IS SEXUAL RECEPTIVITY OF THE DOES A HERITABLE TRAIT? PRELIMINARY RESULTS IN DIVERGENT SELECTION SCHEME

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ABSTRACT

Sexual receptivity of the does at insemination greatly influences fertility and is generally induced by hormones or by technical devices called "bio-stimulations". In the research context of more sustainable farming systems, an original alternative would be to exploit the genetic pathway to increase the receptivity level of the does at insemination. The purpose of the present experiment was to estimate the heritability of rabbit does receptivity and to test a divergent selection scheme on sexual receptivity. The experiment spanned two generations, the founder generation (G0) made of 140 rabbit does and the G1 generation comprising two divergently selected lines with 70 does each. The selection rate of the G0 females to form the G1 lines was 24/140. The selection tests consisted in 18 successive receptivity tests at the rate of three per week. A total of 4695 tests from 273 females were analyzed. The average receptivity was 56.5%. The heritability of Ri, the elementary performance (the 0/1 result of a single test) was estimated at 0.01±0.02 from an animal model and at 0.02 from the sire and dam variance components. The heritability of the average receptivity of a doe was 0.05±0.02 with an animal model and 0.08 from the sire and dam variance components. In agreement with the low estimated heritability, the realized heritability was not different from zero. The occurrence of pseudo-pregnancy during the tests as a consequence of uncontrolled ovulations could have interfered with receptivity and the tests results. Our prospect is to model Ri by analyzing the sequences of tests results as chronological series. Moreover, trying to establish a typology of the sequences, taking pseudo-pregnancy into account, would improve the modelling and hence, the estimation of heritability.

Key words: Rabbit, selection experiment, sexual receptivity, heritability.

INTRODUCTION

In European rabbit meat production, reproduction is generally performed by artificial insemination (AI), associated with a management system called "single batch". In this system, all rabbits does are submitted to a specific operation on the same day (e.g., all does are inseminated on the same day), and a next cycle is performed 6 weeks later. In this context, the economic value of fertility is increased, since a doe which had not been fertilized at one insemination series keeps unproductive for 6 weeks. It has long been assumed that the rabbit doe is in permanent estrus. However, it has been demonstrated that does alternate periods of acceptance (oestrus) and of refusal of mating (dioestrus), whose durations are highly variable between animals (Moret, 1980; Theau-Clément *et al.*, 2011). A female rabbit is called 'receptive' when she accepts mating, indicated by her position of lordosis in the presence of a buck. At insemination, a rabbit doe can be receptive or not. Receptive does produce three to four times more rabbits at weaning than non-receptive ones, particularly when they are lactating (Theau-Clément, 2008). Consequently, receptivity is often induced by injection of PMSG and/or alternatives to the use of hormones, called "biostimulations" (Theau-Clément, 2008; Renouf *et al*., 2008). In the research context of more sustainable farming systems, a totally original alternative would be to exploit the genetic pathway to increase the receptivity level of the does at insemination.

The purpose of the present experiment was to estimate the heritability of rabbit does receptivity and to test a divergent selection scheme on sexual receptivity.

MATERIALS AND METHODS

Animals and experimental design

The selection experiment used the INRA1777 strain (New-Zealand White breed). Two generations were performed. G0 was the founder generation (line 'F') and a divergent selection procedure gave rise to the high (H) and low (L) receptivity lines in G1.
At each generation, 140 primiparous does were used, distributed into two batches, conducted at a 6 week-interval (Figure 1).

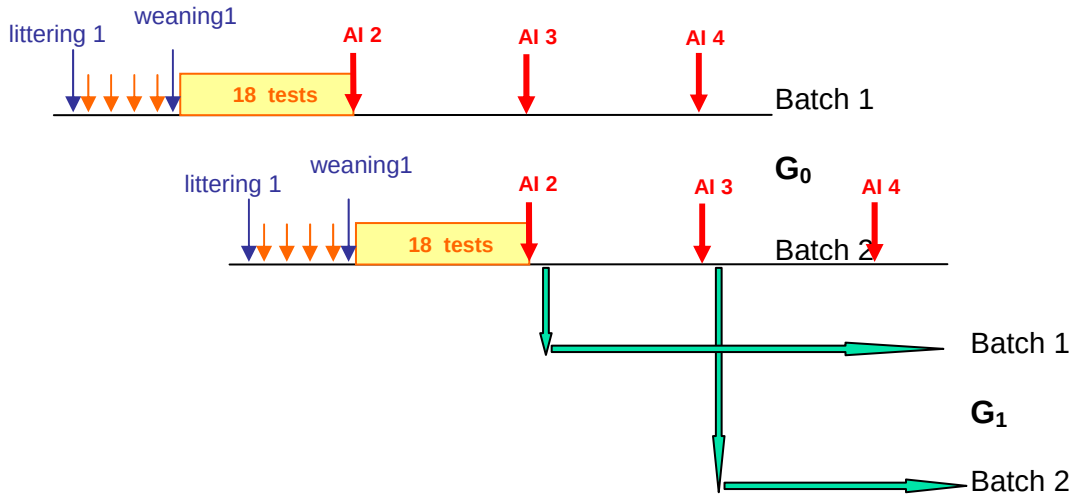

Figure 1: The two selection generations (G0 and G1), and the two batches within each (AI = Artificial Insemination)

Thirty INRA1777 bucks are kept in a building apart for the replacement. A total of 66 vasectomized INRA2266 bucks were housed in the same room as the females for the receptivity tests. After the 1st littering, the females were tested for their receptivity once a week until weaning. They were then submitted to intensive testing for 6 weeks, with 3 tests per week, leading to a total of 18 tests. The test consisted in observing during 2 min the behavior of the female after she was introduced in a tester buck cage: at the first trial, the female had either a lordosis position (then classified receptive) or not. If not, a second trial was done with another buck. After the tests period, the does continued their production phase. The breeding values for receptivity were estimated after the tests period. The estimation was performed by the BLUP with an animal model based on the results of the extensive testing, using the PEST software (Groeneveld and Kovac, 1990). The production of the G1 lines utilized the top 24 females to form the high line (of which 16 were efficient) and the bottom 24 females to form the low line (of which 14 were efficient). Eight males were used to breed the high line and eight for the low line. As shown on figure 1, batch 1 of G1 stemmed from AI n° 3 and 2 of the two G0 batches and batch 2 of G1 stemmed from AI n° 4 and 3 of the two G0 batches. In order not to penalize the reproduction of non-receptive females, the does received a subcutaneous injection of 25 IU of PMSG (Chronogest - Intervet) two days before AI.

Statistical analysis

Two variables were analysed as Ri, the receptivity as the elementary record, an all or none variable (0/1) and Rm, the average receptivity of the rabbit does on the whole testing period (18 tests). Ri was analyzed as a continuous variable.

To test and estimate the effects of the line and of the batch, an analysis of variance was applied to Ri using proc GLM of SAS (2001) with the fixed effect of the line (3 levels, F: corresponding to the founder population in G0, L: the low line in G1 and H: the high line in G1), of the batch (2 levels) and of their interaction.

The realized heritability has been calculated according to the formulas $h^2 = R / S$, where S is the selection differential, i.e., the difference in average receptivity between the top and bottom dams in G0 and R the response to selection after one cycle of divergent selection, i.e., the difference between the average receptivity of the two lines, H and L.

The heritability coefficients have been estimated using two mixed linear models: an animal model on one hand (model 1) and a sire and dam model on the other hand (model 2). The second model may suggest the presence of maternal (and/or dominance) effects on the performance, indicated by a higher dam component of the variance compared to the sire one.
For Ri, the fixed effects of the models were the combination line*batch (6 levels) and the operator (5 levels), while for Rm, the only fixed effects of the models was the line*batch combination. The effect of the operator was not included in the model since the operator changed between tests of a female.
The random effects in model 1 for Ri were the additive genetic effect of the rabbit doe, the permanent environmental effect and a residual effect, while for Rm they were only the additive genetic effect and a residual effect. In model 2, three random effects were considered for Ri: that of the sire, of the dam and of the permanent environment of the rabbit doe, which accounts for the repetition of the test; the latter effect was not included in model 2 for Rm.
In model 2, two heritability estimates were calculated: h^2_s calculated as 4 times the ratio of the sire component of the variance to the total variance, and h^2_{sd}, calculated from 2 times the sum of the sire and dam components of the variance. Model 1 was performed using the VCE software (Neumaier and Groeneveld, 1998) and model 2 using the Proc VARCOMP procedure of SAS (2001).

RESULTS

Generation/line and batch means

The means of receptivity by generation-line and batch are shown in Table 1. Receptivity showed no differences between generation-lines, but was systematically lower in batch 2. Moreover, the interaction between generation-line and batch was significant. This interaction lied in the differences between the two batches within a line. In G1, for example, this difference is 8.6 percent points in the L line vs. 17.7 percent points in the H line.

Table 1: Means of receptivity (%) by generation / line and batch

Generation / line	Number of does	Number of tests	All	Batch	
				1	2
G0 / F	135	2289	56.3±1.2	59.8±1.7^{ab}	53.5±1.5^{c}
G1 / L	69	1201	57.6±1.5	62.1±2.2^{a}	53.5±2.0^{bc}
G1 / H	69	1205	55.5±1.5	64.8±2.1^{a}	47.1±2.0^{c}

Superscripts indicate differences between means (Bonferoni test)

Realized heritability

The selection differential which was measured by the difference between the top and the bottom dams in G0 was 91.2 - 19.1 = 72.1%. The selection response which was estimated by the difference between the lines H and L in G1 was: H-L = 55.5 - 57.6 = -2.1 percentage point, which was not different from zero. As a consequence the realized heritability was not different from zero (-0.03).

Estimated heritability

The estimated heritability coefficients are shown in Table 2.

Table 2: Heritability estimated by two models for Ri, the instant receptivity and Rm, the average does receptivity. Ratio of the variance of the permanent environmental effect (varEP) to the total variance (varT), for Ri only.

	Ri	Rm
Model 1 (animal model)	h^2 = 0.01±0.02 varEP/varT = 0.19±0.02	h^2 = 0.05±0.07
Model 2 (sire and dam effects)	h^2s = 0.004 h2sd = 0.024 varEP/varT = 0.19±0.01	h^2s = 0.03 h^2sd = 0.08

Heritability of the individual performance Ri, had very low values whatever the model used. For the average receptivity Rm, this estimate was also very low (0.05 with an animal model or 0.03 from the sire component of the variance). The estimation from the sire and dam components was higher.
The permanent environmental effects accounted for about 19% of the total variance of Ri, leading to a repeatability coefficient of 21% in model 1. So, individual differences between rabbits does were mostly accounted for by permanent environmental effects.

DISCUSSION

Realized and estimated heritability are in agreement and lead to conclude that receptivity is a lowly heritable trait. This was an argument for deciding to stop the selection experiment at the end of the G1, even if one generation may be insufficient to assess the inheritance of a trait.

The differences between females appeared therefore not to be due to additive genetic effects. They were mostly accounted for by permanent environmental effects, not excluding the possibility of dominance effects. Indeed, the difference between the sire and dam components for Rm points to dominance (and/or maternal) effects. The significant interaction between line and batch, however, indicated the presence of a genetic source of variability. Lines H and L differed in the second batch of G1 more than in the first batch (Theau-Clément *et al.,* 2012). What could constitute these permanent environmental effects? Several causes were hypothesised: a conditioning effect of the early experience by the rabbit does of the receptivity test was not confirmed by our first investigations. Permanent environmental effects could also be due to the micro-environment of the rabbit does within the room. Our attempts to identify such effects were fruitless.

Our results raised the question of the biological significance of the trait measured. Is receptivity measured following this protocol (18 tests at a 2 or 3 day-interval) the same trait as receptivity measured in another context? In other words, is receptivity altered by the recording protocol? A troubling result was that fertility scores at AI performed just after the test series were systematically lower (50-70%) than for AI performed 6 or 12 weeks later (80-95%). This could be due to 'pseudo-pregnancy', a physiological status due to uncontrolled ovulations (out of any mating or GnRH injection) and the presence of corpora lutea, just like during pregnancy (Boiti *et al.,* 2006). These ovulations occurring during the testing protocol could be a consequence of the tests, and could interfere with subsequent receptivity. Blood samples have been collected at inseminations and the dosage of progesterone will allow assessing the presence of corpora lutea.

Ri was analysed by a mixed model with simple repeatability, which assumes that the covariance of repeated measurements does not depend on the time interval between them. According to this model, two sequences as different as 00001111 and 01010101 lead to the same repeatability. A simple repeatability model would therefore not be appropriate for such traits. The prospect is to model Ri by

analysing the sequence of the test results as chronological series. Moreover, trying to establish a typology of the sequences, taking pseudo-pregnancy along with different susceptibilities of the females into account, would improve the modelling.

CONCLUSION

Our protocol designed to measure the sexual receptivity of does consisted in performing a series of 18 tests at a 2 or 3 day-interval. In this context, the sexual receptivity of the rabbit females seems to be lowly heritable. The occurrence of pseudo-pregnancies, due to uncontrolled ovulations and the presence of corpora lutea, could have interfered with receptivity. Our prospect is to model the data as chronological series, taking pseudo-pregnancy into account, what might improve the estimation of heritability.

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