Genetic Improvement Of Litter Size In Rabbits

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Introduction

Breeding programs in rabbits are more recent than those developed in other species. In France and Spain breeding programs began in the seventies (Matheron (1982) and Estany et al. (1989)) and since then a large number of reviews have discussed the advances made in this area (Rouvier (1980); Baselga et al. (1982); Matheron (1982); Matheron and Poujardieu (1984); Rochambeau (1988); Blasco (1996); Garreau et al. (2004); Baselga (2004); Khalil and Al-Saef (2008)).

Fortunately, gone are the days when Matheron (1982) complained about the absence of genetic experiments involving litter size. Since then, the number of selection experiments dealing with litter size improvement has increased considerably. In this paper, an overview of the advances made on selection on litter size in rabbits is given.

Direct selection for litter size

Litter size in rabbits is considered as one of the most important economic components on intensive meat production (Armero and Blasco (1992); Eady and Garreau (2008)). Most of the maternal lines are selected by litter size at weaning (Table 1) since this trait reflects both the prolificacy as well as the milking and nursing ability of the doe.

Nowadays, there is no doubt that the heritability of litter size is low, around 0.10 (for a review see Blasco (1996); Garreau et al. (2004); among others). Responses estimated were below 0.1 rabbits per generation (Table 1). These results are in agreement with those found in pigs by several authors (reviewed by Rothschild and Bidanel (1998)).

The increase observed in litter size after numerous generations of selection was usually due to an increase in ovulation rate (0.18 oocytes/generation in line V and 0.8 oocytes in 13 generations of selection in line A1077; García and Baselga (2002a) and Brun et al. (1992), respectively). However, this response was likely due to a decrease in foetal mortality in other line studied (line A; García and Baselga (2002b)).

Hyperprolific lines. When selection is performed in closed lines, as usually happens in rabbits and pigs, responses are greatly penalized since large selection intensities cannot be

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This study was supported by MCYT AGL2008-05514-C02-01

Table 1. Direct and correlated responses to direct selection on litter size at weaning (LSW) or number of born alive (NBA).

Line	Generations studied	Selection criterion	Estimated response (rabbits/gen)	Method of selection	Methodology used to estimate the response	Correlated response	Authors
V	15-21	LSW	0.085	BLUP	Cryopreserved control	Ovulation rate	García and Baselga (2002a)
V	0-21	LSW	0.09 (0.003)	BLUP	BLUP/REML		
A	17-26	LSW	0.085	INDEX	Cryopreserved control	Foetal survival	García and Baselga (2002b)
A	1-26	LSW	0.175 (0.0034)	INDEX	BLUP/REML		
Prat	3	LSW	0.09 per year	BLUP	BLUP/REML		Gómez et al. (1996)
1077	18	LSW	0.07	INDEX	BLUP/REML		Rochambeau (1998)
1077	18	LSW	0.08	INDEX	Control	Ovulation rate*	
2066	18	NBA	0.12	INDEX	BLUP/REML		Rochambeau (1998)

* Response was estimated by Brun et al. (1992) after 13 generations of selection.

Table 2. Estimates of heritabilities and genetic correlations (standard error) in rabbits.

	Heritability			Genetic correlation				
	OR	PS	LS	OR-LS	PS-LS	OR-PS	OR-ES	OR-FS
Blasco et al. 1993	0.21 (0.11)	0.23 (0.10)	0.27 (0.21)	0.36 (0.31)	0.87 (0.08)	-0.14 (0.35)	0.04 (0.45)	-0.41 (0.39)
Bolet et al. 1994	0.24 (0.04)	0.08 (0.06)	0.11 (0.03)					
Laborda et al. 2010	0.16 (0.05)	0.09 (0.05)	0.09 (0.03)	0.29 (0.19)		-0.43 (0.27)	-0.12 (0.31)	-0.51 (0.27)

OR: ovulation rate; PS: prenatal survival; LS: litter size; ES: embryo survival; FS: foetal survival.

applied. Many hyperprolific selection experiments have been carried out in pigs obtaining successful results (for a review see Rothschild and Bidanel (1998)). To our knowledge, only one hyperprolific line has been founded so far in rabbits (Cifre et al. (1998)). In this experiment a large selection intensity was applied. The hyperprolific does were required to have a parity with 17 or more young born alive or to be included in the group of the best 1% when all parities were considered. Responses in litter size were estimated by comparison to the V line. It was observed that the hyperprolific line (H) showed higher litter size at birth and weaning from third parity onward. At this time the H line is being selected by litter size at weaning.

These puzzling results obtained after selection for litter size in closed populations led to the search for alternative methods of selection: experiments of selection for uterine capacity and ovulation rate for improving indirectly litter size, development of two experiments of canalising selection: on litter size and on birth weight. On the other hand, the increase of litter size has led to undesirable effects in some selection lines which have driven the creation of maternal lines selected for new traits. These topics will be discussed in the next sections.

Selection for components of litter size: ovulation rate and uterine capacity.

An approach to increasing litter size is to select for its components, ovulation rate (OR) and prenatal survival (PS). Fertilization rate, generally, exceed 90 to 95% and is not considered as a limiting factor to increasing litter size. Prenatal losses are the mayor limiting factor of litter size in rabbits, like in pigs and mice. Approximately 30 % of ova shed are lost during prenatal development (Adams (1960); Blasco et al. (1993)). Around 10-14% of the total losses occur before implantation time (day 7 of gestation) while post-implantation mortality (fetal mortality) comprises around 20-23% of the total losses (Adams (1960)).

Genetic parameters. The efficiency for improving litter size depends on the genetic parameters of its components. There are very few estimates of genetic parameters for OR and PS in rabbits (Table 2). Ovulation rate has higher heritability than litter size, but this heritability is lower than in pigs and mice (Blasco et al. (1993); Rosendo et al. (2007)). Genetic correlation between OR and litter size is positive and low. Prenatal survival has a low heritability similar to litter size, and a high correlation with litter size. The low estimate of heritability is close to the values published in pigs (0.11, Rosendo et al. (2007)) and mice (Clutter et al. (1990)). The strong correlation between PS and litter size agrees with other estimates published in pigs (see review by Blasco et al. (1993) and Rosendo et al. (2007)).

Few selection experiments for components of litter size have been reported in rabbits: two divergent selection experiments for uterine capacity and one selection experiment for OR.

Selection for uterine capacity (UC). The first genetic parameters estimated (Blasco et al. (1993)) suggested that prenatal survival could be a good candidate to improve more efficiently litter size in rabbits. Selection for increase UC was proposed as a mean to change

PS (Bennet and Leymaster, (1989)). Uterine capacity was defined by Christenson et al. (1987) as the maximum number of fetuses that the female is able to support at birth when ovulation rate is not a limiting factor. In rabbits, Blasco et al. (1994) proposed using unilateral ovariectomy to measure uterine capacity.

Two divergent selection experiments for UC were performed in rabbits. In the experiment 1, selection was performed on number of dead fetuses from implantation to birth. After 4 generations of selection it was observed that the number of dead fetuses did not change and no significant response was obtained in litter size and its components (Bolet et al.(1994)). In the experiment 2, selection was made on litter size in unilateral ovariectomized females, which includes both embryo and fetal survival. Selection for UC through 10 generations was successful, although it does not seem to be more effective than direct selection for litter size. In mice, similar results have been obtained (Kirby and Nielsen (1993)). Analyses based on genetic trends showed that divergence in UC between lines was 1.5 rabbits born (Blasco et al. (2005)). Response was asymmetric; no differences were found between the High and a cryopreserved control line, whereas the Low and control lines differed by 1.08 kits (Mocé et al. (2005)). The correlated response on litter size was also asymmetric and divergence between both lines was 2.35 kits. The Low uterine capacity line had 1.88 kits less than the control line, while the High uterine capacity line differed with the control line in 0.5 kits. (Santacreu et al. (2005)). The correlated response in litter size in the Low line was associated with a lower PS (at least 7%). The major part of the embryo mortality was produced before 72 hr of gestation. Moreover, embryos from Low line had a less advanced stage of development at 72 hr of gestation than embryos from High line (Mocé et al. (2004)).

A complex segregation analysis performed by Argente et al. (2003) found evidence of major genes with a moderate effect on uterine capacity and a large effect on number of implanted embryos. A F2 population was created by reciprocal mating between the two lines divergently selected for uterine capacity in order to identify SNPs for five candidate genes. The most relevant results were found for progesterone receptor gen (PGR). One SNP was found in the promoter region, 2464G>A. The GG genotype, the genotype more frequent in the High line, had 0.5 kits and 0.5 implanted embryos more than AA genotype. Also, GG genotype showed less expression of progesterone receptor than AA genotype (Peiró et al. (2010)).

Selection for ovulation rate. Only one selection experiment for ovulation rate has been carried out so far in rabbits. After eight generations of selection, OR increased in 1.21 ova (0.15 ova/generation) but the correlated responses per generation in litter size and number of implanted embryos were 0.04 kits and 0.10 embryos (Laborda et al. (2010)). The correlated response in litter size was low, and similar to the response obtained in other experiments of selection for litter size in rabbits (Table 1). The low response in litter size was due to a correlated decrease in embryo, fetal and prenatal survival (1%, 3% and 4%, respectively). These results were similar to those obtained after selection for ovulation rate in pigs (Johnson et al. (1984); Rosendo et al. (2007)) and mice (Bradford (1969); Land and Falconer (1969)). A two-stage selection experiment for ovulation rate and litter size is being carried out in Valencia. Animals belonging to the 6th generation of the rabbit line selected for ovulation rate were used for the creation of this new line. It is likely that prenatal survival will be increased by selecting for litter size females which have been previously selected for ovulation rate.

Selection to reduce the variability in litter size

Litter size in politocous species shows a high variability. In theory, if environmental variability of the litter size decreases, its heritability will increase in turn, and therefore response to selection will also increase. The underlying idea is that environmental variation of a trait can be determined in part by genes (San Cristobal et al. (1998)). In order to unravel the genetic of the environmental variance for litter size in rabbits, a novel divergent selection experiment for environmental variability of litter size is currently carried out in Spain. After three generations of divergent selection, results show that environmental variance of litter size appears to be under genetic control, and environmental variance seems to be negatively correlated with litter size (Argente et al. (2010)). These results are encouraging, although results from more generations will be necessary to achieve a definitive conclusion.

Canalising selection for rabbit birth weight

Many authors have observed that variability for birth weight within a litter is high in rabbits (Bolet et al. (1996); Argente et al. (1999)) and pigs (Quesnel et al. (2008)). Mortality on heterogenous litters is bigger than mortality on homogenous ones (in rabbits; e.g. Poigner et al. (2000); in pigs; Mesa et al. (2006)). Furthermore, some studies in pigs showed that losses from birth to weaning were moderately genetically linked with an increase in the within-litter variability in birth weight (Wolf et al. (2008); Damgaard et al. (2003)). Based on the previous results, it is likely that pre-weaning survival and therefore, litter size at weaning, will increase if heterogeneity in birth weight is reduced. However, this strategy could not be risk exempt since unfavourable genetic correlation seems to exist between number of piglets born alive and within-litter variability of birth weight (Wolf et al. (2008); Damgaard et al. (2003)). Thus, a decrease in the heterogeneity in birth weight in the litters could provoke a negative effect on the litter size. On the other hand, in rabbits Argente et al. (1999) did not find phenotypic correlation between litter size and the within-litter variability in birth weight. The divergent selection experiment on within-litter homogeneity of birth weight that is being carried out in France (Garreau et al. (2003)) will be helpful to better understand all these issues.

After 7 generations of selection, the difference in standard deviation for birth weight between lines was 19% of the standard deviation mean (Bolet et al. (2008)). The response was asymmetrical, since higher response was obtained in the homogeneous line. Besides, most of the response was obtained in the first generation of selection because a higher selection intensity was applied (Garreau et al. (2008)). A favourable correlated response for litter size at weaning and for survival from birth to weaning was also observed, although number of born alive was not significantly different between the two lines (Bolet et al. (2008)). Once again, results obtained are promising but more generations are needed to draw conclusions.

Litter size and weight at weaning.

There are very few estimates of genetic correlations between litter size and growth traits. Last studies show positive and negative correlations but generally low (García and Baselga (2002a); Garreau et al. (2000); Gómez et al. (1998)). On the other hand, it is known that the size of the litters affects growth traits of the young rabbits from birth to weaning (e.g. Drummond et al. (2000); Poigner et al. (2000)) as well as the productive performance of the future reproductive females (Rommers et al. (2001)). Thus, larger litters show a lower average birth weight, lower birth-to–weaning growth rate, and a higher mortality than smaller litters.

In a study conducted in a line selected for litter size at weaning for 20 generations, no correlated responses on growth traits were observed (García and Baselga (2002a)). The correlated response was estimated by comparison to a cryopreserved control population and litter size at birth was included as a covariate in the model. These authors concluded that selection for litter size at weaning did not worsen the genetic potential of the rabbits to growth. However, Brun and Ouhayoun (1994) observed lower weaning and adult weight in the line A1077 versus its control line in the 13 generation. In agreement with these results, Rochambeau (1998) reported that the individual weight at weaning decreased after 18 generations of selection for litter size in lines A1077 and A2026 (-3.4g and -4.4g per generation, respectively). These results brought about the modification of the selection objectives and the line 1077 was selected for both number of born alive at birth and individual weight at 63 days from generation 23 onwards. After 9 generations of selection, a positive correlated response on weaning weight (+60 g) was observed, although a negative genetic trend of maternal effects on weaning weight (-10 g) was also noticed (Garreau and Rochambeau (2003)). These results led to the creation of a new line, 1777, derived from the line 1077. This new line is selected for number of born alive at birth and direct and maternal effects on weaning weight. The weights given to each of the characters are 0.50 for the maternal effect and 0.25 for each of the others. Although results obtained in the first three generations seem promising (0.13 born rabbits per generation and 7.5 and 7.2 gr for the direct and maternal effects of weaning weight per generation; Garreau et al. (2005)). Results from more generations will be necessary to reach a definitive conclusion.

Conclusion

In rabbit, the response in litter size has been low using both direct and indirect selection. Two novel experiments of canalising selection are being developed for improving more efficiently litter size. Results obtained in both experiments are promising but more generations are necessary to reach definitive conclusions.

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