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Selection for ovulation rate in rabbits: Direct and correlated responses estimated with a cryopreserved control population¹

P. Laborda,*² M. A. Santacreu,* A. Blasco,* and M. L. Mocé*³

*Instituto de Ciencia y Tecnología Animal, Universidad Politécnica de Valencia, 46071 Valencia, Spain

ABSTRACT: The aim of this work was to evaluate the response in 10 generations of selection for ovulation rate in rabbits using a cryopreserved control population. Selection was based on the phenotypic value of ovulation rate estimated at d 12 of second gestation by laparoscopy. To produce the control population, embryos from 50 donor females and 18 males, belonging to the base generation of the line selected for ovulation rate, were recovered. A total of 467 embryos (72-h embryos) were vitrified and stored in liquid N₂ for 10 generations. The size of both populations was approximately 10 males and 50 females. The number of records used to analyze the different traits ranged from 99 to 340. Data were analyzed using Bayesian methodology. A difference between the selected and the control populations of 2.1 ova (highest posterior density interval (HPD_{95%})

[1.3, 2.9]) was observed in ovulation rate (OR), but it was not accompanied by a correlated response in litter size (LS; -0.3; HPD_{95%} [-1.1, 0.5]). The number of implanted embryos (IE) increased with selection in 1.0 embryo (HPD_{95%} [-0.6, 2.0]), but this increase was not relevant. Prenatal survival, embryonic survival, and fetal survival (FS) were calculated as LS/OR, IE/OR, and LS/IE, respectively. Prenatal survival was reduced with selection (-0.12; HPD_{95%} [-0.20, -0.04]), basically because of a decrease in FS (-0.12; HPD_{95%} [-0.19, -0.06]). Embryonic survival could have slightly decreased (-0.05; HPD_{95%} [-0.12, 0.02]). In summary, comparison with a control population showed that ovulation rate in rabbits increased with selection without any correlated response in litter size, basically because of a decrease in fetal survival.

Key words: cryopreserved control population, fetal survival, litter size, ovulation rate, rabbit, selection

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INTRODUCTION

Selection for ovulation rate has been unsuccessful as a means of indirectly improving litter size in pigs (Cunningham et al., 1979; Rosendo et al., 2007; Leymaster and Christenson, 2000) and mice (Land and Falconer, 1969; Bradford, 1969), despite the increase in ovulation rate. The lack of correlated response in

litter size has been associated with an increase in the postimplantation mortality [see Bradford (1969) for mice and Freking et al. (2007) for pigs]. Response to selection for ovulation rate in rabbits was assessed in previous studies using predicted genetic trends (Laborda et al., 2011, 2012). Predicted genetic trends have the disadvantage of being dependent on the model and on the estimated genetic parameters of the traits analyzed (Sorensen and Johansson, 1992). The limited number of data in this type of experiment and the scarce number of experiments lead to estimation of genetic parameters with high SE, especially genetic correlations; therefore, the correlated responses estimated with genetic trends have low precision. For inference, information from the estimated genetic trends can be complemented with the results obtained from the comparison between a control population and the selected population. Control populations are less model depen-

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²Corresponding author: patlavi@dca.upv.es

³Present address: Departamento de Producción Animal y Ciencia y Tecnología de los Alimentos, Universidad Cardenal Herrera-CEU, Edificio Seminario, 46113 Moncada, Valencia, Spain.

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dent, but they depend on the limited experimental facilities that should be shared by the selected and the control populations. Cryopreserved control populations are less common in selection experiments, although they present lower genetic drift and absence of unintended selection, allowing a better use of the facilities (Hill, 1972).

The aim of this study was to estimate direct response to selection for ovulation rate and correlated responses on litter size and its components by contrasting the selected population to a cryopreserved control population.

MATERIALS AND METHODS

All experimental procedures involving animals were approved by the Polytechnic University of Valencia Research Ethics Committee.

Animals

Animals came from an experiment of selection for ovulation rate described by Laborda et al. (2011) and from a cryopreserved control population, detailed below. The ovulation rate line was selected for 10 generations; then, selection was relaxed for 1 generation. Females from generation 11 of the selected line and females from the control population were used to assess direct and correlated responses. Animals of both populations were housed at the experimental farm of the Universidad Politécnic de Valencia in individual cages. They were kept under controlled 16 h light:8 h dark photoperiods and fed a commercial diet. Matings were planned to avoid inbreeding. Laparoscopies were performed on all does at d 12 of their second gestation. Details of the technique are given by Santacreu et al. (1990).

Embryo Transfer and Control Population

To produce the control population, embryos from 50 donor females and 18 males, belonging to the base generation of the line selected for ovulation rate, were recovered. Details of the process of embryo recovery are available in Mocé et al. (2009). A total of 467 embryos (72-h embryos) were vitrified and stored in liquid N₂ until transfer. Embryos were vitrified and thawed according to the method described by Vicente et al. (1999). Recipient females (n = 40) were nulliparous females of 19 to 20 wk of age, synchronized by intramuscular administration of 1 mg buserelin acetate (Hoechst; Marion Roussel, Madrid, Spain) 21 d before the transfer. Only females that presented vulva color associated with receptive status were induced to ovulate with a second administration of buserelin acetate. The second dose was administered 60 to 63 h before transfer (Vicente et al., 1999). To perform the transfers, rabbits were anesthetized with an intramuscu-

lar administration of xylazine (Rompun 2%; Bayer AG, Leverkusen, Germany) at a rate of 4 mg/kg BW; 5 min later an intravenous dose of ketamine HCL and chlorbutol (Imalgène 500; Merial S.A., Lyon, France) at a rate of 15 to 30 mg/kg BW was administered in the marginal ear vein. Embryo transfers were performed by using the laparoscopic technique described by Besenfelder and Brem (1993).

After parturitions, 1 to 2 daughters from each recipient female were randomly selected. Males were selected within each male family (i.e., 1 son of each male was selected). The control population consisted of 45 does and 10 males. This control population was contemporary to the 10th generation of the line selected for ovulation rate. To eliminate the possible effects of cryopreservation, the control does were mated to produce the next generation; 1 to 2 daughters from each female were randomly selected, and a total of 54 control females contemporary to generation 11 of the selected line were obtained. Males were selected within each male family. Animals from the control population contemporary to generation 11 of the selected line were used to assess direct and correlated responses.

Traits

Litter size (**LS**) was estimated as the total number of kits born per litter; the number of kits born alive per litter (**NBA**) and the number of kits weaned per litter (**NW**), together with LS, were measured in a maximum of 4 parities in each female. Ovulation rate (**OR**), estimated as the number of corpora lutea in both ovaries, and the number of implanted embryos (**IE**), estimated as the number of implantation sites, were measured by laparoscopy at d 12 of second gestation. Both the right and the left ovulation rates (**ROR** and **LOR**) and number of implanted embryos (**RIE** and **LIE**) were measured. Ovulatory difference (**OD**) was defined as the difference between the ROR and LOR, expressed as an absolute value; implantatory difference (**ID**) was defined as the difference between RIE and LIE, expressed as an absolute value. Embryonic survival (**ES**) was calculated as IE/OR, fetal survival (**FS**) was calculated as LS/IE, and prenatal survival (**PS**) was calculated as LS/OR. Females had a second postmortem measurement of OR, ROR, LOR, and OD. The BW of the female was measured at d 12 of second gestation, at laparoscopy time (**WOR**). The number of females and number of records used to analyze the traits in the selected and the control populations are shown in Table 1.

Statistical Analysis

Bayesian inference was used. The model assumed for OR, ROR, LOR, OD, LS, NBA, and NW was

Table 1. Number of records used to analyze the traits ovulation rate (OR), right and left ovulation rates (ROR and LOR), ovulatory difference (OD = |ROR – LOR|), litter size (LS), number of kits born alive (NBA), number of kits weaned (NW), number of implanted embryos (IE), number of implanted embryos on the right and left uterine horns (RIE and LIE), implantatory difference (ID = |RIE – LIE|), embryonic survival (ES), fetal survival (FS), prenatal survival (PS), and weight at second gestation (WOR) in the selected and control populations

Population	Trait											
	OR	OD, ROR, LS,	LOR	NBA	NW	IE	ID, RIE,	LIE	ES	FS	PS	WOR
Control (n = 54)	91	88	162	162	48	46	48	47	48	48		
Selected ¹ (n = 56)	92	92	178	177	53	53	53	52	52	53		

¹Here n = number of females.

$$y_{ijklmn} = \text{Line}_i + L_j + P_k + YS_l + p_{im} + e_{ijklmn}$$

where Line_i is the effect of the line (2 categories: control and selected), L_j is the effect of lactation state of the doe (2 categories: lactating and nonlactating does when mated), P_k is the effect of parity (4 categories for LS, NBA, and NW; 2 categories for OR and OD), YS_l is the effect of year-season (3 categories), p_{im} is the permanent environmental effect of doe, and e_{ijklmn} is the residual of the model. The model for IE, RIE, LIE, ID, ES, FS, PS, and WOR had neither the parity effect nor the permanent environmental effect of doe because records came only from the second parity, and the year-season effect had only 2 categories. Bounded uniform priors were used for all unknowns with the exception of the permanent effect, which was considered normally distributed with mean 0 and variance $I\sigma_p^2$, where I is a unity matrix and σ_p^2 is the permanent effect variance of the trait. Residuals were normally distributed with mean 0 and variance $I\sigma_e^2$. The priors for the variances also were bounded uniform positive.

Features of the marginal posterior distribution of differences between line means were estimated by using the Gibbs sampling algorithm. Chains of 1,000,000 samples each were used, with a burning period of 200,000. One sample out of each 50 was saved to avoid high correlations between consecutive samples. Monte Carlo SE were small. Convergence was tested using the Z criterion of Geweke.

RESULTS AND DISCUSSION

Table 2 shows raw means and SD for the traits measured in the control population; the values of the traits OR, LS, NBA, NW, IE, and survival rates are in agreement with values published by other authors in maternal rabbit lines

Table 2. Means, SD, SE, and units of ovulation rate (OR), right and left ovulation rates (ROR and LOR), litter size (LS), number of kits born alive (NBA), number of kits weaned (NW), number of implanted embryos (IE), number of implanted embryos on the right and left uterine horns (RIE and LIE), ovulatory difference (OD = |ROR – LOR|), implantatory difference (ID = |RIE – LIE|), embryonic survival (ES), fetal survival (FS), prenatal survival (PS), and adult weight at second gestation (WOR) in the control population

Trait	Mean	SD	SE	Unit
OR	14.4	2.2	0.2	ova
ROR	7.6	2.4	0.3	ova
LOR	6.7	2.3	0.2	ova
OD	3.5	2.6	0.3	ova
LS	9.2	2.9	0.2	kits
NBA	8.3	3.3	0.3	kits
NW	6.8	3.3	0.3	kits
IE	11.8	3.1	0.5	embryos
RIE	6.0	2.3	0.4	embryos
LIE	5.9	2.5	0.4	embryos
ID	3.4	2.6	0.4	embryos
ES	0.84	0.18	0.03	—
FS	0.85	0.15	0.02	—
PS	0.70	0.17	0.02	—
WOR	4211	494	72.5	g

(Brun et al., 1992; García et al., 2001; García and Baselga, 2002; Piles et al., 2006; Theau-Clement et al., 2009; Ragab and Baselga, 2011). The value of WOR agrees with other estimates of pregnant female BW in commercial rabbit lines (for example, see Feugier and Fortun-Lamothe, 2006; Martínez-Vallespín et al., 2011). No values for the traits OD and ID have been found in the literature.

Features of the marginal posterior distributions of the differences between the selected and control populations for the traits measured are presented in Tables 3, 4, 5, and 6. We considered a relevant response to selection (value **R**) when the difference between populations (value **D**) was at least 10% of the mean of the control population [i.e., an increase of 1% per generation (10 generations)]. Using Bayesian inference, we can calculate the probability of the difference between populations being greater or less than zero (P_0) and the probability of having a relevant response to selection (P_R), which is the probability of the difference being greater than the value R when D is positive or less than R when D is negative.

Ovulation Rate

As shown in Table 2, OR was 14.4 in the control population. A difference between the selected and control populations of at least 1.4 ova (value R; Table 3) was expected to assess that response to selection had been

Table 3. Features of the estimated marginal posterior distributions of the differences between the selected and the control lines for ovulation rate (OR), right and left ovulation rates (ROR and LOR), ovulatory difference (OD = |ROR – LOR|), and weight at second gestation (WOR)¹

Trait (unit)	D	HPD _{95%}	R	P ₀	P _R	k
OR (ova)	2.1	1.3, 2.9	1.4	1.00 ^a	0.95 ^a	1.4 ^a
ROR (ova)	0.8	-0.1, 1.4	0.8	0.98 ^a	0.49 ^a	0.1 ^a
LOR (ova)	1.4	0.6, 2.0	0.7	1.00 ^a	0.98 ^a	0.8 ^a
OD (ova)	-0.6	-1.4, 0.1	-0.3	0.94 ^b	0.76 ^b	0.0 ^b
WOR (g)	267	101, 441	420	1.00 ^a	0.04 ^a	115 ^a

¹D = posterior mean of the difference between the selected and the control population, HPD_{95%} = greatest posterior density interval of the difference at 95%, R = 10% of the mean of the control population (1% per generation, 10 generations), P₀ = probability of D being ^agreater than zero or ^bless than zero, P_R = probability of response (probability of D being ^agreater than R or ^bless than R), and k = limit for the interval ^a[k, +∞) or ^b(-∞, k] having a probability of 95%.

successful. There was a difference of 2.1 ova between the selected and control populations (value D; Table 3), which represents an increase of 1.5% per generation. The probability of this difference being greater than R was 0.95 (Table 3). This was a relevant response, at least 1.4 ova (k = 1.4; Table 3). The response estimated with genetic trends was 1.3 ova in Laborda et al. (2011). A small response to selection was observed in ROR (D = 0.8 ova, P₀ = 0.98; Table 3). In LOR, the difference between populations was 1.4 ova (k = 0.8 ova; Table 3), showing a relevant response in the left ovary (P_R = 0.98; Table 3). The response in ROR is similar to the response estimated by Laborda et al. (2011; 1.1 ova). The genetic trend of LOR estimated by Laborda et al. (2011) showed a correlated response to selection of 0.5 ova, but the genetic correlation between OR and LOR was estimated with low precision (highest posterior density interval [HPD_{95%}; 0.23, 1.00]). Therefore, no conclusions regarding the response in LOR can be drawn.

Adult BW at second gestation increased 267 g with selection (Table 3). This difference was positive with a probability of 1.00 but did not reach 10% of the mean of the control population (Table 3). When the variable WOR was used as a covariate to analyze OR, the difference between lines in OR practically did not change (from 2.1 to 1.8). Quirino et al. (2009) reported a genetic correlation between OR and WOR of 0.49 in the same rabbit line; however, no other study has been found dealing with genetic correlations between OR and BW of the adult female rabbit.

Number of Implanted Embryos

The IE increased with selection (1.0 embryo; Table 4), but the probability of this difference being greater than R was low (0.36; Table 4), showing no relevant

Table 4. Features of the estimated marginal posterior distributions of the differences between the selected and the control line for the number of implanted embryos (IE), number of implanted embryos on the right and left uterine horns (RIE and LIE), and implantatory difference (ID = |RIE – LIE|)¹

Trait (unit)	D	HPD _{95%}	R	P ₀	P _R
IE (embryos)	1.0	-0.6, 2.0	1.2	0.92 ^a	0.36 ^a
RIE (embryos)	0.5	-0.4, 1.5	0.6	0.86 ^a	0.42 ^a
LIE (embryos)	0.4	-0.6, 1.5	0.6	0.80 ^a	0.37 ^a
ID (embryos)	-0.8	-1.8, 0.0	-0.3	0.97 ^b	0.89 ^b

¹D = posterior mean of the difference between the selected and the control population, HPD_{95%} = greatest posterior density interval of the difference at 95%, R = 10% of the mean of the control population (1% per generation, 10 generations), P₀ = probability of D being ^agreater than zero or ^bless than zero, and P_R = probability of response (probability of D being ^agreater than R or ^bless than R).

correlated response in IE. Little can be said about the correlated responses in RIE and LIE (see P_R in Table 4) because of their large HPD_{95%} interval. It seems that the correlated response in RIE agrees with the genetic trend (0.8 embryos; Laborda et al., 2012). The correlated response in LIE should be taken with caution as it happens with the response in LOR.

Laborda et al. (2011, 2012) suggested that an increase in OD could have been related to the lacking correlated response in LS in the line selected for OR. The increase in OD together with the absence of embryo uterine transmigration could have caused an associated increase in ID, disfavoring FS and therefore PS in the overcrowded uterine horn. The estimated genetic correlation of OR with ID was positive; however, no correlated response was observed on ID after 10 generations (Laborda et al., 2012). Moreover, the genetic correlation of ID with PS and LS was estimated with low precision, and nothing could be concluded. Contrary to what was expected, in this experiment, OD and ID were less in the selected population than in the control population (P₀ = 0.94 and P₀ = 0.97 in Tables 3 and 4, respectively). The difference between populations in OD and ID had a probability of obtaining a relevant response against the selected population of 0.76 and 0.89, respectively. These results should be taken with caution because of the large HPD_{95%} intervals and because OD and ID are highly variable traits (coefficients of variation of 74% and 77%, respectively; calculated from Table 2).

Survival Rates

Prenatal survival was lower in the selected population than in the control population (D = -0.12 ova, P₀ = 1.00; Table 5). It had a probability of 87% of being less than -0.07 (value R; Table 5), indicating a relevant correlated response in PS against the selected line.

Table 5. Features of the estimated marginal posterior distributions of the differences between the selected and the control lines for embryonic survival (ES), fetal survival (FS), and prenatal survival (PS)¹

Trait	D	HPD _{95%}	R	P ₀	P _R	k
ES	-0.05	-0.12, 0.02	-0.08	0.91 ^b	0.17 ^b	0.01 ^b
FS	-0.12	-0.19, -0.06	-0.08	1.00 ^b	0.86 ^b	-0.06 ^b
PS	-0.12	-0.20, -0.04	-0.07	1.00 ^b	0.87 ^b	-0.05 ^b

¹D = posterior mean of the difference between the selected and the control population, HPD_{95%} = greatest posterior density interval of the difference at 95%, R = 10% of the mean of the control population (1% per generation, 10 generations), P₀ = probability of D being ^agreater than zero or ^bless than zero, P_R = probability of response (probability of D being ^agreater than R or ^bless than R), and k = limit for the interval ^a[k, +∞) or ^b(-∞, k] having a probability of 95%.

Most of the response in PS was due to a decrease in FS. There was a difference of -0.12 between lines (value D; Table 5), having a probability of 0.86 of being relevant. Embryonic survival had a probability of 91% of being less in the selected than in the control population (D = -0.05; Table 5) and was responsible for the low correlated response observed in IE. However, this correlated response was not relevant (P_R = 0.17; Table 5). Laborda et al. (2012) observed no correlated response estimated with genetic trends in ES because the genetic correlation between OR and ES was close to 0; however, this correlation was estimated with low precision. Responses in FS and PS estimated with the cryopreserved control population were similar to the responses estimated with genetic trends. The possible causes for the decrease in PS were discussed by Laborda et al. (2011, 2012).

Litter Size

In rabbits, direct response to selection for LS has been usually close to 1% per generation (see review in Mocé and Santacreu, 2010). Selection for OR should have a greater response than direct selection for LS to be considered as an alternative. Litter size, NBA, and NW presented no relevant differences between the selected and control populations (0.06, 0.13, and 0.10, respectively; Table 6). These results corroborate the results obtained by Laborda et al. (2011) with genetic trends, where no correlated response to selection was observed in LS.

In rabbits selected for OR, the genetic correlation between OR and LS was estimated with low precision, as in the experiments of selection for OR in other polytocous species [see Cunningham et al. (1979) and Rosendo et al. (2007) for pigs and Bradford (1969) and Land and Falconer (1969) for mice]. Therefore, conclusions about its value should be taken with caution. However, the correlated response in LS estimated with the control population supports the idea that the correlation between OR and LS should be close to 0; the use of a control population

Table 6. Features of the estimated marginal posterior distributions of the differences between the selected and the control lines for litter size (LS), number of kits born alive (NBA), and number of kits weaned (NW)¹

Trait	D	HPD _{95%}	R	P ₀	P _R	k
LS (kits)	-0.3	-1.1, 0.5	-0.9	0.74 ^b	0.06 ^b	0.4 ^b
NBA (kits)	-0.3	-1.2, 0.6	-0.8	0.74 ^b	0.13 ^b	0.5 ^b
NW (kits)	-0.2	-0.9, 0.6	-0.7	0.68 ^b	0.10 ^b	0.5 ^b

¹D = posterior mean of the difference between the selected and the control population, HPD_{95%} = greatest posterior density interval of the difference at 95%, R = 10% of the mean of the control population (1% per generation, 10 generations), P₀ = probability of D being ^agreater than zero or ^bless than zero, P_R = probability of response (probability of D being ^agreater than R or ^bless than R), and k = limit for the interval ^a[k, +∞) or ^b(-∞, k] having a probability of 95%.

strengthens the results obtained with genetic trends for most of the traits, giving evidence of the adequacy of the model and the genetic parameters estimated.

In conclusion, comparison with a control population shows that 10 generations of selection for OR in rabbits has increased OR in about 2 ova, but it has not been accompanied by a correlated response in litter size, mainly because of a decrease in FS.

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