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

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Abstract

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 analysing 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

diallel cross, heterosis, longevity, maternal lines, Rabbits

1 | INTRODUCTION

Longevity is one of the most important functional traits directly related to farm benefits and associated with disease resistance and rabbit welfare. Improving the length of productive life of rabbit doe is desirable to overcome the negative consequences of high replacement rate (Prieto et al., 2014). The annual replacement rate in meat rabbits is about 120% (Ramon & Rafel, 2002) with nearly 50% of the dead or culled does being replaced during their first three parities (Rosell, 2003). All along these parities, the cost of purchasing, rearing and maintaining the rabbit does

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has not yet been recovered. Moreover, the high replacement rates increase the proportion of young does on the farm, which are more difficult to handle and significantly less productive than the older ones (Sánchez et al., 2004). Additionally, this high replacement increases pathological problems related to the introduction of animals from other farms. Therefore, longevity is related to disease resistance and animal welfare as well as its direct relation to farm profitability.

There are a number of issues involved in the genetic improvement of longevity: it shows low heritability (Piles, et al., 2006; Sánchez et al., 2008) and it is recorded late in the animal's life when they die or are culled. Sánchez et al. (2008) considered the number of parturitions that a female had as selection criterion for founding a new line. This founding procedure was proved to be successful because this line had a very similar production level compared to lines selected for a long time for prolificacy (Ragab & Baselga, 2011), but with better survival rates. Another divergent selection experiment for functional longevity in the INRA 1,077 rabbit line was carried out in France (Garreau et al., 2008). The authors found a significant difference in longevity between the two lines (+0.92 inseminations (39 days)). Culling and mortality rates were lower in the line selected for increasing longevity than in that selected to reduce longevity. Functional longevity has a low heritability, as has been said before, but variation between genetic groups has been observed (Piles, et al., 2006; Sánchez et al., 2008). So, it would be possible to exploit the genetic variation between the lines to optimize the crosses between them.

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

2 | MATERIALS AND METHODS

2.1 | Ethical statement

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

2.2 | Animals and Management

Four maternal lines of rabbits were available in this study for conducting a diallel crossing that produced sixteen genetic groups (the four lines and twelve simple crosses). The lines A, V, H and LP (L) lines were described previously by Ragab and Baselga (2011), and at the beginning of the experiment, the lines were on the 45th, 40th, 24th and 10th generation of selection, respectively. Data for the present study were recorded from January 2009 to October 2011 on animals allocated to four Spanish farms. The crossbreeding experiment was carried out in four experimental farms located in four Spanish cities; León farm (farm 1, located in León city northwest Spain), Castellón farm (farm 2, located in Castellón de la Plana city, Valencian Community, east Spain), Tarragona farm (farm 3, located in Tarragona city, Tarragona Province, northeast Spain) and the farm belonging to the Universitat Politècnica de València (farm 4, Valencia, Valencian Community, east Spain). The total number of does was 7,211, distributed as follows: farm 1 (1822), farm 2 (1987), farm 3 (1612) and farm 4 (1,790).

The genetic groups involved in this experiment corresponded to the four lines, AA, HH, LL and VV, and the respective single crosses, AH, HA, AL, LA, AV, VA, HV, VH, HL, LH, VL and LV, where the first letter refers to the sire line, and the second to the dam line of the genetic group. All the crossbred groups and VV animals were raised in farms 1 and 2; does from VV and HH were raised in farm 3, and VV, AA and LL animals were bred in farm 4. The line V was present in all farms to connect data between farms and to be used as a reference line.

Management differed slightly across farms. Does in farms 1 and 2 were grouped in a single batch mated every 42 days by applying artificial insemination with semen from a paternal line (10-20 $\times$ 10^6 spermatozoa per dose) while in farms 3 and 4, does were grouped into 6 batches and weekly natural mating was applied. In all farms, the first mating was around 18 weeks of age, for males and females. The does were served 10–12 days postkindling and a pregnancy test was carried out by abdominal palpation on day 12 after mating. Litters were weaned at 28 days. All animals were fed ad

libitum on a standard commercial pelleted diet, and they were reared under a constant photoperiod of 16:8 hr (light/dark). As a general management practice, does were never culled due to productive reasons, that is low prolificacy or fertility was never a reason for culling except when there were also signs of disease.

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

2.3 | Trait definition and statistical model

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

$$h_m(t|x_m(t)) = h_0(t) * \exp\left\{x_m(t) * \beta\right\},$$

where the hazard ($h_m(t|x_m(t))$ of the doe at time t) affected by the covariates indicated in the vector $x_m(t)$ is the product of a baseline hazard at time t, $h_0(t)$, and the exponential effect of the components of $x_m(t) = \{GFYS_i(t), NBA_j(t), GPPO_k(t), PS_l(t)\}$. $\beta_{GFYS_i(t)}$ is the vector comprising the fixed effect of genetic group-farm-year-season combination i of the doe m at time t; this is a time-dependent factor with 145 levels. The changes of the levels occurred at fixed calendar dates, leading to levels comprising a period of approximately 90 days. This combination factor, among others, accounts for possible interactions between genetic groups and the environmental factors. $\beta_{NBA_j(t)}$ is the vector comprising the fixed effect time-depen- dent factor of the number born alive class j at time t, with 9 classes defined as follows: nulliparous, 0, 1 to 2, 3 to 4, 5 to 6, 7 to 8, 9 to 10, 11 to 12 and > 12 born alive; for this factor, levels changed at every parity. $\beta_{GPPO_k(t)}$ is the vector comprising the effect of the combination k between the genetic group and positive palpation order at time t; this was also fitted as a time-dependent factor with 80 levels. It allows for taking into account the possible effect of the interaction between the genotype and the parity order. This factor allowed us to assume a different pattern of risk accumulation during the life of the animals for the different genetic groups, that is assuming the genetic group effect as a time-dependent factor. $\beta_{PS_l(t)}$ is the vector comprising the time-dependent effect of the physiological status l of the doe at time t. This factor reflects the combination between the reproductive status of the does (pregnant, non-pregnant and unknown) and the lactational status of does (lactating or non-lactating).

Data analysis was conducted using the Survival Kit 6.0 software (Ducrocq et al., 2010). The model was solved to get the estimates of the differences between all the genetic groups and the VV group, as well as the (co)variance matrix between these estimates. The contrasts were defined as the differences on log-hazard between V line (Reference line) and the other genetic groups, within the different PPO levels.

In these contrasts, the part of the genetic effects accounted for by GFYS was considered by adding the average of the effect of the GFYS levels in which the lines of interest were involved. From these contrasts and their variance-covariance structure, the differences between direct and maternal genetic effects of the lines, as well as the direct heterosis, were estimated by generalized least squares according to the Dickerson model (Dickerson, 1969). The significance of the estimated contrasts and heterosis was assessed setting the first type error at $\alpha = 0.05$. Dickerson model was the model of choice because of its common use to analyse crossbreeding and relative simplicity where the expected performance Y_c of the type c of doe can be written, following the Dickerson´s model as:

$$Yc = \mu + \sum_{i=1}^{n} \lambda_j g_j^I + \sum_{i=1}^{n} \beta_k g_k^M + lm \neq \sum \gamma_{lm} h_{lm}^I,$$

where n is the number of lines; g_j^I the direct genetic effect of the line i, being λ_j the gene proportion which j contributes to c; g_k^M is the maternal genetic effect of the line k, being β_k the gene proportion which k contributes to the dams of c; h_{lm}^I is the direct heterosis between lines i and j, being γ_{im} the contribution of the lines a l and m to the heterosis of c.

TABLE 1 Summary statistics for rabbit's functional longevity of censored and uncensored records in the data set

	Censored[a] records 2,784 (38.61%)	Uncensored[b] records 4,427 (61.39%)
Minimum time (day)	5	3
Maximum time (day)	895	873
Average time (day)	334.43	196.82

[a]Records from does that had not completed their productive life.

[b]Records from does that had completed their productive life.

3 | RESULTS

The contrasts for the log-hazard between the four maternal lines, globally and for the different productive cycles are presented in Table 2. The presented contrasts could be used to calculate the relative risk of elimination or death of a doe as the exp(log-hazard). Line L showed the highest capacity to overcome the risk factors that can lead to death or culling. The L line showed hazard ratios with respect to A, H and V lines of 0.77 (exp (−0.26)), 0.82 and 0.78, respectively, being the log-hazard ratio significant for the cases involving A and V lines. These figures mean a high risk of culling was observed in females from A, H and V lines were 1.29, 1.22 and 1.28 times the risk of L does. No overall significant differences between A, H and V lines were found. Performing the same set of contrasts within positive palpation order (number of productive cycle), it was observed that at the first cycle, A and V does had 1.84 and 1.51, respectively, more risk of being eliminated from the herd than H line does. During the second and third cycle, no significant differences were observed between lines. The occurrence of global significant differences between A and V lines with respect to L line was due to the fact that during the last cycles, significant differences between lines were observed. In the fourth cycle, there was 1.36 times more risk of death or culling for a V doe than for an L doe, whereas in the fifth parity this ratio was 2.14. In the fifth cycle, the risk ratios of A, V and H lines with respect to L were significant, showing the values of 2.3, 2.14 and 3.15, respectively.

Concerning the general differences between crossbred does, (considering together each cross and its reciprocal, Table 3) and line V, there were no significant differences between the crossbred groups and line V, except for the cross between A and H lines, which was favourable to line V. Analysing the same differences by productive cycle, significant differences were found at the first cycle and during cycles equal or higher to the 5th. In the first cycle, the groups HL and LH, and LV and VL showed favourable and significant differences with respect to V line for the associated risk. However, the does of the groups HA and AH had a risk of elimination from the herd 1.3 times greater than that of V line at their first cycle. Moreover, in general, no significant differences were found at the third and fourth cycles, except a significant difference in favour of crosses LH and HL at the third cycle. At cycle orders ≥ 5, the crossbreds had higher associated hazards than V line. The differences were important, and the relative risk ranged from 1.32 to 2.34.

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

Differences in direct genetic effects between lines are presented in Table 5. There are two results that merit attention. The first one is that line V had the highest associated risk and its differences were significant with respect to the lines H and L. In the case of the H line, the difference to the V line is due to a high and important risk associated with V line at the first productive cycle, but in the case of the L line, the difference is established during the fourth and later productive cycles. The second important result refers to the fact that the direct effect of the L line had the lowest associated hazard, especially at cycles ≥ 5. At these cycles, the relative risks of the L line with respect to those of lines A, H and V were only 0.39, 0.49 and 0.53, respectively. Also, from Table 5 it can be concluded that no significant differences were observed between A and V lines, either globally or at any cycle.

TABLE 2 Contrasts (standard errors) between rabbit lines for the global log-hazard (GR) and for the log-hazard associated with the consecutive positive palpation order (OPP)

Contrast[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th 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)*

[a]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line).

*Significant difference at $\alpha = 0.05$.

TABLE 3 Contrasts (standard errors) between crossbred groups[a] and V line rabbits for the global log-hazard (GR) and for the log-hazard associated with the consecutive positive palpation order (OPP)

Contrast[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th OPP
AH- VV[b]	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)*

[a]One cross and its reciprocal are considered together.

[b]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line; All-VV = The contrast between all crossbred and V line).

*Significant difference at $\alpha = 0.05$.

TABLE 4 Contrasts (standard errors) between reciprocal crosses[a] of rabbits for the global log-hazard (GR) and for the log-hazard associated with the consecutive positive palpation order (OPP)

Contrast[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th 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)

[a]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line).

*Significant difference at $\alpha = 0.05$.

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

Contrast[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th 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)*

[a]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line).

*Significant difference at $\alpha = 0.05$.

The observed differences in global risk between lines regarding maternal genetic effects were small and in general, not significant, except between lines H and V in favour of V line (Table 6). Nevertheless, over the course of the life of the animals, some significant differences were observed. During the first productive cycle, the difference in the maternal genetic effect between A, H and L lines and the V line was found to be significant and favourable to the last line. Late in the life of the animals, a negative maternal effect was associated with the H line, compared to the maternal effects of lines A and L. The estimated differences in maternal effects approximately match the observed differences between any cross and its reciprocal. The estimated values for the direct heterosis depended on the lines involved in the cross (Table 7). In general, the heterosis for the global log-hazard was not significant, except for the cross AH, which had an unfavourable value (positive risk associated with the cross). However, when different lifetime periods are considered, it is

important to note that later cycles are always associated with significant and relevant, but unfavourable, heterosis effects. On the contrary, at earlier ages some favourable effects were observed.

4 | DISCUSSION

In the present study, L line had the lowest risk of death or culling. This result was in accordance with previous reports by EL Nagar et al. (2020) who stated that the L rabbit line had a longer functional longevity than the A, V, H and R rabbit lines. Also, Theilgaard et al. (2007) reported the high capability of the L line to recover from stress and to manage its body resources better than V line. The differences favouring L line were expected because this line was founded by selecting females from commercial farms that showed an extremely long productive life which was measured as a function of the number of parties; ≥ 25 parities and prolificacy near or above the average of the Spanish commercial rabbit population (Sánchez et al., 2008). Nevertheless, for the other lines, neither the foundation nor the selection process relied on any longevity criteria (Ragab & Baselga, 2011). In a study comparing L and V lines for longevity, Sánchez et al. (2008) reported that the mean of the relative risk between L and V lines was 0.80 (exp (−0.22)), which indicated that it was 1.24 times more likely for a V doe to be culled or to die than for an L doe. Moreover, the relative risks between V and L lines at their foundation and in present generations were reported to be 1.55 and 1.56, respectively, always in favour of L line (EL Nagar, 2015).

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

In the fifth cycle, a better survival rate was also observed for the V line than for the H line, compensating for the higher risk associated with the V line at early cycles. These different ways of cumulating risk for the different genetic types supposes that the interaction between PPO and genetic type is significant, and this implies that the pattern of risk along the successive PPO was different for the different genetic types. In this regard, however, El Nagar et al. (2020) showed that, in a single farm, with the same purebred lines as were used in this study, they followed a similar lifetime risk pattern. This risk decreased as the order of positive palpation increased. In that study, the largest hazard difference was 1.30 between the OPP1 and OPP3 in L line. Sánchez et al. (2004) attributed the high risk associated with the first two parties to the fact that the does are still growing and kindling would be an important risk factor. The same tendency was observed by Lenoir et al. (2013) who reported that in the Hycole D line, the risk associated with the first parity (1.47) was greater than that for the second parity (1.22). On the contrary, in pigs, Tarrés et al. (2006) found that the risk of culling a sow increased in higher parity orders.

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

It should be noted that the increased risk associated with crossbred does began at the fifth cycle, when the cost of the does had already been recovered. Additionally, Rosell (2003) reported that around 50% of the dead and culled does are in one of the first three kindlings. Therefore, based on these two

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

Contrast[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th 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)

[a]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line).

*Significant difference at α = 0.05.

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

Genetic groups[a]	GR	1st OPP	2nd OPP	3rd OPP	4th OPP	≥5th 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)*

[a]Line of buck × line of doe (A = A line; L = LP line; H = H line; V = V line).

*Significant difference at $\alpha = 0.05$.

factors, the importance of using crossbreed instead of purebred does in the commercial farms appear especially with the high levels of culling due to productivity causes.

In another study (Piles, et al., 2006) where lines A, V and Prat were evaluated, no significant differences were found between the direct genetic effects of A and V lines. However, the relative risk between both lines in that study was higher than in our work. In that study, significant differences in direct genetic effects between A and Prat lines were found. In the present study, it was not possible to detect overall significant difference in the direct genetic effects. For instance, between A and H lines and between L and H lines, the differences between direct genetic effects generated in certain cycles were compensated by differences of the opposite sign generated during other cycles.

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

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

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

5 | CONCLUSIONS

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

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data sets used and analysed during the current study are available from the corresponding author on reasonable request.

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