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1 **TITLE**

2 **Genetic analysis of functional longevity in a complete diallel**  
3 **crossing experiment involving four maternal rabbit lines**

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29 **Running Head (Short title):** CROSSBREEDING EFFECTS ON DOE RABBIT

30 LONGEVITY.

31

## ABSTRACT

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In a diallel cross between four maternal lines of rabbits, the four maternal lines and the corresponding crossbred females (does) were evaluated concerning functional longevity, estimating their crossbreeding components. Sixteen genetic groups were produced by using four maternal lines of rabbit (A, V, H and LP (L)). The groups were distributed over 4 Spanish farms. In all farms, the V line was present as the reference group. A total of 7,211 does' longevity records were recorded. Using a Cox proportional hazard model of fixed effects, survival analysis was performed to study longevity analyzing the hazard of death or culling. Does from lines A, H and V had similar risks of death or of being culled and they were more susceptible compared with those from line L. The lowest hazard was associated with L line does. No significant differences were found between the average of all crosses and the V line except when comparing the V line to the cross between A and H lines, favouring the former (1.30 higher risk of replacement for AH animals). Significant differences between reciprocal crosses were observed between VH and HV, in favour of HV (0.72 of relative risk of replacement) and between LH and HL, in favour of HL (0.76 of relative risk). Line V had the highest risk due to the direct genetic effects and these differences were significant with the lines H (1.40 of relative risk) and L (1.43 of relative risk). The differences in maternal genetic effects were small and not significant except between lines H and V in favour of V line (0.75 of relative risk). The estimated direct heterosis effects do not always follow the same trend but they showed the importance of the crossing between specialized lines to produce crossbred does for intensive meat rabbit production.

**KEYWORDS:** Rabbits, maternal lines, diallel cross, longevity, heterosis.

## INTRODUCTION

55

56 Longevity is one of the most important functional traits directly related to farm benefits  
57 and associated with disease resistance and rabbit welfare. Improving the length of  
58 productive life of rabbit doe is desirable to overcome the negative consequences of  
59 high replacement rate (Prieto *et al.*, 2014). The annual replacement rate in meat rabbits  
60 is about 120% (Ramon and Rafel, 2002) with nearly 50% of the dead or culled does  
61 being replaced during their first three parities (Rosell, 2003). All along these parities  
62 the cost of purchasing, rearing and maintaining the rabbit does has not yet been  
63 recovered. Moreover, the high replacement rates increase the proportion of young  
64 does on the farm, which are more difficult to handle and significantly less productive  
65 than the older ones (Sánchez *et al.*, 2004). Additionally, this high replacement  
66 increases pathological problems related to the introduction of animals from other  
67 farms. Therefore, longevity is related to disease resistance and animal welfare as well  
68 as its direct relation to farm profitability.

69 There are a number of issues involved in the genetic improvement of longevity: it  
70 shows low heritability (Piles *et al.*, 2006b; Sánchez *et al.*, 2008) and it is recorded late  
71 in the animal's life when they die or are culled. Sánchez *et al.* (2008) considered the  
72 number of parturitions that a female had as selection criterion for founding a new line.  
73 This founding procedure was proved to be successful because this line had a very  
74 similar production level compared to lines selected for a long time for prolificacy (Ragab  
75 and Baselga, 2011), but with better survival rates. Another divergent selection  
76 experiment for functional longevity in the INRA 1077 rabbit line was carried out in  
77 France (Garreau *et al.*, 2008). The authors found a significant difference in longevity  
78 between the two lines (+ 0.92 inseminations (39 days)). Culling and mortality rates  
79 were lower in the line selected for increasing longevity than in that selected to reduce

80 longevity. Functional longevity has a low heritability, as has been said before, but  
81 variation between genetic groups has been observed (Piles *et al.*, 2006b; Sánchez *et*  
82 *al.*, 2008). So, it would be possible to exploit the genetic variation between the lines to  
83 optimize the crosses between them.

84 Crossbreeding has been documented in pigs, beef cattle and sheep to have a  
85 substantial impact on traits directly related to fertility and health, and therefore also  
86 indirectly on longevity. To our knowledge, very few studies have been carried out to  
87 study genetic variability of rabbit longevity among breeds, lines and crossbreds. In a  
88 study, conducted by Piles *et al.* (2006a), involving three Spanish maternal rabbit lines  
89 selected for litter size at weaning (A, V, Prat), complete diallel crossing was carried out  
90 to estimate crossbreeding parameters of functional longevity. They found favourable  
91 and significant heterosis between the lines V and Prat, and between lines A and Prat.  
92 In a different experiment by Lukefahr and Hamilton (2000) involving Californian (CAL),  
93 New Zealand White (NZW) and the crossbred does CAL x NZW, a higher longevity  
94 was observed for NZW than for CAL; crossbred does behaved similarly to NZW. The  
95 objective of our study was to evaluate functional longevity of crossbred and purebred  
96 does from a complete diallel cross of four maternal lines of rabbits and the  
97 corresponding crossbreeding parameters. These lines are currently in use by the  
98 Spanish rabbit production sector.

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## MATERIALS AND METHODS

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### **Ethical statement**

103 Animal manipulations and the experimental procedures were approved by the Ethical  
104 Committee of the Universitat Politècnica de València (Valencia, Spain), according to  
105 Council Directives 98/58/EC (European Economic Community, 1998).

106

## 107 **Animals and Management**

108 Four maternal lines of rabbits were available in this study for conducting a diallel  
109 crossing that produced sixteen genetic groups (the four lines and twelve simple  
110 crosses). The lines A, V, H and LP (L) lines were described previously by Ragab and  
111 Baselga (2011), at the beginning of the experiment the lines were on the 45<sup>th</sup>, 40<sup>th</sup>, 24<sup>th</sup>  
112 and 10<sup>th</sup> generation of selection respectively. Data for the present study were recorded  
113 from January 2009 to October 2011 on animals allocated to four Spanish farms. The  
114 crossbreeding experiment was carried out in four experimental farms located in four  
115 Spanish cities; León farm (farm 1, located in León city northwest Spain), Castellón farm  
116 (farm 2, located in Castellón de la Plana city, Valencian Community, east Spain),  
117 Tarragona farm (farm 3, located in Tarragona city, Tarragona Province, northeast  
118 Spain) and the farm belonging to the Universitat Politècnica de València (farm 4,  
119 Valencia, Valencian Community, east Spain). The total number of does was 7211,  
120 distributed as follows: farm 1 (1822), farm 2 (1987), farm 3 (1612) and farm 4 (1790).  
121 The genetic groups involved in this experiment corresponded to the four lines, AA, HH,  
122 LL and VV, and the respective single crosses, AH, HA, AL, LA, AV, VA, HV, VH, HL,  
123 LH, VL and LV, where the first letter refers to the sire line, and the second to the dam  
124 line of the genetic group. All the crossbred groups and VV animals were raised in farms  
125 1 and 2; does from VV and HH were raised in farm 3, and VV, AA and LL animals were  
126 bred in farm 4. The line V was present in all farms to connect data between farms and  
127 to be used as a reference line.

128 Management differed slightly across farms. Does in farms 1 and 2 were grouped in a  
129 single batch mated every 42 days by applying artificial insemination with semen from  
130 a paternal line (10-20x10<sup>6</sup> spermatozoa per dose) while in farms 3 and 4, does were

131 grouped into 6 batches and weekly natural mating was applied. In all farms, the first  
132 mating was around 18 weeks of age, for males and females. The does were served  
133 10-12 days post-kindling and a pregnancy test was carried out by abdominal palpation  
134 on day 12 after mating. Litters were weaned at 28 days. All animals were fed *ad libitum*  
135 on a standard commercial pelleted diet and they were reared under a constant  
136 photoperiod of 16:8 h (light/dark). As a general management practice, does were never  
137 culled due to productive reasons, i.e. low prolificacy or fertility was never a reason for  
138 culling except when there were also signs of disease.

139 The complete data set included records of sixteen genetic groups, involving 7,211  
140 does, 38.61% of them having censored longevity records because the does were  
141 removed before the end of their productive lives or the experiment finished before their  
142 death or culling date. The maximum, minimum and average length of productive life  
143 for censored and uncensored records is presented in Table 1.

144

#### 145 **Trait definition and Statistical Model**

146 In this study functional longevity in rabbits was defined as the time in days between  
147 the date of first positive palpation of a doe and the date of death or culling due to non-  
148 productive reasons (Sánchez et al., 2004). Survival analysis methodology was  
149 followed to analyse rabbit does' longevity data. But taking into account the high  
150 proportion of does dying in the first parturition, Weibull model was discarded because  
151 of the misfit of its data (Sánchez et al., 2004; Piles et al., 2006b). So, the model of  
152 choice was the Cox proportional hazard model (Cox, 1972) following this equation for  
153 the hazard:

$$154 \quad h_m(t|x_m(t)) = h_0(t) * \exp\{x_m(t) * \beta\}$$



155 where, the hazard ( $h_m(t|\mathbf{x}_m(t))$ ) of the doe at time  $t$ ) affected by the covariates indicated  
 156 in the vector  $\mathbf{x}_m(t)$  is the product of a base line hazard at time  $t$ ,  $h_0(t)$ , and the  
 157 exponential effect of the components of  $\mathbf{x}_m(t) = \{ \mathbf{GFYS}_i(t),$   
 158  $\mathbf{NBA}_j(t), \mathbf{GPPO}_k(t), \mathbf{PS}_l(t) \}$ .  $\beta_{\mathbf{GFYS}_i(t)}$  is the vector comprising the fixed effect of  
 159 genetic group-farm-year-season combination  $i$  of the doe  $m$  at time  $t$ ; this is a time-  
 160 dependent factor with 145 levels. The changes of the levels occurred at fixed calendar  
 161 dates, leading to levels comprising a period of approximately 90 days. This  
 162 combination factor, amongst others, accounts for possible interactions between  
 163 genetic groups and the environmental factors.  $\beta_{\mathbf{NBA}_j(t)}$  is the vector comprising the  
 164 fixed effect time-dependent factor of the number born alive class  $j$  at time  $t$ , with 9  
 165 classes defined as follows: nulliparous, 0, 1 to 2, 3 to 4, 5 to 6, 7 to 8, 9 to 10, 11 to 12,  
 166 and >12 born alive; for this factor, levels changed at every parity.  $\beta_{\mathbf{GPPO}_k(t)}$  is the  
 167 vector comprising the effect of the combination  $k$  between the genetic group and  
 168 positive palpation order at time  $t$ ; this was also fitted as a time-dependent factor with  
 169 80 levels. It allows for taking into account the possible effect of the interaction between  
 170 the genotype and the parity order. This factor allowed us to assume a different pattern  
 171 of risk accumulation during the life of the animals for the different genetic groups, i.e.  
 172 assuming the genetic group effect as a time-dependent factor.  $\beta_{\mathbf{PS}_l(t)}$  is the vector  
 173 comprising the time-dependent effect of the physiological status  $l$  of the doe at time  $t$ .  
 174 This factor reflects the combination between the reproductive status of the does  
 175 (pregnant, non-pregnant, and unknown) and the lactational status of does (lactating or  
 176 non-lactating).  
 177 Data analysis was conducted using the Survival Kit 6.0 software (Ducrocq *et al.*, 2010).  
 178 The model was solved to get the estimates of the differences between all the genetic  
 179 groups and the VV group, as well as the (co)variance matrix between these estimates.

180 The contrasts were defined as the differences on log-hazard between V line  
 181 (Reference line) and the other genetic groups, within the different PPO levels.  
 182 In these contrasts, the part of the genetic effects accounted for by GFYS was  
 183 considered by adding the average of the effect of the GFYS levels in which the lines  
 184 of interest were involved. From these contrasts and their variance-covariance structure  
 185 the differences between direct and maternal genetic effects of the lines, as well as the  
 186 direct heterosis, were estimated by generalized least squares according to the  
 187 Dickerson model (Dickerson, 1969). The significance of the estimated contrasts and  
 188 heterosis were assessed setting the first type error at  $\alpha=0.05$ . Dickerson model was  
 189 the model of choice because of its common use to analyze crossbreeding and relative  
 190 simplicity where the expected performance  $Y_c$  of the type c of doe can be written,  
 191 following the Dickerson's model as:

$$192 \quad Y_c = \mu + \sum_{i=1}^n \lambda_j g_j^I + \sum_{i=1}^n \beta_k g_k^M + \sum_{l \neq m} \gamma_{lm} h_{lm}^I$$

193 Where,  $n$  is the number of lines;  $g_j^I$  the direct genetic effect of the line  $i$ , being  $\lambda_j$  the  
 194 gene proportion which  $j$  contributes to  $c$ ;  $g_k^M$  is the maternal genetic effect of the line  
 195  $k$ , being  $\beta_k$  the gene proportion which  $k$  contributes to the dams of  $c$ ;  $h_{lm}^I$  is the direct  
 196 heterosis between lines  $i$  and  $j$ , being  $\gamma_{lm}$  the contribution of the lines  $l$  and  $m$  to the  
 197 heterosis of  $c$ ;

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## RESULTS

200 The contrasts for the log hazard between the four maternal lines, globally and for the  
 201 different productive cycles are presented in Table 2. The presented contrasts could be  
 202 used to calculate the relative risk of elimination or death of a doe as the  $\exp(\log$   
 203 hazard). Line L showed the highest capacity to overcome the risk factors that can lead

204 to death or culling. The L line showed hazard ratios with respect to A, H and V lines of  
205 0.77 (exp (-0.26)), 0.82 and 0.78 respectively being the log-hazard ratio significant for  
206 the cases involving A and V lines. These figures mean a high risk of culling was  
207 observed in females from A, H and V lines were 1.29, 1.22 and 1.28 times the risk of  
208 L does. No overall significant differences between A, H and V lines were found.  
209 Performing the same set of contrasts within positive palpation order (number of  
210 productive cycle), it was observed that at the first cycle, A and V does had 1.84 and  
211 1.51, respectively, more risk of being eliminated from the herd than H line does. During  
212 the second and third cycle, no significant differences were observed between lines.  
213 The occurrence of global significant differences between A and V lines with respect to  
214 L line was due to the fact that during the last cycles, significant differences between  
215 lines were observed. In the fourth cycle there was 1.36 times more risk of death or  
216 culling for a V doe than for an L doe, whereas in the fifth parity this ratio was 2.14. In  
217 the fifth cycle the risk ratios of A, V and H lines with respect to L were significant,  
218 showing the values of 2.3, 2.14 and 3.15, respectively.

219 Concerning the general differences between crossbred does, (considering together  
220 each cross and its reciprocal, Table 3) and line V, there were no significant differences  
221 between the crossbred groups and line V, except for the cross between A and H lines,  
222 which was favorable to line V. Analyzing the same differences by productive cycle,  
223 significant differences were found at the first cycle and during cycles equal or higher  
224 to the 5<sup>th</sup>. In the first cycle, the groups HL and LH, and LV and VL showed favourable  
225 and significant differences with respect to V line for the associated risk. However, the  
226 does of the groups HA and AH had a risk of elimination from the herd 1.3 times greater  
227 than that of V line at their first cycle. Moreover, in general, no significant differences  
228 were found at the third and fourth cycles, except a significant difference in favour of

229 crosses LH and HL at the third cycle. At cycle orders  $\geq 5$ , the crossbreds had higher  
230 associated hazards than V line. The differences were important and the relative risk  
231 ranged from 1.32 to 2.34.

232 Table 4 shows the differences between the estimates of log hazard associated with  
233 reciprocal crosses, to give a first indication of the magnitude of maternal effects  
234 involved in the crosses. The only significant contrasts were found between VH and HV  
235 and between LH and HL. In the first case, when the V line was used as a dam line the  
236 hazard ratio associated to VH was reduced to 0.72, but when line H was the dam in  
237 the cross between H and L lines, the risk of culling or death was 1.31 times higher than  
238 in the reciprocal cross. The significant difference between HV and VH crosses is a  
239 consequence of the differences between them during the first cycle, while for the case  
240 of LH and HL crosses the difference is established late in the doe's life. For the contrast  
241 between AH and HA crosses no overall significant differences were detected; during  
242 the first cycle the risk was higher for the cross HA (1.95) but in the later cycles the  
243 higher risk was observed on the reciprocal cross (1.89).

244 Differences in direct genetic effects between lines are presented in Table 5. There are  
245 two results that merit attention. The first one is that line V had the highest associated  
246 risk and its differences were significant with respect to the lines H and L. In the case  
247 of the H line, the difference to the V line is due to a high and important risk associated  
248 to V line at the first productive cycle, but in the case of the L line, the difference is  
249 established during the fourth and later productive cycles. The second important result  
250 refers to the fact that the direct effect of the L line had the lowest associated hazard,  
251 especially at cycles  $\geq 5$ . At these cycles, the relative risks of the L line with respect to  
252 those of lines A, H and V, were only 0.39, 0.49 and 0.53, respectively. Also, from Table

253 5 it can be concluded that no significant differences were observed between A and V  
254 lines, either globally or at any cycle.

255 The observed differences in global risk between lines regarding maternal genetic  
256 effects were small and in general, not significant, except between lines H and V in  
257 favour of V line (Table 6). Nevertheless, over the course of the life of the animals, some  
258 significant differences were observed. During the first productive cycle the difference  
259 in the maternal genetic effect between A, H and L lines and the V line was found to be  
260 significant and favourable to the last line. Late in the life of the animals, a negative  
261 maternal effect was associated with the H line, compared to the maternal effects of  
262 lines A and L. The estimated differences in maternal effects approximately match the  
263 observed differences between any cross and its reciprocal. The estimated values for  
264 the direct heterosis depended on the lines involved in the cross (Table 7). In general,  
265 the heterosis for the global log hazard was not significant, except for the cross AH,  
266 which had an unfavorable value (positive risk associated to the cross). However, when  
267 different lifetime periods are considered, it is important to note that later cycles are  
268 always associated with significant and relevant, but unfavourable, heterosis effects.  
269 On the contrary, at earlier ages some favourable effects were observed.

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## DISCUSSION

272 In the present study, L line had the lowest risk of death or culling. This result was in  
273 accordance with previous reports by EL Nagar *et al.* (2020) who stated that the L rabbit  
274 line had a longer functional longevity than the A, V, H and R rabbit lines. Also,  
275 Theilgaard *et al.* (2007) reported the high capability of the L line to recover from stress  
276 and to manage its body resources better than V line. The differences favouring L line  
277 were expected because this line was founded by selecting females from commercial

278 farms that showed an extremely long productive life which was measured as a function  
279 of the number of parities;  $\geq 25$  parities and prolificacy near or above the average of the  
280 Spanish commercial rabbit population (Sánchez *et al.*, 2008). Nevertheless, for the  
281 other lines, neither the foundation nor the selection process relied on any longevity  
282 criteria (Ragab and Baselga, 2011). In a study comparing L and V lines for longevity,  
283 Sánchez *et al.* (2008) reported that the mean of the relative risk between L and V lines  
284 was 0.80 (exp (-0.22)), which indicated that it was 1.24 times more likely for a V doe  
285 to be culled or to die than for an L doe. Moreover, the relative risks between V and L  
286 lines at their foundation and in present generations, were reported to be 1.55 and 1.56,  
287 respectively, always in favour of L line (EL Nagar, 2015).

288 The selection criteria of L line, during its foundation, was based on survival ability until  
289 very late ages, i. e. more than 28 parities. Therefore, it makes sense that the  
290 differences in survival ability we have observed between all the lines and the L females  
291 are essentially set at late parities.

292 In the fifth cycle, a better survival rate was also observed for the V line than for the H  
293 line, compensating for the higher risk associated to the V line at early cycles. These  
294 different ways of cumulating risk for the different genetic types supposes that the  
295 interaction between PPO and genetic type is significant, and this implies that the  
296 pattern of risk along the successive PPO was different for the different genetic types.  
297 In this regard, however, El Nagar *et al.* (2020) showed that, in a single farm, with the  
298 same purebred lines as were used in this study, they followed a similar life-time risk  
299 pattern. This risk decreased as the order of positive palpation increased. In that study,  
300 the largest hazard difference was 1.30 between the OPP1 and OPP3 in L line. Sánchez  
301 *et al.* (2004) attributed the high risk associated with the first two parities to the fact that  
302 the does are still growing and kindling would be an important risk factor. The same

303 tendency was observed by Lenoir *et al.* (2013) who reported that in the Hycole D line,  
304 the risk associated with the first parity (1.47) was greater than that for the second parity  
305 (1.22). On the contrary, in pigs, Tarrés *et al.* (2006) found that the risk of culling a sow  
306 increased in higher parity orders.

307 Crossbred does at the beginning of their reproductive career seemed to show some  
308 superiority over line V, but they failed to maintain this situation in the final stages of  
309 their productive life. This result may be attributed to the fact that in purebred does,  
310 such as line V, the inbreeding had a negative effect on longevity rather than on the  
311 crossbred does. However, EL Nagar *et al.* (2020) reported that the inbreeding did not  
312 seem to have an unfavourable effect on longevity for the A, V, H, L and R rabbit lines.  
313 Moreover, the crossbred does have a higher production level than purebred does  
314 which, with time, could increase the risk of culling or death. However, EL Nagar *et al.*  
315 (2020) stated that the greatest risk of culling or death associated with low litter sizes  
316 could be linked to underlying pathological and/or stress disorders, since no voluntary  
317 culling for production reasons was practiced in the experimental farm.

318 It should be noted that the increased risk associated with crossbred does began at the  
319 fifth cycle, when the cost of the does had already been recovered. Additionally, Rosell  
320 (2003) reported that around 50 % of the dead and culled does are in one of the first  
321 three kindlings. Therefore based on these two factors, the importance of using  
322 crossbreed instead of purebred does in the commercial farms appear especially with  
323 the high levels of culling due to productivity causes.

324 In another study (Piles *et al.*, 2006a) where lines A, V and Prat were evaluated, no  
325 significant differences were found between the direct genetic effects of A and V lines.  
326 However, the relative risk between both lines in that study was higher than in our work.  
327 In that study, significant differences in direct genetic effects between A and Prat lines

328 were found. In the present study, it was not possible to detect overall significant  
329 difference in the direct genetic effects. For instance, between A and H lines and  
330 between L and H lines, the differences between direct genetic effects generated in  
331 certain cycles were compensated by differences of the opposite sign generated during  
332 other cycles

333 In relation to the maternal effects, Piles *et al.* (2006a) found a similar value to our  
334 overall life-time estimate between A and V lines, in their case, as in our experiment, it  
335 was not declared to be significantly different to zero. In our study, as we considered  
336 the interaction with PPO, we have, however, assessed that in the first parity there was  
337 a clearly higher risk associated to the maternal effects of the V line.

338 Regarding the heterosis effects, the difference in the sign of the estimates at earlier  
339 and later ages could be explained by the higher elimination rate during early cycles in  
340 purebred groups and the high production levels of crossbred does. Piles *et al.* (2006a)  
341 found favorable heterosis in crosses between A, Prat and V line but it was only  
342 significant between A and Prat lines. In dairy cattle, the crossbred cows showed higher  
343 longevity compared with the purebred cows, which means favourable and beneficial  
344 heterosis and supports the idea that crossbreeding could be considered as a useful  
345 tool to improve the production longevity in the Danish dairy cattle population (Clasen  
346 *et al.*, 2017). Similar findings were reported by Jönsson, (2015) in Swedish dairy cattle.  
347 In order to have a complete overview of the present diallel crossing experiment, litter  
348 size and litter size components of the different genetic groups were compared by  
349 Ragab *et al.* (2014 and 2016). Moreover, growth, slaughter, carcass and meat quality  
350 traits in the same purebred and their crossbred genetic groups were compared by  
351 Mínguez *et al.* (2015, 2016 and 2017).



352 In all the reported contrasts and estimates of the genetic parameters, the interaction  
353 between genetic types and farms had not been considered. We have done so because  
354 our experimental design did not allow for studying the genetic types as nested to the  
355 farms, since all the genetic types are not presented in all the farms. Thus, in spite of  
356 having partially accounted for this interaction effect during the estimation of the genetic  
357 type effects, when defining the contrasts of interest we averaged the value of the  
358 genetic type effects across the farms in which that particular type was presented. In  
359 spite of the obvious limitation, this procedure allows, at least, the differences between  
360 a given genetic type in different farms to be regarded. This could not be achieved if the  
361 GFYS interaction, which was a significant effect, were ignored in the model for  
362 estimating the genetic type effects. From these genetic type effects the reported  
363 contrasts and genetic parameter estimates have been derived. Reporting our  
364 estimates as averages across farms, and not nested within farm, also enables the lines  
365 and their genetic crossbreeding parameters, in an average environment. Although, as  
366 we have already indicated, we absolutely accept that this rank could be different in the  
367 different farms, and this is why we initially fit the interaction effect.

368

369

## CONCLUSIONS

370 Relevant differences between L line and the other lines might be consequence of the  
371 foundation criterion more related to longevity used to create this line. The heterosis did  
372 not seem to have a great effect on functional longevity. However, in general, the  
373 crossbred does show higher longevity compared to that of purebred lines used to  
374 create the cross, especially in the early reproductive cycles, which are the most  
375 important from a practical point of view.

376

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383

## CONFLICT OF INTERESTS

385 The authors declare that they have no competing interests.

386

## DATA AVAILABILITY STATEMENT

388 The datasets used and analysed during the current study are available from the  
389 corresponding author on reasonable request.

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461

## TABLES

462 **Table 1** Summary statistics for rabbit's functional longevity of censored and  
463 uncensored records in the data set

	<b>Censored<sup>†</sup> records</b>	<b>Uncensored<sup>‡</sup> records</b>
	2784 (38.61%)	4427 (61.39%)
Minimum time (day)	5	3
Maximum time (day)	895	873
Average time (day)	334.43	196.82

464 <sup>†</sup>Records from does that had not completed their productive life. <sup>‡</sup>Records from does  
465 that had completed their productive life.

466 **Table 2** Contrasts (standard errors) between rabbit lines for the global log hazard (GR)  
 467 and for the log hazard associated with the consecutive positive palpation order (OPP)

Contrast <sup>†</sup>	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AA-HH	0.06(0.16)	0.61(0.24)*	0.40(0.25)	-0.04(0.25)	-0.38(0.22)	-0.31(0.26)
AA-LL	0.26(0.11)*	0.29(0.19)	0.05(0.20)	0.18(0.22)	-0.07(0.18)	0.83(0.27)*
AA-VV	0.00( 0.10)	0.20(0.15)	0.21(0.17)	-0.10(0.18)	-0.38(0.15)*	0.09(0.21)
HH-VV	-0.05(0.13)	-0.41(0.20)*	-0.19(0.21)	-0.06(0.20)	0.00(0.18)	0.40(0.18)*
LL- HH	-0.20(0.16)	0.33(0.25)	0.35(0.25)	-0.22(0.26)	-0.31(0.23)	-1.15(0.26)*
LL-VV	-0.25(0.10)*	-0.08(0.17)	0.16(0.17)	-0.28(0.19)	-0.31(0.15)*	-0.75(0.21)*

468 <sup>†</sup>Line of buck x line of doe (A = A line; L= LP line; H = H line; V = V line). \*Significant  
 469 difference at  $\alpha = 0.05$ .

470

471 **Table 3** Contrasts (standard errors) between crossbred groups<sup>†</sup> and V line rabbits for the  
 472 global log hazard (GR) and for the log hazard associated with the consecutive positive  
 473 palpation order (OPP)

Contrast <sup>†</sup>	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AH-VV	0.26(0.08)*	0.31(0.13)*	-0.06(0.16)	-0.04(0.16)	0.24(0.16)	0.85(0.16)*
AL-VV	0.03(0.09)	0.04(0.14)	-0.15(0.17)	-0.16(0.17)	0.00(0.15)	0.42(0.16)*
AV-VV	-0.07(0.09)	-0.21(0.14)	-0.10(0.15)	-0.21(0.17)	-0.14(0.15)	0.28(0.16)
HV-VV	0.01(0.09)	-0.07(0.14)	-0.12(0.15)	-0.33(0.17)	-0.02(0.15)	0.60(0.15)*
LH-VV	-0.07(0.08)	-0.38(0.14)*	-0.08(0.14)	-0.34(0.17)*	-0.10(0.15)	0.57(0.14)*
LV-VV	-0.04(0.09)	-0.45(0.15)*	-0.29(0.16)	0.03(0.17)	-0.01(0.16)	0.54(0.15)*
All-VV	0.02(0.06)	-0.13(0.09)	-0.13(0.10)	-0.18(0.11)	0.00(0.10)	0.54(0.10)*

474 <sup>†</sup>One cross and its reciprocal are considered together. <sup>‡</sup>Line of buck x line of doe (A= A  
 475 line; L= LP line; H = H line; V = V line; All-VV = The contrast between all crossbred and V  
 476 line). \* Significant difference at  $\alpha = 0.05$ .

477

478



479 **Table 4** Contrasts (standard errors) between reciprocal crosses<sup>†</sup> of rabbits for the global  
 480 log hazard (GR) and for the log hazard associated with the consecutive positive palpation  
 481 order (OPP)

Contrast <sup>†</sup>	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AH-HA	0.04(0.13)	-0.67(0.22)*	0.14(0.28)	-0.29(0.28)	0.34(0.27)	0.64(0.26)*
AL-LA	-0.02(0.14)	0.05(0.23)	-0.36(0.29)	0.18(0.29)	-0.06(0.26)	0.08(0.26)
AV-VA	-0.05(0.15)	0.31(0.25)	-0.02(0.27)	-0.21(0.29)	-0.42(0.26)	0.11(0.28)
HV-VH	-0.32(0.15)*	-1.20(0.23)*	-0.13(0.26)	-0.31(0.29)	-0.01(0.25)	0.03(0.24)
LH-HL	0.27(0.13)*	0.06(0.23)	0.34(0.24)	0.20(0.29)	0.10(0.26)	0.65(0.23)*
LV-VL	-0.17(0.15)	-0.19(0.26)	-0.17(0.28)	-0.18(0.29)	-0.19(0.27)	-0.13(0.24)

482 <sup>†</sup>Line of buck x line of doe (A= A line; L= LP line; H = H line; V = V line). \*Significant  
 483 difference at  $\alpha = 0.05$ .

484

485 **Table 5** Contrasts (standard error) for direct genetic effects on the global log hazard (GR)  
 486 and for the log hazard associated with the consecutive positive palpation order (OPP)  
 487 between the different genetic groups of rabbits

Contrast †	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AA-HH	0.20(0.19)	0.62(0.29)*	0.50(0.31)	-0.08(0.32)	-0.31(0.29)	0.21(0.32)
AA-LL	0.21(0.15)	0.22(0.25)	-0.14(0.28)	0.14(0.30)	-0.10(0.26)	0.94(0.32)*
AA-VV	-0.15(0.14)	-0.22(0.23)	0.08(0.25)	-0.36(0.27)	-0.56(0.24)	0.31(0.28)
HH-VV	-0.34(0.16)*	-0.84(0.26)*	-0.42(0.28)	-0.28(0.29)	-0.25(0.26)	0.10(0.25)
LL-HH	-0.02(0.19)	0.40(0.30)	0.64(0.31)*	-0.22(0.33)	-0.21(0.29)	-0.72(0.31)*
LL-VV	-0.36(0.14)*	-0.44(0.24)	0.22(0.26)	-0.50(0.28)	-0.47(0.24)*	-0.62(0.27)*

488 †Line of buck x line of doe (A= A line; L= LP line; H = H line; V = V line). \*Significant  
 489 difference at  $\alpha = 0.05$ .

490

491 **Table 6** Contrast (standard error) for maternal genetic effects on the global log hazard  
 492 (GR) and for the log hazard associated with the consecutive positive palpation order  
 493 (OPP) between the different genetic groups of rabbits

Contrast †	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AA-HH	-0.14( 0.10)	-0.01(0.16)	-0.10(0.19)	0.04(0.20)	-0.07(0.18)	-0.53(0.18)*
AA-LL	0.05( 0.10)	0.07(0.16)	0.19(0.20)	0.05(0.20)	0.03(0.18)	-0.10(0.18)
AA-VV	0.15( 0.10)	0.42(0.17)*	0.12(0.19)	0.27(0.20)	0.19(0.18)	-0.23(0.18)
HH-VV	0.29( 0.10)*	0.43(0.16)*	0.23(0.19)	0.22(0.20)	0.25(0.18)	0.30(0.17)
LL-HH	-0.19( 0.10)	-0.07(0.16)	-0.29(0.18)	-0.01(0.20)	-0.09(0.18)	-0.42(0.17)*
LL-VV	0.11( 0.10)	0.36(0.17)*	-0.06(0.19)	0.22(0.20)	0.16(0.18)	-0.13(0.17)

494 †Line of buck x line of doe (A= A line; L= LP line; H = H line; V = V line). \*Significant  
 495 difference at  $\alpha = 0.05$ .

496

497 **Table 7** Estimates (standard error) for the direct heterosis for the global log hazard (GR)  
 498 and for the log hazard associated with the consecutive positive palpation order (OPP) in  
 499 the different genetic groups of rabbits

Genetic groups <sup>†</sup>	GR	1 <sup>st</sup> OPP	2 <sup>nd</sup> OPP	3 <sup>rd</sup> OPP	4 <sup>th</sup> OPP	≥5 <sup>th</sup> OPP
AH	0.28(0.12)*	0.35(0.17)*	-0.06(0.19)	0.03(0.19)	0.45(0.18)*	0.62(0.19)*
AL	0.16(0.12)	-0.02(0.17)	-0.34(0.19)	0.04(0.20)	0.34(0.18)	0.76(0.20)*
AV	-0.08(0.10)	-0.31(0.15)*	-0.21(0.16)	-0.16(0.18)	0.05(0.16)	0.23(0.18)
HV	0.04(0.11)	0.14(0.16)	-0.02(0.17)	-0.30(0.18)	0.00(0.16)	0.42(0.16)*
LH	0.10(0.12)	-0.13(0.18)	-0.07(0.18)	-0.16(0.20)	0.05(0.18)	0.76(0.18)*
LV	0.09(0.10)	-0.41(0.16)*	-0.38(0.17)*	0.17(0.18)	0.14(0.16)	0.91(0.17)*

500 <sup>†</sup>Line of buck x line of doe (A= A line; L= LP line; H = H line; V = V line). \*Significant  
 501 difference at  $\alpha = 0.05$ .