WORLD RABBIT SCIENCE 2001, VOL.9 (2), 77-86.

VARIANCE COMPONENTS AND RESPONSE TO SELECTION FOR REPRODUCTIVE, LITTER AND GROWTH TRAITS THROUGH A MULTI-PURPOSE INDEX

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ABSTRACT : Variance components and genetic trends were estimated for number of services/parturition (NS), parturition interval (PI), number born alive (NB), number weaned/litter born (NW), litter weaning weight (LW), 30-d individual weaning (WW) and 70-d (W70) weights and a multiple-trait selection index (MI) in rabbits from a closed population in Botucatu, Southeast Brazil. Phenotypic values for two litter (NW and LWW), and two individual performance (WW and W70) traits were included in the index. Individual selection according to the multiple-trait index was practised for a 2.6-yr period (January 1992 through July 1994). Performance records collected for five years (July 1989 through July 1994) on 2,162 parturitions, 2,122 litters, and 10,440 individuals were included in the analyses. The general model used to estimate variance components and breeding values included the random effects of animal, maternal genetic, and permanent dam effects (for reproductive and litter traits) or common litter effects (for individual weight traits), and fixed effects of parity, parturition date, sex (for individual weight traits) and covariates of the inbreeding coefficient of the dam (for reproductive and litter traits) or of the rabbit and its dam (for individual weight traits). Inbreeding coefficients ranged from 0 to 0.36. For reproductive and litter traits, estimates of permanent dam effects ranged from 0.03 to 0.09 and estimates of direct heritability ranged from 0.02 to 0.05. The estimated genetic correlation between NS and PI was 0.73. For WW, W70, and MI, estimates of direct and maternal heritabilities and direct-maternal genetic correlation were 0.08, 0.08 and 0.28; 0.18, 0.05 and 0.76; and -0.35, 0.59 and -0.46, respectively. Estimated common litter effects for WW and W70 were 0.44 and 0.26, respectively. Estimates of direct genetic trends/yr for NS, PI, NB, NW and LW were -0.0037 ± 0.0003 services, -0.200 ± 0.030 d, 0.034 ± 0.010 young/litter, 0.039 ± 0.006 young/litter, and 35.2 ± 4.6 g, respectively. Estimates of direct and maternal genetic trends/yr were 6.74 ± 0.39 g and 1.58 ± 0.60 g for WW; 17.20 ± 1.22 g and 8.35 ± 0.71 g for W70; and 4.91 ± 0.65 and -2.34 ± 0.39 for MI. Individual weight traits showed meaningful genetic trends with multiple-trait selection, whereas reproductive and litter traits showed slight, but favourable genetic changes. It seems possible to achieve slow, but simultaneous improvement of litter and growth traits with a multiple-trait selection program in rabbits.

Les composantes de la variance et les paramètres génétiques ont été estimés pour le nombre d'accouplements nécessaires par mise bas (NS), l'intervalle entre deux mises bas consécutives (PI), le nombre de lapereaux nés vivants par portée (NB), le nombre sevrés par portée née (NW), le poids de portée au sevrage (LW), le poids individuel lors du sevrage à 30 jours (WW) puis à 70 jours (W70) et enfin pour un index de sélection multi-caractères (MI), chez des lapins élevés en population fermée à Botucatu dans le sud-est du Brésil. L'index de sélection comprend deux valeurs phénotypiques liées à la portée (NW et LW) et deux valeurs individuelles (WW et W70). Une sélection individuelle d'après la valeur de l'index multi-caractères a été effectuée pendant 2,6 années (de janvier 1992 à juillet 1994). La mesure des caractères a été effectuée sur une période totale de 5 ans, de juillet 1989 à juillet 1994. Les données collectées portent sur 2162 mises bas et 2122 portées. L'analyse des performances individuelles a été effectuée sur 10 440 lapereaux. Le modèle général utilisé pour estimer la variance et les paramètres d'élevage incluait d'une part les effets aléatoires de l'animal, de la génétique maternelle, ainsi l'effet maternel permanent (pour les caractères de reproduction ou relatifs à la portée) ou l'effet moyen de portée (pour les caractères individuels), et d'autre part les effets fixes de la parité, de la date de mise bas, du sexe (pour les poids individuels), ainsi que le coefficient de consanguinité de la mère (pour les caractères de reproduction ou reliées à la portées), ou des lapereaux et de leur mère (pour les caractères individuels) comme covariables. Les coefficients de consanguinité variaient de 0,0 à 0,36. Pour les caractères de reproduction ou relatifs à la portée, les estimées des effets permanents de la mère varient de 0,03 à 0,09. Les estimées de l'héritabilité directe varient de 0,02 à 0,05. L'estimation de la corrélation génétique entre NS et PI est de 0,73. Les estimations de l'héritabilité directe, de l'héritabilité maternelle et celle de la corrélation génétique entre les effets direct et maternel ont été de 0,08 – 0,08 et 0,28 pour WW, de 0,18 – 0,05 et 0,76 pour W70 et enfin de -0,35 de 0,59 et de -0,46 pour MI. Les estimées de l'effet commun de portée ont été 0,44 et 0,26 pour WW et W70 respectivement. Les estimées des effets génétiques annuels directs pour NS, PI, NB, NW et LW ont été de -0,0037 ± 0,0003 accouplements, -0,200 ± 0,030 jours, 0,034 ± 0,010 lapereaux nés par portée, 0,039 ±006 lapereaux sevrés par mise bas, et 35,2 ± 4,6 g respectivement. Les estimées des effets génétiques annuels directs et maternels ont été de 6,74 ± 0,39 g et 1,58 ± 0.60 g pour WW, de 17,20 ±1,22 et 8,35 ± 0,71 g pour W70 et enfin de 4,91 ± 0,65 et -2,34 ± 0,39 pour MI. Les caractères individuels pondéraux montrent une réponse génétique nette à la sélection avec l'index multi-caractères utilisé par les auteurs, tandis que les caractères de reproduction ou relatifs aux portées montrent une évolution génétique plus faible mais dans le sens favorable. Ainsi, grâce à une sélection avec un index multi-caractères il semble possible d'obtenir chez le lapin une amélioration lente mais simultanée des caractères relatifs aux portées et de ceux relatifs à la croissance.

INTRODUCTION

The conventional approach to a breeding program for meat rabbit production improvement has been the establishment of specialized lines through selection. Dam lines are frequently selected for litter size and sire lines for average daily gain from weaning to market age. These lines are subsequently combined in a crossbreeding program to obtain market fryers (ROCHAMBEAU, 1997; BASELGA, 1998). However, in countries where the rabbit industry has not yet reached a high level of organization, it may not be possible to select and maintain specialized sire and dam lines. An alternative approach could be the development of a multi-purpose line, achieved through simultaneous selection for prolificacy and growth performance traits.

Reported estimates of direct and maternal heritability for parturition interval and number of services/parturition are close to zero, indicating that selection for these traits would be rather ineffective (BASELGA, 1983, 1998; KHALIL and SOLIMAN, 1989). Although selection for litter size has been effective, response to long-term selection for this trait has been lower than expected (MGHENI and CHRISTENSEN, 1985a; VANGEN, 1993). It was hypothesised that inbreeding depression partially masks the accumulated genetic progress; when lines independently selected for litter size are crossed, the total progress is uncovered (ROUVIER, 1991). Selection for increased growth rate and market weight, on the other hand, has effectively improved these traits (MGHENI and CHRISTENSEN, 1985 b; LUKEFAHR *et al.*, 1996; MOURA *et al.* 1997; ROCHAMBEAU *et al.*, 1998). Nevertheless, long-term selection for growth rate has also been shown to decrease fitness due to inbreeding depression and unintended changes in adult body weight and age at maturity (ROCHAMBEAU *et al.*, 1989; HOLDER *et al.*, 1999). For example, in rabbits, selection for higher growth rate can increase adult weight and produce new giant breeds which are late maturing and prone to leg disease (BLASCO *et al.*, 1998).

Weaning and 70-day individual weights are traits of economic relevance in the breeding of rabbits for meat production. The relative importance of maternal and direct additive effects for growth traits should be considered in rabbit breeding programs because maternal genetic and common litter effects can be much larger than direct additive effects for weaning weight and even for market weight (FERRAZ and ELER, 1994; LUKEFAHR *et al.*, 1996, MCNITT and LUKEFAHR, 1996).

The objectives of this study were to estimate variance components and genetic trends for fertility related, and litter and individual performance traits in a rabbit population selected according to a multiple-trait index.

MATERIAL AND METHODS

Location and Management

The experiment was conducted at the Rabbit Production Unit of the "Faculdade de Medicina Veterinária e Zootecnia", UNESP, located in Botucatu, Southeast Brazil (at a latitude of 22 º South). The maternity facility consisted of an open, east-west oriented building equipped with 150 commercial wire cages (0.80 x 0.60 x 0.45 m) fitted with metal feeders, and nipple drinkers. Light, ventilation, and temperature were natural except for a plastic adjustable curtain protecting against a predominant south wind.

Males and females were first mated at 150 and 120 days of age, respectively. Matings were performed continuously, on a daily basis, five days a week (Monday through Friday). Ventral palpation was performed 10 to 12 days after mating to determine pregnancy. Does that failed to conceive were remated on the next weekday. Parturition-mating interval was 10 to 15 days. Each breeding buck hutch was adjacent to eight female cages. The females from those cages were mated to the same buck for 40 days. Males were then moved to the next group of females. This rotation of males was repeated every 40 days to assure that mating pairs were randomly formed. Doe culling criteria included three consecutive reproductive failures, whereas buck's included lack of libido and low fertility. Does and bucks were culled if health problems such as sore hocks, respiratory trouble, wryneck or abscesses occurred. Culled animals were replaced with young selected seed stock. Number born alive was recorded within 16 h after kindling and cross fostering was not practised. Litters were weaned at 30 d of age and transferred to a growing facility, structurally similar to the maternity building. After receiving an identification, litters were mixed and the young rabbits were randomly assigned to wire cages, eight per cage. A pelleted ration containing approximately 18% CP, 2,750 kcal DE/ kg and 12% CF was available on an *ad libitum* basis to all animals.

Population and Selection Program

The Botucatu rabbit is an albino, medium-sized line, descendant of Norfolk 2000 hybrids imported from England in 1971. Further information on the origin of the hybrids were provided elsewhere (MOURA *et al.*, 2000). The population has been kept closed during at least 15 generations of local adaptation with approximately 120 dams and 15 sires. Non-systematic selection and avoidance of matings between close relatives were practised from 1971 to 1991. Facility and resource constraints precluded the development of maternal and paternal specialized lines from the Botucatu rabbit population. In January 1992, a selection program was initiated based on the multiple-trait index proposed by POLASTRE *et al.* (1989). During the selection period, matings between close relatives were not avoided and generations overlapped. Parent-offspring and brother-sister matings may have occurred at times due to the above-mentioned system of rotation of breeding bucks. Emphasis was placed on litter size and market weight, but the index combined phenotypic values of four traits:

I_x = - 8084 - 1157 (number weaned) - 0.733 (individual weaning weight) + 3.202 (litter weaning weight) + 2.19 (70-d weight)

where I_x is the phenotypic value of the multiple-trait index for individual x.

Table 1 : Descriptive statistics for number of services/parturition (NS), parturition interval (PI), number born alive (NB), number weaned (NW), litter weaning weight (LW), individual weaning (WW), 70-d (W70) weights, multiple-trait index (MI) and respective covariates[a]

Trait	Number of records	Mean	SD	CV	Range
NS[b]	2,162	1,317	0.637	48.4	
Dam inbreeding		0.0587	0.0554		0 to 0.33
PI, d	1,630	49.49	15.18	30.7	
Dam inbreeding		0.0557	0.0540		0 to 0.33
NB	2,122	6.66	3.14	47.1	
NW	2,122	4.80	3.02	62.9	
LW, g	2,122	2,922	1,763	60.3	
Dam inbreeding		0.0588	0.0554		0 to 0.33
WW, g	10,440	680.4	132.9	21.84	
Dam inbreeding		0.0559	0.0523		0 to 0.33
Rabbit inbreeding		0.0803	0.0578		0 to 0.36
W70, g	9,170	1,890	253	13.39	
MI	9,170	-2.15	20.80	-968.55	
Dam inbreeding		0.0567	0.0525		0 to 0.33
Rabbit inbreeding		0.0805	0.0578		0 to 0.36

[a] Total of 133 sires and 551 dams.
[b] A square-root transformation was performed on this trait, but numbers in the table were back transformed.

The index was based on genetic parameters estimated from the Selecta breed by the paternal half-sib intra-class correlation method (POLASTRE *et al.*, 1991, 1992b). Selecta was an albino medium-sized breed that originated from a pool of other breeds (New Zealand White, Californian, Bouscat Giant) and the Norfolk hybrid, in a commercial rabbit farm during the 1970's (MOURA *et al.*, 1991). Relative economic weights were 100, 1, 5, and 10, respectively, for the four traits. The correlation between the index and the aggregate breeding value was estimated at 0.738. Selection was applied to the individual progeny. An additive adjustment factor for parity was adopted mainly to compensate for the lower performance of litters originated from the first parturition of a female. Additive adjustment factors for month of birth were also used but were less important because comparisons were made among contemporary animals. Approximately 28% of the females and 11% of the males were first selected at 70 d of age up to July 1994. Prior to reproduction, selected animals were inspected; those presenting health problems or visible defects were immediately culled.

Estimation of (co)variance components

A computer program developed by POLASTRE *et al.* (1992a) was used to store data, to assist selection, and to compute inbreeding coefficients according to WRIGHT (1922) and MALECOT (1948). Selection was initiated in 1992 but performance records had been collected for five years (July 1989 through July 1994), in order to account for the base population and selection generations. Data on 2,162 parturitions and 1,630 parturition intervals from 551 does were included in the analyses of number of services/parturition (NS) and parturition interval (PI). A square root transformation was adopted for the former variable. Does were born between February 1989 and February 1994. Records on 2,122 litters for number born alive (NB), number weaned/litter born (NW), and litter-weaning weight (LW) were included in the analyses of litter traits. For individual weights, 10,440 records for weaning weight (WW) and 9,170 records for 70 d weight (W70) and the multiple-trait index (MI) were included. Pedigree data of the population traced back to 1987. Descriptive statistics for all traits and respective covariates are presented in Table 1. The relationship matrix included 890 individuals for reproductive and litter traits and 10,615 for individual traits. Variance and covariance components were estimated by using the Multiple Trait Derivative Free Restricted Maximum Likelihood Program (BOLDMAN *et al.*, 1993). A bivariate model was employed for NS and PI, whereas univariate models were adopted for the other traits, all of the general form

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \in$$

where

y is the vector of observations, β is the vector of fixed effects, **a** is the vector of random additive genetic effects, **m** is the vector of random maternal genetic effects, **c** is a vector of uncorrelated random effects, **X**, $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are incidence matrices relating β, **a**, **m**, and **c** to y, and $\in$ is the vector of random residual effects.

Four alternative models were employed for estimation of (co)variance components, depending on the traits considered:

Model 1 (NS and PI, NB, NW, LW) - included the fixed effects of parity (12 levels), parturition date (yr-mo combination, 62 levels), and the covariate for inbreeding coefficient of the dam; the random additive genetic, and uncorrelated permanent dam effects;

Model 2 (NB, NW, LW) - included the fixed effects of parity (12 levels), parturition date (yr-mo

Table 2 : Estimates of direct heritability (h^2_d), permanent dam effects (c^2), phenotypic standard deviation (psd), direct genetic trend and regression coefficient for dam inbreeding (b_d) of, and direct genetic (r_g), permanent dam (r_c), and residual correlations (r_e) between number of services per parturition (NS) and parturition interval (PI) from Model 1[a]

Trait	h^2_d	c^2	psd	r_g	r_c	r_e	b_d[b]	Genetic trend b ± SE (P-value)
NS	0.03	0.03	0.2285				0.15	-0.0037 ± 0.0003 (0.000)
				0.73	0.87	0.71		
PI, d	0.02	0.04	14.61				-5.95	-0.200 ± 0.030 (0.002)

[a] Model 1 included the fixed effects of parity, parturition date, and the covariate for inbreeding coefficient of the dam; the random additive genetic, and uncorrelated permanent dam effects.
[b] Change in the corresponding trait if the inbreeding coefficient increases from 0 to 1.

combination, 62 levels), and the covariate for inbreeding coefficient of the dam; the random additive and maternal genetic effects, and the direct-maternal correlation;

Model 3 (WW, W70, MI) - included the fixed effects of parity (12 levels), parturition date (yr-mo combination, 61 levels), sex (2 levels), and the covariates for inbreeding coefficient of the rabbit and of its dam; the random additive and maternal genetic effects, and the direct-maternal correlation.

Model 4 (WW, W70, MI) - included the fixed effects of parity (12 levels), parturition date (yr-mo combination, 61 levels), sex (2 levels), and the covariates for inbreeding coefficient of the rabbit and of its dam; the random additive and maternal genetic effects, the direct-maternal correlation, and uncorrelated common litter effects.

Single trait models were first run to obtain initial values for the two-trait model. Convergence was considered to have been reached when the variance of function values (-2 log L) in the simplex was less than 10^{-9}. Successive runs were carried out to ensure convergence to a global maximum. No convergence was attained with Model 4 for MI.

The estimable functions of parturition date or birth date effects obtained from the mixed-model analyses were plotted to illustrate environmental changes. Average annual breeding values were regressed on dam's, litter's or rabbit's year of birth to estimate linear genetic trends. For each trait, genetic trends were based on the estimates from the model that showed the best fit (i.e., the lowest log likelihoods).

RESULTS AND DISCUSSION

Average inbreeding of all weaned rabbits increased at an annual rate of 1.44% between 1989 and 1994, and 92.3% of all weaned rabbits in that period were inbred. The estimated regression coefficients for inbreeding covariates (Tables 2, 3 and 4) show the change in the corresponding trait if the inbreeding coefficient increases from 0 to 1. Inbreeding of dam was negatively associated with litter traits (Table 3) and MI, but positively associated with WW and W70 (Table 4). Inbreeding of rabbit was negatively associated with WW, W70 and MI (Table 4). Given the large number of inbred rabbits and the unfavourable association between inbreeding and most performance traits, the inclusion of inbreeding covariates in the models seemed appropriate; otherwise, the expected merit of a parent with a large number of inbred progeny could be underestimated.

Table 3 : Estimates of direct heritability (h^2_d), maternal heritability (h^2_m), direct-maternal correlation (r_{dm}), permanent dam effects (c^2), phenotypic standard deviation (psd) and regression coefficients for dam inbreeding (b_d) from alternative models, and direct genetic trend for number born alive (NB), number weaned (NW) and litter weaning weight (LW)

Trait	h^2_d	h^2_m	r_{dm}	c^2	psd	b_d[a]	Genetic trend b ± SE (P-value)
Model 1[b]							
NB	0.05	_	_	0.09	3.029	-4.20	0.034 ± 0.010 (0.023)
NW	0.03	_	_	0.09	2.893	-3.21	0.039 ± 0.006 (0.003)
LW, g	0.03	_	_	0.07	1,684.4	-1,565	35.2 ± 4.6 (0.002)
Model 2[c]							
NB	0.18	0.05	-0.78	_	3.062	-4.23	_
NW	0.13	0.04	-0.78	_	2.915	-3.57	_
LW, g	0.09	0.05	-0.66	_	1,691.4	-1,684	_

[a] Change in the corresponding trait if the inbreeding coefficient increases from 0 to 1
[b] Model 1 included the fixed effects of parity, parturition date, and the covariate for inbreeding coefficient of the dam; the random additive genetic, and uncorrelated permanent dam effects.
[c] Model 2 included the fixed effects of parity, parturition date, and the covariate for inbreeding coefficient of the dam; the random additive and maternal genetic effects, and the direct-maternal correlation.

Variance Components

Estimated genetic, phenotypic and environmental parameters for NS and PI are provided in Table 2. Direct heritability and permanent dam

Table 4 : Estimates of direct heritability (h^2_d), maternal heritability (h^2_m), direct-maternal correlation (r_{dm}), common litter effect (c^2), phenotypic standard deviation (psd) and regression coefficients for the rabbit (b_r) and its dam (b_d) inbreeding for weaning weight (WW), 70-d weight (W70) and multiple-trait index (MI)

Trait	h^2_d	h^2_m	r_{dm}	c^2	psd	b_r[a]	b_d[a]
Model 3[b]							
WW, g	0.48	0.25	-0.39	_	132.12	-29.2	127.1
W70, g	0.39	0.11	-0.45	_	263.82	-220.1	227.8
MI	0.28	0.76	-0.46	_	25.10	-30.8	-24.0
Model 4[c]							
WW, g	0.08	0.18	-0.35	0.44	134.16	-17.8	117.1
W70, g	0.08	0.05	0.59	0.26	252.53	-193.1	145.1

[a] Change in the corresponding trait if the inbreeding coefficient increases from 0 to 1

[b] Model 3 included the fixed effects of parity, parturition date, sex, and the covariates for inbreeding coefficient of the rabbit and of its dam; the random additive and maternal genetic effects, and the direct-maternal correlation.

[c] Model 4 included the fixed effects of parity, parturition date, sex and the covariates for inbreeding coefficient of the rabbit and of its dam; the random additive and maternal genetic effects, the direct-maternal correlation, and uncorrelated common litter effects.

variance represented small proportions of the total phenotypic variance for NS and PI; however, genetic, permanent dam and residual correlations between these traits were positive and high. For NS, BASELGA (1983, 1998) reported heritability estimates to be null (based on literature reviews) when matings were performed once a week, on a fixed day, which differed from the daily schedule adopted in the present study. In Egypt, estimates of 0 and 0.17 ± 0.14 were obtained for NS with Bouscat and Giza White rabbits, respectively, in an every-other-day mating schedule (KHALIL and SOLIMAN, 1989). Our estimate of heritability for PI is in agreement with the range of estimates reported involving a semi-intensive reproductive rate (i.e., 10 to 20 d parturition-mating intervals, LEBAS *et al.*, 1996), which was between 0.01 and 0.10 (BASELGA 1983, 1998).

From Model 1, estimates of permanent dam effects for NB, NW, and LW were twice to three times as high as estimates of direct heritability (Table 3). Direct heritability estimates from Model 2 are higher than those from Model 1, and are likely to be overestimated because permanent dam effects were ignored. These results corroborate those of another study conducted in Brazil with New Zealand White and Californian rabbits (FERRAZ and ELER, 1994). In that study, estimates of permanent dam effects ranged from 0.02 to 0.13, and were at least of the same magnitude as heritability estimates, which ranged from 0 to 0.13. In specialized dam strains, ROCHAMBEAU *et al.* (1994, 1998) reported heritability estimates for similar traits to be between 0.03 and 0.08, whereas GÓMEZ *et al.* (1998) reported higher values for NB (0.13) and NW (0.08). Maternal heritabilities estimated in an alternative analysis for NB, NW and LW (Model 2) were between 0.04 and 0.05 for all three traits. A strong antagonism between direct genetic and maternal genetic effects was revealed in this analysis by the high and negative estimates of correlation of -0.66 and -0.78.

Estimates of direct heritability for WW and W70 from the complete model (Model 4) coincided at 0.08 (Table 4), but were lower than expected. FERREIRA *et al.* (1999), in a comparison of several model designs, showed that the inclusion of maternal genetic effects with genetic correlation between direct and maternal effects and permanent environmental effect resulted in lower estimates of direct heritability of birth, weaning and yearling weights in beef cattle. The estimate of maternal heritability of WW (Model 4) surpassed that of W70. Common litter effects accounted for more variation in individual weights at both ages than did additive and maternal genetic effects, but seemed to have reduced its relative importance with the advancement of age. These results confirm the relevance of maternal effects, both genetic and environmental, for WW, but also suggest their gradual reduction after weaning. The direct-maternal genetic correlation was negative for WW, but positive for W70. Negative relationships between direct and maternal genetic effects for weaning weight have been established in other species (DICKERSON, 1947; FERREIRA *et al.*, 1999) and may reflect the antagonism between growth and maternal ability. In contrast, FERRAZ and ELER (1994) reported a value close to zero for this correlation in Californian rabbits. However, they included linear and quadratic effects of litter size at weaning in the model, which may partially explain this lack of agreement. Although Model 4 show the best fit for WW and W70, no convergence was attained for MI. Presumed complex genetic relationships among litter and individual performance traits (GÓMEZ *et al.*, 1998) in addition to the negative genetic correlations between direct and maternal effects for litter and individual traits may partially explain this difficulty. High estimates of direct and maternal heritabilities for WW, W70 and MI (Table 4) were obtained from the alternative model (Model 3). They may be overestimated because common litter effects were ignored. An antagonism was also revealed between direct and maternal genetic effects by the negative direct-maternal correlation.

Environmental Changes

Environmental changes in NS and PI reflected a cyclic, seasonal pattern within years for both traits. Maximum annual peaks in NS (approx. one phenotypic SD) and PI (0.7 to 1.7 SD) occurred between March and June each year, which corresponds to the second half of the decreasing day length period in the Southern hemisphere. Minimum peaks were less evident, but seemed to be concentrated in late winter and early spring months (from July through September) for both traits. A larger number of services were required per conception in the winter months in Egypt, compared to fall and spring for native and exotic breeds of rabbits, but no matings were performed in the summer (KHALIL and SOLIMAN, 1989).

Seasonal effects of temperature and length of daylight on doe reproduction and milk production were evident on the environmental changes in NB, NW and LW. A striking minimum peak, common to all three traits, observed in July 1991, was attributed to a suspected feed toxin. It was responsible for a large number of abortions, stillbirths and an increase in pre-weaning mortality, causing drastic reductions in NB, NW, and LW. Overall, during the selection period (from January, 1992 through July, 1994), the amplitude of the fluctuations diminished and a slight decline seem to have occurred for all three traits.

Environmental changes for WW, W70 and MI largely reflect seasonal variation due to temperature (Figure 1). Overall, fluctuations for WW and MI decreased after selection started, probably due to a more standardised management, but a declining environmental trend was observed for W70. A possible explanation is that prior to selection, the breeding stock was moved into an entirely new facility. With the advancement of selection, overcrowding became a problem and, consequently, environmental conditions may have slowly deteriorated.

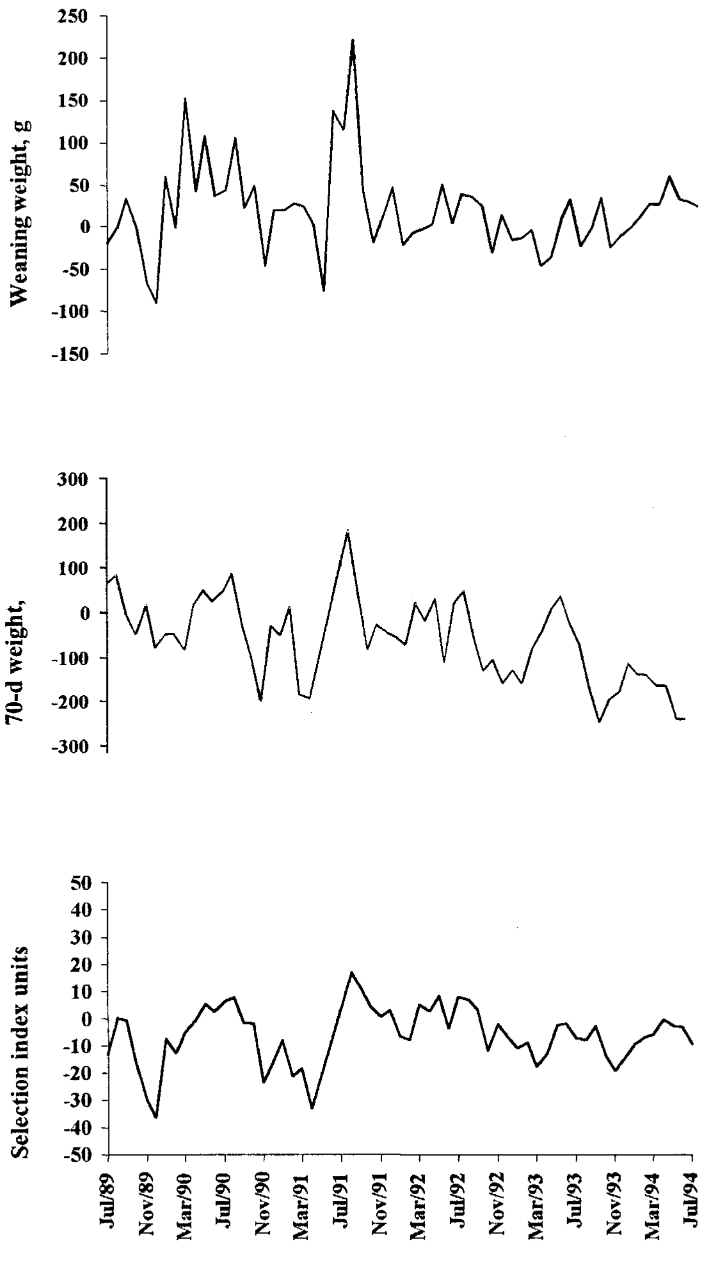

Figure 1 : Environmental changes in 30-d weaning and 70-d weights and in the multiple-trait selection index

Response to selection

Genetic trends for NS and PI are consistent with low estimates of heritability and a high estimate of genetic correlation, which anticipated slight, but favourable, parallel changes (Table 2). Estimated annual direct genetic trends for NB, NW, and LW (Table 3) were positive and significant, indicating that the response to selection was favourable. The estimated trend was more pronounced for NW and LW, traits included in the selection index, than for NB. The average trend for NW, of approximately 0.04 young/litter per yr, is in the lower range of responses obtained with European dam lines. Spanish and French specialized lines, after being submitted to long-term selection exclusively for NB or NW, presented average responses in the range of 0.03 to 0.13 young/litter per generation with generation intervals ranging from 9 to 12 mo (GÓMEZ and SANTACREU, 1996; ROCHAMBEAU *et al.*, 1998).

Estimated genetic trends for WW, W70 and MI are illustrated in Figure 2. A positive direct linear trend was observed for WW, but no maternal linear trend was detected. It is likely that the negative direct-

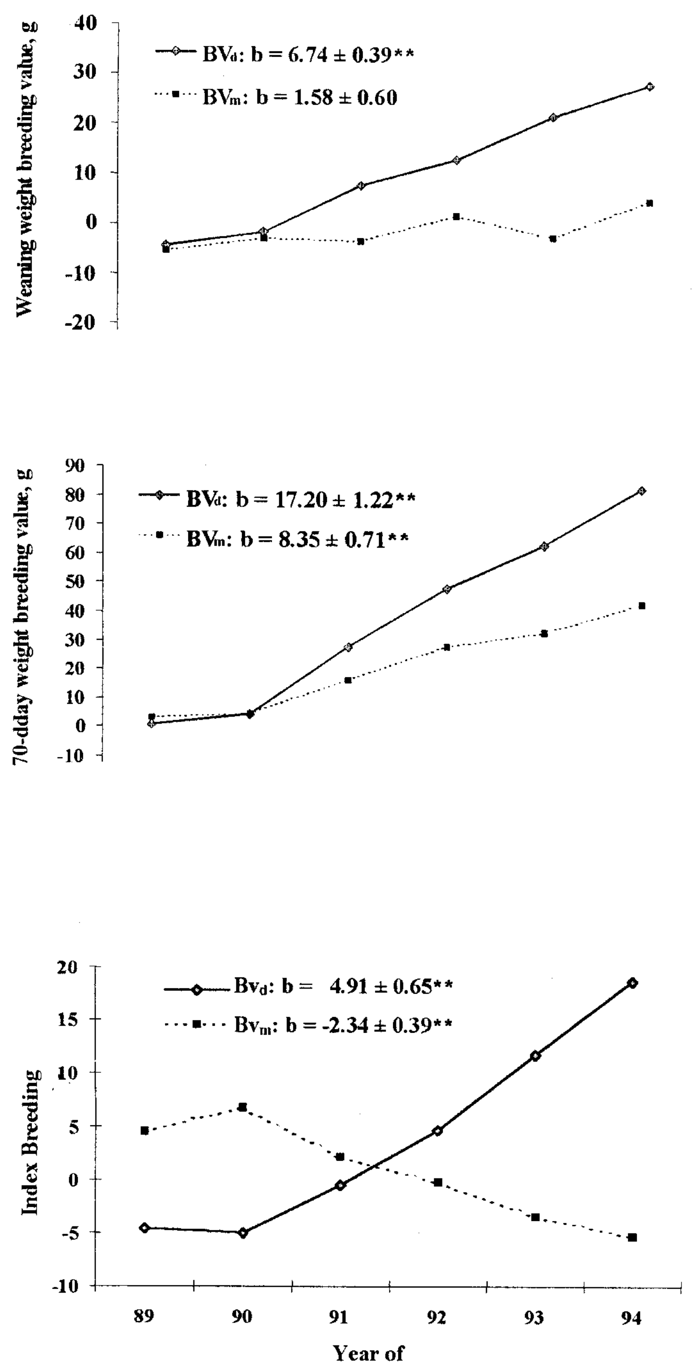

Figure 2 : Estimated direct (BV_d) and maternal (BV_m) genetic trends for weaning (upper panel) and 70-d (central panel) weights and multiple-trait index (lower panel)

maternal genetic correlation diminished the direct response to selection for WW. A negative correlation has been often pointed out as one of the causes of response to selection below that expected in long-term selection experiments with rabbits (BASELGA, 1998). Direct and maternal linear trends were favourable for W70, suggesting a more consistent response to selection for this trait, which received a higher relative economic weight in the selection index. Specialized paternal lines selected exclusively for growth rate for several generations presented average linear trends ranging from 23.4 to 29.1 g/generation with a generation interval of six months (ESTANY *et al.*, 1992, LUKEFAHR *et al.*, 1996), which is higher than the values obtained in the present study. A positive direct and a negative maternal trend were observed for MI, reflecting the antagonism between direct and maternal effects.

Based on an average theoretical selection intensity of 1.46 (28 % of the females and 11% of the males), POLASTRE *et al.* (1989) estimated expected responses to MI selection in the Selecta breed to be 0.031 young, 35.4g, 263g and 185g per year for NW, WW, LWW, and W70, respectively. Direct genetic trends estimated in this study are only 5 to 10% of these values, except for NW. Selection intensity below that expected, in addition to the antagonism between direct and maternal effects, may decrease response to selection (ROCHAMBEAU *et al.*, 1989).

No indication of fertility impairment as a consequence of combined short-term selection for litter and individual growth performance traits was detected in the present study. Model adjustment for dam inbreeding, culling of does after three consecutive reproductive failures, as well as the short selection period could have contributed to these results. Studies combining prolificacy and growth traits into a multi-purpose line were not very frequent in rabbits. Some lines ended up, after a few generations, in focusing on either growth rate or litter size. Selection for litter weight at 60 d of age emphasised growth rate predominantly (RAFEL *et al.*, 1990). In selecting for a complex trait, total litter weight at weaning per doe per yr ROCHAMBEAU *et al.* (1988) emphasised litter size predominantly. Long-term selection experiments, in which single-trait selection was practised over several generations, have often been associated with fertility impairment. ROCHAMBEAU *et al.* (1989) reported decreased fertility and shortened reproductive life span from a study involving 12 generations of selection for average daily gain in rabbits. The authors attributed reduced fitness to inbreeding depression, because the effective number of individuals per generation was small. Six generations of selection for litter size at two weeks of age also affected fertility unfavourably (NARAYAN *et al.*, 1985). Accumulation of inbreeding in lines selected for litter size has been shown to partially mask the response to selection (ROUVIER, 1991) and could, therefore, affect fertility. Accordingly, a large number of studies in mice have reported a decline in fitness, including fertility problems resulting from unidirectional long-term selection for body weight as reviewed by BRIEN (1986). Inbreeding depression and decreased fitness of extreme phenotypes were among the presumed causes of poor male libido and female sterility. It is possible that with short-term multiple-trait selection, as practised in the present study, a weak genetic correlation between the selected and unselected fitness traits prevailed, whereas long-term selection for growth traits may generate a stronger negative correlation with fitness and the cessation of response to selection (BARRIA and BRADFORD, 1981). Therefore, if selection had been carried out for a longer period of time, undesirable effects on fertility traits could have arisen.

In countries where the rabbit industry has not yet reached a high level of organization, it may not be possible to select and maintain specialized sire and dam lines for a subsequent crossbreeding program. An alternative could be the development of a multi-purpose line, through simultaneous selection for prolificacy and growth performance traits. Genetic trends for reproductive, litter and growth traits from the present study suggest that it is possible to achieve slow, but simultaneous improvement of litter and growth traits with a multiple-trait selection program in rabbits. This approach, albeit less efficient than the conventional one, would be justifiable in such special circumstances.

Acknowledgements : This research project has been partially funded by grants from CNPq, FAPESP and FUNDUNESP, Brazil. The authors would like to thank Mrs. Irene F. Arruda for technical assistance.

Received : February 12th, 2001
Accepted : June 4th, 2001

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