Original article

Selection response of growth rate in rabbits for meat production

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Summary – Genetic and environmental trends in 2 lines of rabbit (B and R) selected on individual weight gain (WG) from weaning (4 wk) to slaughter (11 wk) were estimated using mixed model methodology. Line B was derived from the California breed and line R was a synthetic of stock of different origin. The data were collected from a single herd and comprised 7 718 individuals in line B and 9 391 in line R, the lines having 12 and 9 generations of selection respectively. Realized responses in the 2 lines were 2.7% and 2.2% of the initial mean per year respectively and showed that selection on WG was effective but was less than expected. Selection on slaughter weight (SW) and effects of selection on other economic traits are discussed. It is concluded that selection on either WG or SW is a simple method for improving growth rate in rabbit sire line stocks.

selection / growth rate / rabbit / mixed model

Résumé – Réponse à la sélection pour la croissance chez le lapin de chair. *On a estimé les tendances génétiques et environnementales dans 2 lignées de lapin (B et R), sélectionnées sur le gain de poids (WG) entre le sevrage (28 jours) et l'abattage (77 j), en utilisant la méthodologie du modèle mixte. La lignée B est issue de la race californienne; la lignée R est une souche synthétique. Les données, recueillies dans un seul élevage, incluaient 7 718 individus de la lignée B et 9 391 de la lignée R, représentant respectivement 12 et 9 générations de sélection. Les réponses à la sélection dans les 2 lignées, respectivement 2,7% et 2,2% de la moyenne par an, montrent que la sélection a été efficace, mais avec des réponses inférieures aux valeurs espérées. La sélection sur le poids d'abattage (SW) et les effets de la sélection sur d'autres caractères économiques sont discutés. On conclut que la sélection sur WG, ou sur SW, est une méthode simple pour améliorer la vitesse de croissance des souches paternelles de lapin.*

sélection / vitesse de croissance / lapin / modèle mixte

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INTRODUCTION

Most breeding schemes concerning rabbits for meat production involve a specialized sire line selected exclusively on growth rate and 1 or 2 dam lines in which litter size is the major trait in the selection objective (Rouvier, 1981; Baselga and Blasco, 1989).

Selection for litter size has been discussed by Matheron and Rouvier (1977) who proposed use of a family index to increase the rate of response. More recently, Estany *et al* (1988a) assessed the advantages of introducing mixed model methodology (Henderson, 1973) in the selection of dam lines. However, not much attention has been paid to improving the efficiency of selection in sire or dual purpose lines. Although it has been suggested that the heritability of growth rate is high enough to make phenotypic selection efficient, little theoretical and experimental evidence has been presented. Three selection experiments based on the individual performance of average daily growth between 28 and 77 d or live weight at 112 d have been carried out (Rochambeau, 1988). Observed responses to selection were lower than expected.

The main aim of this paper was to evaluate the genetic trends achieved in 2 strains of rabbits selected on growth rate for 9 and 12 generations respectively.

MATERIALS AND METHODS

Rabbit stocks and selection

Two closed lines of rabbits (in this paper referred to as line B and line R) were used in the experiment. Founder animals in line B were chosen randomly from a base population of California rabbits (49 females and 14 males). Line R was a synthetic line created after 2 generations of crossing from a pool of animals of 3 commercial sire lines (71 females, 14 males). Animals were reproduced within a nested mating structure, avoiding matings of animals with common grandparents. Generations were discrete. Although animals from 2 different generations were not mated they could be contemporary, because the last litters of one generation were produced at the same time as the first litters of the next generation. The experiment was designed to have 20 males and 80 females per generation.

Selection for growth rate started in 1980 for line B and in 1984 for line R. Young animals were selected according to individual weight gain (WG) from weaning (4 wk old) to slaughter (11 wk old), referred to a seasonal mean and corrected by a moving average computed every 2 wk. Males were selected within their sire families in order to reduce inbreeding. Individuals were identified and weighed at weaning (WW) and slaughter (SW). Selection started when most of the does had 1 litter weaned. Selection continued for 2 months, so most of the replacement came from the first litters. Selection operated on an average of 240 candidates of each sex per generation.

At the end of the test, selected animals were culled for health problems independently of performance. Selected bucks and does were first mated at $\approx$ 20 wk of age, while later matings were made weekly 10 d after parturition. Females failing to conceive after 3 services were culled. Also, does could be culled at weaning

for health problems. Mating of close relatives was avoided; the maximum relationship of mates allowed was 0.125. Moreover, to minimize the rate of inbreeding, no more than 2 male progeny were selected from the same sire. The total number of generations, sires, dams and individuals per line is summarized in table I.

Table I. Numbers by line of generations (G), sires (S), dams (D) and individuals (I) at slaughter used in the experiment.

Line	G	S	D	I
B	12	210	751	7 718
R	9	177	640	9 391

All animals were housed on a single farm and reared in the same environment. Young rabbits remained in the dam's cage until weaning. Cross-fostering was not practised. Later, rabbits were placed in growing cages of 8 individuals and fed *ad libitum* with a standard granulated feed. Temperature inside the fattening units could range from 5–34°C.

Statistical methods

The following animal model was used to estimate environmental and genetic effects for each trait analyzed (WG, WW and SW) in each line (B and R):

$$Y_{ijkl} = m + s_i + l_j + a_k + p_l + e_{ijkl}$$

where m = overall mean; s_i = the fixed effect of the ith year–season at birth (each season consisted of 13 wk); l_j = the fixed effect of the jth litter size class born alive (litter size was coded in the following manner: line B, $j = 1$: $1 - 3$ newborn rabbits, $j = 2 - 11$: $4 - 13$, and $j = 12$: 14 or more. Line R, $j = 1$: $1 - 3$, $j = 2 - 12$: $4 - 14$, and $j = 13$: 15 or more); a_k = the random additive genetic effect of the kth animal; p_l = the random maternal effect of the lth doe on all its progeny (excluding dam additive effect); e_{ijkl} = the random error. No sex effect was included as there is no sexual dimorphism at this age (Gómez and Blasco, 1992).

All pedigrees were known so a complete relationship matrix was incorporated to account for the covariances between animal effects. Residual and maternal effects were assumed uncorrelated with each other and with animal effects. In order to reduce computational requirements, the model was fitted using an equivalent reduced animal model (Quaas and Pollak, 1980) and a single-trait pseudoexpectation approach to estimate variance components (Schaeffer, 1986). This is an iterative procedure based on quadratic forms similar to those used in the Residual Maximum Likelihood (REML) procedure (Patterson and Thompson, 1971). It gives and approximate REML solution, but it is less demanding in computing time (REML is very demanding because it requires inverting a large matrix, whereas the pseudoexpectation approach does not require any matrix inversion). However it is not totally free of selection bias as the REML solutions are. It seems to underestimate the parameters, although the bias is not large (Ouweltjes *et al*, 1988). As we did

not have facilities to maintain control lines, the averages of the individual genetic predictors in each generation were used to estimate genetic trends (Sorensen and Kennedy, 1984). The standard errors (SE) of the trends were calculated without taking genetic drift into account. Cummulative genetic responses were expressed as contrasts between base and final generations, and genetic drift was considered when calculating their standard errors (Sorensen and Kennedy, 1983). Environmental changes were estimated by using the estimable functions of year–season effects.

Realized phenotypic selection differentials per generation were obtained after correcting the data for the fixed effects included in the model described above and weighting for the number of progeny each individual contributed to the next generation (Falconer, 1989). Selection intensity was estimated by dividing the selection differentials by the standard deviation (SD) of adjusted phenotypic values. Inbreeding coefficients were computed for all animals using the algorithm described by Tier (1990).

Estimated responses were compared with those predicted by applying the algorithm of Wray and Thompson (1990) to the obtained selection intensities and inbreeding coefficients. This algorithm takes into account the reduction in genetic variance caused by gametic disequilibrium and inbreeding.

RESULTS

Overall means and standard deviations

Components of variance, estimated by the pseudoexpectation method, are shown in table II expressed as a proportion of phenotypic variances. These are the estimates of the base population before selection. SEs were not computed due to the high requirements in computing cost.

Table II. Additive genetic (h^2) and maternal variances (p^2) of each recorded trait, expressed as a proportion of phenotypic variance, and estimated by the pseudoexpectation method. Base population parameters.

	Line B			Line R		
Item	WW	SW	WG	WW	SW	WG
h^2	0.15	0.19	0.21	0.15	0.15	0.17
p^2	0.27	0.14	0.10	0.18	0.12	0.10

WW: weaning weight; *SW*: slaughter weight; *WG*: weight gain.

The overall means and standard deviations of traits after fitting random effects in the 2 lines are presented in table III. The means refer to the base generation genetic level and therefore they can be considered as the means at the beginning of the experiment. Line R was heavier at weaning than line B but its weight gain was less. These differences were somewhat more favourable to line B when only seasons

Table III. Estimated line means and phenotypic standard deviations (*SD*) of recorded traits in the base generation (in g), estimated by the BLUP animal model of the complete data.

Trait	Line B		Line R	
	Mean	*SD*	*Mean*	*SD*
WW	583	109	628	107
SW	2 220	282	2 233	278
WG	1 634	247	1 600	240

WW: weaning weight; SW: slaughter weight; WG: weight gain.

in common were taken into account. Phenotypic variances were also slightly higher in line B. Coefficients of variation ranged from 12.4–18.7%, the highest being for *WW* in line B.

Environmental influences

Figure 1 shows the effect of year–season on *WG*. The corresponding figures for *WW* and *SW* were very similar to figure 1. Environmental changes were dramatically influenced by the cyclical pattern of seasonal effects within years. The amplitude of the cycles could be as high as one phenotypic SD, as is the case of *SW* in line R, and ranged from ≈ 0.7 to 0.9 SD for *WG*. As expected, maximum values correspond to winter and minimum values to summer. Differences between 2 successive seasons could add up to 0.7 phenotypic SD for WG. Long-term environmental trends showed a significant increase in all cases. However, they were not monotonic and can be explained by a large husbandry improvement during 1984. At the end of that year the feed was improved and its quality remained similar for the last 4 yr of the experiment. The trend of year–season effects on time were nearly parallel in the 2 lines so there was no interaction between line and year–season.

Figure 2 shows the effect of litter size class on *WW* and *WG*. Linear regression of litter size effect on litter size was significant ($p < 0.05$) in line B and R for *WW* (-34.0 ± 2.8 and -30.0 ± 2.7) and for *SW* (-41.5 ± 3.3 and -37.4 ± 4.4) but was not significant for *WG*. Linear regression fitted well, the coefficient of determination being 0.85 or higher. Litter size effects were more important than year–season effects only for *WW*. SDs of year–season effects were 3.8 and 6.3-fold those corresponding to litter size class effects for *WG* in lines R and B respectively.

Genetic trends

Estimated genetic trends in each line are presented in table IV. Genetic trend was estimated as a linear regression of the average estimated breeding value on generation number. Cumulative estimated genetic responses are relative to the base level for foundation individuals of zero. As a univariate model has been applied for each trait, correlated responses could be biased (Johansson and Sorensen, 1990).
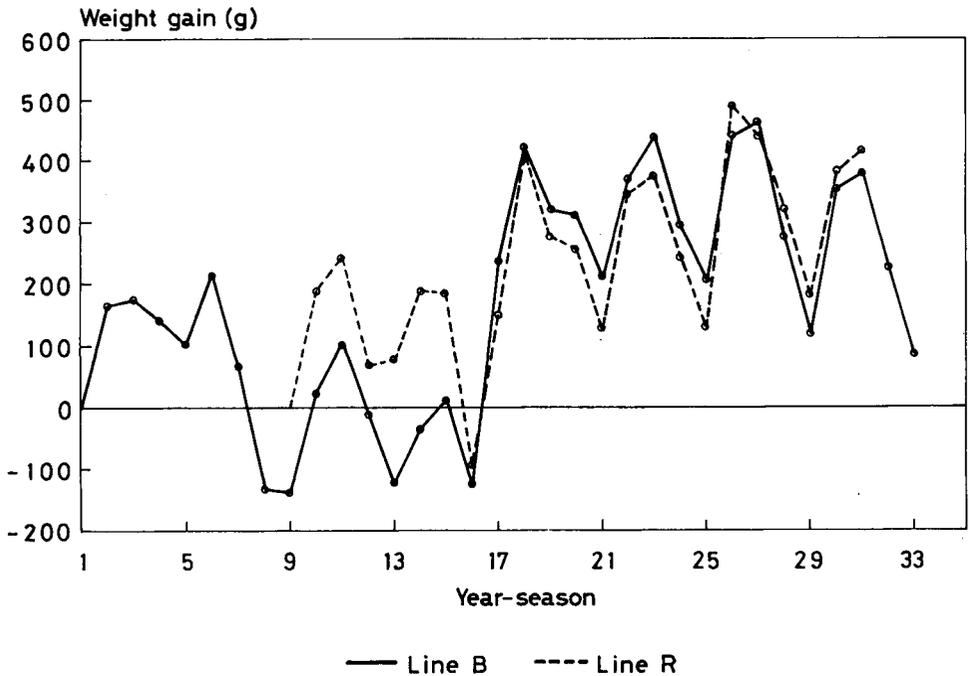
Fig 1. Environmental changes in weight gain from weaning to slaughter.

However, since correlations of WG with WW and SW are close to zero and unity respectively (Camacho, 1989), the bias should be small.

Direct responses for WG were significant and positive in both lines. Line B showed a higher rate of improvement per generation (2.0% of the base population mean in line B and 1.6% in line R) and on a year basis (2.7% *vs* 2.2%). Total genetic progress was 22.2% and 13.2% of the initial means in line B and R respectively. Genetic improvement in WG was mostly associated with a correlated gain in SW. Genetic change in WW was not statistically significant.

Selection differentials for individual selection, selection intensities and mean inbreeding coefficients for each sex and generation are shown in table V. Selection was 1.5–2-fold more intensive in males than in females. Rates of inbreeding per generation were 1.27% in line B and 0.81% in line R and are comparable to those predicted from theory (Wray and Thompson, 1990), and close to the predicted rate without selection (0.78%).

Responses based on realized selection intensities and inbreeding coefficients were also calculated (table V). Responses are predicted with a methodology which
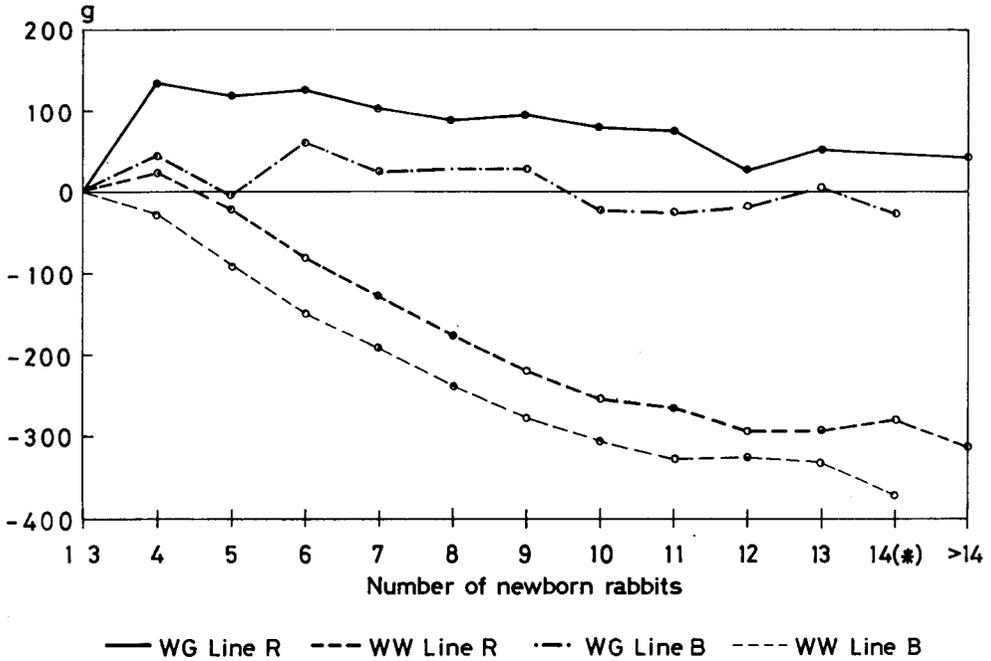
Fig 2. Litter size class effect on weaning weight (WW) and weight gain (WG).

Table IV. Linear genetic trend per generation for response (R) to selection on weight gain and cumulative genetic response (CR) of recorded traits in each line (in g). Values in parentheses are standard errors.

	Line B		Line R	
Trait	R	CR	R	CR
WW	− 1.1 (0.8)	− 22.8 (23.5)	0.3 (0.4)	− 0.9 (16.0)
SW	27.1 (1.4)	296.4 (62.4)	23.4 (1.5)	188.2 (41.7)
WG	32.0 (0.8)	362.0 (67.9)	25.7 (1.5)	210.8 (38.2)

WW: weaning weight; SW: slaughter weight; WG: weight gain.

Table V. Selection differentials (*SD*) for individual selection, selection intensities (*i*), cumulative inbreeding coefficients (*F*) and predicted responses (*R*) per generation for weight gain (in g), using estimated heritabilities of table II.

						Generation						
Item	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	
Line B												
						Males						
SD	282	282	254	257	211	264	283	239	243	192	281	
i	1.14	1.14	1.03	1.04	0.86	1.07	1.15	0.97	0.98	0.78	1.14	
F	0.00	0.00	0.01	0.04	0.05	0.07	0.08	0.09	0.09	0.10	0.12	
						Females						
SD	96	140	94	176	69	129	138	139	141	106	142	
i	0.39	0.57	0.38	0.71	0.28	0.52	0.56	0.56	0.57	0.43	0.58	
F	0.00	0.00	0.02	0.02	0.05	0.05	0.07	0.09	0.10	0.10	0.12	
												Total
R	39.7	41.9	33.2	40.5	25.7	35.8	37.7	33.2	33.5	26.0	36.5	383.7
Line R												
						Males						
SD	176	277	210	205	237	204	266	290				
i	0.73	1.16	0.88	0.85	0.99	0.85	1.11	1.21				
F	0.00	0.00	0.01	0.02	0.02	0.03	0.05	0.06				
						Females						
SD	111	241	186	128	177	128	114	137				
i	0.46	1.01	0.78	0.53	0.74	0.53	0.49	0.57				
F	0.00	0.00	0.01	0.01	0.02	0.03	0.04	0.05				
												Total
R	24.3	42.4	31.1	25.6	32.0	25.1	28.7	31.7				240.9

takes into account the reduction of the variance due to genetic disequilibrium and inbreeding (Wray and Thompson, 1990). Cumulative responses estimated by mixed model methodology (table IV) are found to be 5.9% (line B) and 14.3% (line R) lower than those predicted in table V.

DISCUSSION AND CONCLUSIONS

The use of mixed model methodology to measure genetic change without a control line has been criticized by Thompson (1986). He showed that the realized heritability estimates are highly dependent on the *a priori* parameters used in the estimation. When a control line is not available, Smith (1988) suggests estimating the *a priori* parameters iteratively by REML. Then, when the relationship matrix is complete and the animal model is used, the trend in estimated breeding value may give a reasonable approximation to the genetic response for traits of moderate to high heritability. This has been checked by Mrode *et al* (1989a, b) in beef cattle experiment with a control line.

Genetic responses achieved in both rabbit selection lines showed that individual selection on weight gain from weaning to slaughter age was effective. However, as in other rabbit selection experiments reported (Mgheni and Christensen, 1985; Rochambeau *et al*, 1989), responses were lower than the expected according to the experimental design. While expected responses per generation range from 3–4% of the mean, realized responses were only $\approx$ 1–2% of the mean per generation.

To explain the disagreement between expected and realized responses most authors implicate low selection intensities and maternal effects. Realized selection intensities per generation ranged from 0.570–1.085 (table V), averaging 0.765 for line B and 0.805 for line R. These values were 56.3% (line B) and 59.2% (line R) lower than that planned (1.360) for a population of 80 does and 20 bucks, each doe having 6 offspring and selecting one buck per sire.

Similar results were obtained by Rochambeau *et al* (1989) and are indicative of the difficulties in achieving high selection intensity in practice. Results obtained in this experiment and those outlined by Rochambeau *et al* (1989) showed that selection differentials were only $\approx$ 60% of those planned. Health problems and some particulars in the management of discrete generations are seen as major causes of failure to achieve the expected differentials. Since some diseases occurring in intensive rabbit units are difficult to control, mortality and culling rates of selected animals are important in comparison with other species. Thus, in some generations post-weaning mortality was as high as 30% and culling rates can reach similar values (Torres *et al*, 1987). As pointed out by Baselga *et al* (1988), there is some scope to improve genetic resistance to respiratory diseases by culling affected animals. Because the generations were discrete, selection was not continuous over time. Selection did not start until the number of individuals in the parental generation was close to the given number (480), so replacement animals could only be selected from among animals born later. All these factors tended to decrease theoretical selection differentials and therefore selection opportunities.

A more efficient alternative to individual selection is the use of the BLUP method (Wray, 1989; Wray and Thompson, 1990), because it permits a better seasonal and litter size class effect adjustment and an optimal use of family records. Especially when generations overlap and sequential culling is practised, BLUP produces substantially higher rates of genetic progress than individual selection (Belonsky and Kennedy, 1988). Though litter size class effects can be neglected when selection is on WG, season effects should always be considered.

Recording could be reduced if selection was made on *SW* instead of *WG*. The genetic correlation between the traits has been estimated to be near unity (Camacho, 1989) and there is also evidence that the genetic response in *WG* is associated with correlated response in *SW* (Estany *et al*, 1988b; Camacho, 1989; Rochambeau *et al* 1989). If that is the case, cross-fostering to equalize litter size would be worthwhile to reduce any maternal effect on *SW*. Otherwise, litter size must be taken into account in genetic evaluation models. The use of an index for improvement of *SW* using weights at earlier ages has been suggested (Khalil *et al*, 1986). However, if genetic parameters estimated in lines B and R for *WW* and *SW* are used it seems not to be worthwhile, as rates of response are expected to be improved by only $\approx$ 1% of the rate.

In an economic context growth rate must be considered in relation to other economic traits included in the breeding goal and, in particular, to feed efficiency, body composition and litter size. Unfortunately, estimates of the genetic effects of selection for growth rate on these traits are scarce and not very precise. Nonetheless, results reviewed by Rochambeau (1988) suggest that growth rate is generally well correlated genetically to them, in accordance with some results obtained in the present lines (Camacho, 1989; Blasco *et al*, 1990). Some attention, however, is required with regard to culling rates and failure to rear a litter observed in lines selected for growth rate (Torres *et al*, 1987; Rochambeau *et al*, 1989). Further research is needed to study the effects of selection for growth rate. However, it appears to be a good and simple criterion for improving rabbit sire line breeding stocks for a range of production systems.

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