 1 and 3). Nevertheless, there was no correlated response to weight at slaughter, since the regression coefficient was non-significant (1.5 ± 0.54 ; Fig. 2). However, the computed genetic trend is very small, lower than 0.3% of the mean for all traits. Considering that the weight at slaughter is the weaning weight plus the post-weaning gain, the expected genetic trend for the weight at slaughter should be the genetic trend estimated for weaning weight (1.4 g) plus the number of days of the fattening period (35 days) times the genetic trend of post-weaning daily gain (0.11 g/day). Thus, the expected genetic trend should be 5.25 g, which is different from 1.5 g. This inconsistency, in some sense, is not surprising because the figures are very small and the analyses have been done by separate bivariate models of each growth trait with litter size at weaning. In the same way, one previous, but minor, inconsistency that may partially explain this result, is that the actual estimates of the genetic correlations between litter size and the growth traits

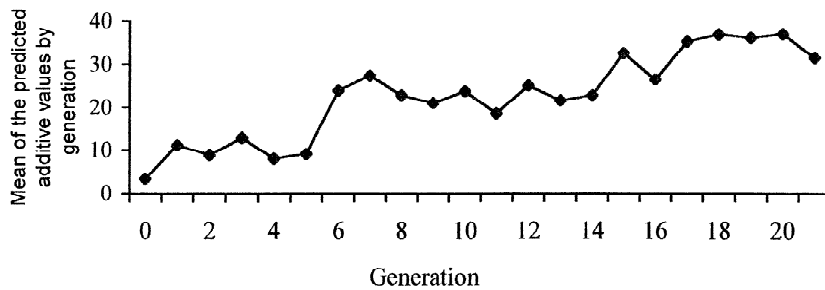


Fig. 1. Genetic trend of weight at weaning (g).

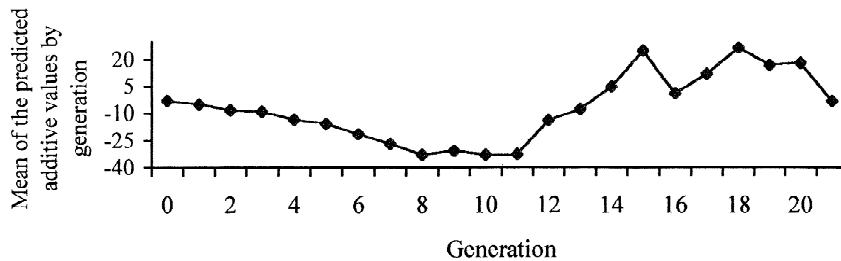


Fig. 2. Genetic trend of weight at slaughter (g).

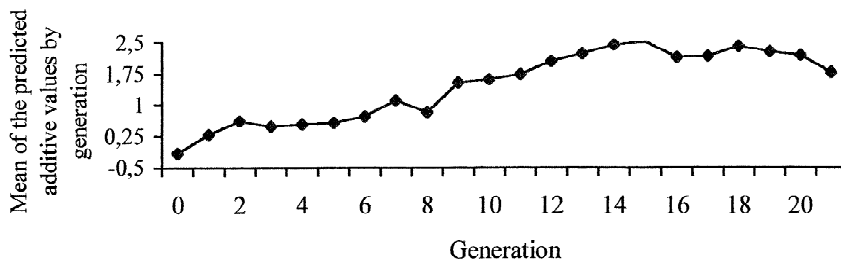


Fig. 3. Genetic trend of daily gain (g/day).

are very small and positive for weaning weight and post-weaning daily gain, but small and negative for weight at slaughter.

4. Discussion

The use of reproductive techniques, like the cryopreservation of embryos and their transfer with high efficiency (Vicente et al., 1999; García et al., 2000), has allowed the establishment of a control population. The advantages indicated by Hill (1972) and Smith (1977) for this methodology have been corroborated in this experiment, as the frozen control

population is less costly to maintain and is more flexible to use, and there is no cumulative genetic drift variance over time if it is compared with a standard unselected control population. Moreover, it is possible to check the model used in order to evaluate the animals when the response estimates are obtained by BLUP methodology or with control population, because of this genetic trend depends on prior values of genetic parameters and the genetic model used (Blair and Pollack, 1984; Thompson, 1986; Ollivier, 1999).

The results of this paper show that there is no correlated response to selection in growth traits evaluated with a control population. They agree with

the estimated correlations between growth traits and number at weaning when the mixed model approach is used, so the genetic correlations are not different from zero. Nevertheless, the genetic trends estimated for weight at weaning and post-weaning daily gain are significant, positive and very small. Qualitatively, both results disagree, but quantitatively the genetic trends are so small that we can not accept a serious discrepancy between both approaches in our data. Comparing both approaches, García and Baselga (2002) obtained good agreement between them when the response to selection of litter size at weaning was analysed for reproductive traits.

Our results showing no difference between the selected and control group tend to be similar those previously reported by Gómez et al. (2000), since the selection for a global objective (litter weight at weaning of the dam and individual daily weight gain) achieved a response in growth traits without impairment of litter size at weaning. However, de Rochambeau et al. (1994) reported that selection for increased litter size resulted in a decrease of individual weight at weaning but the total weight of the litter at weaning increased in two different maternal lines. This consideration has meant the modification of the objective of selection in one maternal line, to include the weight at 63 day, in addition to litter size performances (de Rochambeau, 1998), trying to increase at the same time litter size and individual weight. This is because the production scheme recommended for the farmers is to use a crossbred female, coming from the cross of two maternal lines. These does are mated to bucks of a line specialised for growth traits in order to combine reproductive and growth efficiency in rabbit production. Moreover, the diminution of weights from birth to adulthood when litter size increases could restrict the doe capacity to meet the needs for very high performances. Nevertheless, the least-square means given in Table 2 indicate a suitable capacity for growing in this line, although it is specialised as a maternal line.

Concerning the estimation of genetic parameters, the heritability estimates of described traits were intermediate with other literature estimates of maternal lines. Gómez et al. (1998) obtained estimated heritabilities of 0.41 for individual weight at weaning (32 days), 0.37 for individual weight at 60 days of

age, and 0.34 for average daily gain, after selection during 3 years with overlapping generation for litter size at weaning. de Rochambeau (1998) reported heritabilities of individual weight at weaning equal to 0.08 and 0.09 for two lines selected during 18 generations for litter size at birth and at weaning, respectively. With reference to genetic correlations, the estimates are very different; thus Gómez et al. (1998) indicated that litter size at weaning was negatively correlated with growth traits, especially with individual weight at weaning (-0.25) in a line selected for litter size at weaning. In lines selected for daily gain, Camacho and Baselga (1990) reported positive genetic correlations between reproductive and growth traits.

The main conclusion of this experiment is that there is no correlated response of selection for litter size at weaning on growth, feed intake or feed efficiency traits evaluated to a constant litter size.

Acknowledgements

This work has been supported by the Spanish Research Project AGF97-0803.

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