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- 28 Running Head (Short title): COMPARING FIVE RABBIT LINES IN TERMS OF
- 29 LONGEVITY.

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ABSTRACT

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The objective of the present study was to compare five Spanish rabbit lines in terms of functional longevity. Four of them are maternal lines (A, V, H and LP) founded on different criteria and being selected for litter size at weaning. The fifth line is the paternal line R, founded and selected for post-weaning daily gain from 28 to 63d. The last generations of selection considered in the present study were 44th, 39th, 10th, 8th and 32th generations for lines A, V, H, LP and R, respectively. Cox proportional hazard models under a Bayesian approach were used to perform two comparisons between the lines. The first comparison was done at the origin of the lines, involving the complete data set (from March 1980 to March 2013; records of 15670 does), and the complete pedigree (19405 animals), so the effect of selection was considered. The second comparison was done at two fixed times through the selection processes when all lines shared the same environmental and management conditions (from March 1997 to September 1998 and from March 2011 to September 2012). For the second comparison the same model as the first comparison was used, but excluding the additive effects from the model of analysis, and involving only the data corresponding to each period, so the differences between the lines were not dependent on the additive values of the animals. At their foundation, lines V, H and LP showed a substantial superiority over line A. The line R also had higher risk of death or culling with relevant differences when compared to V, H and LP lines. The line LP had the longest productive life compared to the other lines; this may be a consequence of its foundation process. The maximum relative risks were observed between the lines LP and R (0.239). This means that at foundation it was 0.239 times more likely for a LP doe to be culled/died than for a R female. The interactions between year-seasons and the lines were important and affected the differences

between the lines at their origin. During the two periods of the comparison at fixed time, lines A and R showed low longevity compared to the other lines. However, as the selection process evolves, the differences between these two lines and the other lines were reduced, which demonstrate the importance of natural selection in these lines. The predicted differences between the four maternal lines match well the phenotypic differences computed at the fixed times of comparison, indicating that the genetic model is suitable to describe the longevity records in these populations, although, this was not the case for the paternal line R. It could be concluded that the average longevity of a population greatly depends on the criteria followed for the foundation of this population. Along the generations of selection for litter size, the differences of longevity between lines tend to decrease, due to the action of the natural selection in the lines of lower longevity.

KEYWORDS: line foundation, selection, functional longevity, maternal lines, survival
 analysis, rabbits.

INTRODUCTION

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The success of any selection experiment could be limited by the criteria and procedure used to recruit animals in the base generation, i.e. foundation, this holds for any specie and trait, and it is particularly relevant in rabbit lines. One way to quantify the consequences of considering different foundation criteria is to compare. for the desired traits, performances of lines sharing the same environmental and management conditions at different moments of the selection processes, for example at their origin and after some generations of selection. Longevity is a functional trait directly related to farm profitability; thus, selective breeding to increase the length of productive life could help to reduce costs attributed to replacements. With the aim of creating a maternal line outstanding for its longevity, Sanchez et al. (2008) recruited, from commercial farms, females showing and extraordinary length of productive live (over 25 parturitions) but keeping a prolificacy performance above the mean prolificacy of the Spanish rabbit commercial population. This selection procedure was chosen so because traditional breeding methods, based on limited selection pressure within a close populations, were not expected to be success since the time required to obtain relevant information for accurately ranking the animals within each generation would be rather long (Larzul et al., 2014). The aim of this study was to compare the functional longevity of the aforementioned line, with others raised in the same selection farm. Some of these lines are being selected for litter size at weaning and other is selected for postweaning daily gain. As the comparisons between the functional longevity of the lines are done at their foundation and also at fixed time periods of the selection process of the lines it is possible to assess how the initial genetic differences evolve as consequence of the different selection procedures implemented for each line.

MATERIALS AND METHODS

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Ethical statement

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

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Animals and Management

Data used in the present study were collected from five Spanish lines of rabbits, four of them are maternal (A, V, H, LP) and the fifth is a paternal line (R). These lines are reared at a selection nucleus located in the farm of the Institute for Animal Science and Technology, Universitat Politècnica de València. The records were collected along the generations of selection of these lines from March 1980 to March 2013. The process of foundation of line A began in 1976 sampling New Zealand White (NZW) rabbits, reared by farmers near Valencia (Spain). After three generations without selection, the line is being selected since 1980 by a family index based on litter size at weaning (Estany et al., 1989). Line V was founded in 1980 as a synthetic line, mating crossbred animals that were progeny of four specialized maternal lines, after three generations without selection, the line is being selected (Estany et al., 1989) to increase litter size at weaning since 1982. Line H was founded applying hyperprolific selection and embryo cryopreservation techniques (García-Ximénez et al., 1996; Cifre et al., 1998). Hyperprolific does were assembled from a large commercial population, spread over different Spanish farms. This line was kept since its foundation in 1996 at the nucleus of selection until May, 2004 (10th generation of selection). Line LP was founded selecting females from commercial farms that showed extremely long productive lives and prolificacy near or above the average of the Spanish commercial rabbit population (Sánchez et al., 2008). This line is being selected since 2003 to increase litter size at weaning. In V, H and LP, animals are evaluated for litter size using a repeatability animal model. Line R comes from the fusion of two paternal lines, one founded in 1976 with California rabbits reared by Valencian farmers and the other founded in 1981 with rabbits belonging to specialised paternal lines (Estany et al., 1992). The method of selection has always been individual selection on post-weaning daily gain. The farm where the rabbits are housed has isolated roofs and the ventilation is controlled depending on the indoor temperature. The cages for does (90 cm long, 50 cm wide and 40 cm high) and progeny (80 cm long, 50 cm wide and 30 cm high) are standard flat deck. Management of animals in the different lines is the same, using natural mating; bucks and does began reproduction from 17 to 18 weeks of age. On the day 12 post-mating each does are tested for pregnancy by abdominal palpation, and non-pregnant does are mated back. Does are mated 11 days after kindling, usually one female is always mated to the same buck; litters are examined each morning during the suckling period to remove dead kits. Kits are reared by their own dams, and weaned at 28 days post kindling. Then animals are individually identified by a number tattooed on the left ear and transferred to the fattening cages (8-9 rabbits per cage) until marketing at 63 days. Both breeding animals and progeny are fed ad libitum on pelleted commercial rations. The animals were kept under controlled 16-h light: 8-h dark photoperiods. Mating males and females in the maternal lines always belong to the same generation, i.e. non-overlapping generations mating. In these maternal lines does for the next generations are selected from 25 – 30 % of the best evaluated matings, with

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a limit of 4 does per mating. Each sire contributes a son to the next generation, and is selected from the best mating of the sire.

Management of animals in line R is somewhat different compared to other lines, where in the last generations the does were artificially inseminated and the candidates for selection were genetically evaluated exclusively based on their phenotypic values, i.e. individual selection. Similarly to the maternal lines, in the R line each sire contributes a son to the next generation and does are selected at a rate of around 20%, referred to the average growth of the previous four weeks. Mating was conducted in non-overlapping generations until the 25th generation. The generation interval is about 6 months and the estimated response to selection was about 0.5 g/day per generation (Estany et al. 1992). In maternal lines the generation interval is about 9 months and the response to selection ranged from 0.076 (Tudela et al., 2003) to 0.085 (García and Baselga, 2002) kit weaned per parturition by generation.

For a suitable genetic evaluation of animals in the nucleus, some common culling criteria in commercial farms are not considered; i.e. does with low levels of production or no strong reproductive delay are not culled.

Data and Statistical Models

The analysed trait was the length of the productive life (LPL), this trait was measured as the difference in days between the date of the first positive palpation test and the date of death or culling for involuntary causes (Sánchez et al., 2008). Once again, does were never culled based on production results, therefore, LPL reflected a direct measurement of functional longevity. Date and reason for culling or death are systematically recorded, as well as all the information regarding mating and

parturition dates, pregnancy status after the abdominal palpation and prolificacy. Does removed to free space for females of the next generation or eliminated because of accidents or other technical reasons not related to health status were treated as censored (Piles et al., 2006b). Thus, the record of each animal included the called censoring code, representing (0 = censored; 1 = uncensored) and all the information regarding physiological status of the female during its entire life (reproductive and lactation status), as well as all the prolificacy records and the line to which the animal belonged. Functional longevity was analysed using Cox models. A Weibull model was discarded because of its misfit due to the high proportion of does dying in the first parturition (Sánchez et al., 2004; Piles et al., 2006b). The pedigree file involved 19,405 animals, and the number of does with records was 15,670, out the total number of females with records 5,775 had censored data (Table 1), most of these does were removed before the end of their productive life because of space limitations in the nucleus and the followed breeding program. In order to accomplish the comparison of the LPL between the lines this data set was used either completely, for the comparison at the foundation; or different subsets were extracted, for the comparisons at given periods of the selection process. The number of does for the comparisons at foundation and at fixed times are shown in Table 1. In a first analysis, the complete data set from the foundation of each line until March 2013 was considered, including the full pedigree. In this analysis a complete genetic model (CM) was used fitting the systematic effects of line-year-season combination (LYS), positive palpation order (OPP), and number born alive at each kindling (NBA) as time-dependent factors; in addition to the additive genetic value of the animal as a random effect. In detail, the CM model was:

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$$h_i(t|\mathbf{x'}_i(t)) = h_0(t) \exp\{\mathbf{x'}_i(t)_{LYS}\boldsymbol{\beta}_{LYS} + \mathbf{x'}_i(t)_{OPP}\boldsymbol{\beta}_{OPP} + \mathbf{x'}_i(t)_{NBA}\boldsymbol{\beta}_{NBA} + \mathbf{z'}_i\mathbf{u}\}$$

where $h_i(t|\mathbf{x}'_i(t))$ is the hazard of animal i at time t, for time-dependent factors, $x'_{i}(t) = \{x'_{i}(t)_{LYS_{i}}\}$ affected covariates indicated by by $\mathbf{x}'_{i}(t)_{\text{OPP}}, \mathbf{x}'_{i}(t)_{\text{NBA}}, \mathbf{z}'_{i}$; $h_{0}(t)$ is the baseline hazard function at time t, approximated by a step-wise function given by $h_0(t) = h_{0m}$ for $t \in [\tau_{m-1}, \tau_m]$; m = 1, ..., M +1, where τ_1, \dots, τ_M are the M different ordered survival times, $\tau_0 < \tau_1 < \dots < \tau_M < \infty$ τ_{M+1} ; $\tau_0 = 0$ and $\tau_{M+1} = \infty$. β_{LYS} , is the vector of regression coefficients for the lineyear-season (LYS) combinations with 212 levels, where the year-season was defined by 6 months' time intervals. The number of levels were 63, 63, 17, 20 and 49 for the subsets of A, V, H, LP and R lines, respectively. β_{OPP} , is the vector including the effect of the three levels of the positive palpation order (OPP) (1, 2 and 3 or more positive palpation orders), the changes of level in this factor occurred after every pregnancy test. β_{NBA} , is the vector including the effects of 5 classes of number born alive in each kindling (NBA); the first level corresponded to does that had 0 NBA, the second level to parturitions with 1 to 4 born alive, the third to parturitions with 5 to 8 born alive, and so on until the fifth level which corresponded to parturition with at least 13 born alive. The changes of levels in this time-dependent factor occurred at parturition. Finally, u_i is the additive genetic effect of the animal i, this factor was assumed to follow a priori a multivariate normal distribution with mean 0 and (co)variance G. In order to account for the genetic heterogeneity between the five G was defined as a block-diagonal matrix formed by elements $\mathbf{A}_i \sigma^2_{a,i}$, where \mathbf{A}_i is the numerator relationship matrix of the line i, and $\sigma^2_{a,i}$ is the additive genetic variance for that particular line. The additive genetic variances ($\sigma^2_{a,i}$) were assumed to be known and equal to 0.17, 0.05, 0.29, 0.29 and 0.07 for A, V, H, LP and R lines, respectively (EL Nagar et al., 2020). The prior distributions for the remaining model parameters were defined in the same way as in Sánchez et al. (2006). Baseline hazard step-wise

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function elements h_{0m} for $m=1,\dots,M+1$ were assumed to be independent and 221 identically distributed (i.i.d.) : $p(h_{0m}) \sim \frac{1}{h_{0m}}$, where $0 < h_{0m} < \infty$. This is a long-222 uniform prior which supposes an uniform distribution for the logarithm of h_{0m} . The 223 224 elements of all β were assumed to be i.i.d. following a uniform distribution. 225 In the analysis of the complete data set using CM additive genetic effects account for 226 the genetic responses in the different lines. Thus, the contrast of the differences between each pair of lines based on the year-season levels shared by both lines 227 228 reflect the difference between the lines at their foundation, reflecting genetic differences between the lines when the respective populations were created. The 229 230 periods in which each pair of lines were sharing the same environmental and 231 management conditions were from March 1983 to September 2003 and from March 232 2006 to March 2013 for lines A and V; from March 1997 to September 1998 for lines A and H; from March 2006 to March 2013 for lines A and LP; from March 1990 to 233 234 March 2013 for lines A and R; from March 1997 to September 1998 for lines V and 235 H; from September 2004 to March 2013 for lines V and LP; from March 1990 to 236 September 2003 and from March 2006 to March 2013 for lines V and R; from March 237 1997 to September 1998 for lines H and R; and from March 2006 to September 2013 238 for lines LP and R. The lines H and LP only shared one year-season, for this reason 239 the contrast between them was not estimated. 240 It is possible to compute actual differences between lines at different periods of time 241 shared by some of them, without relying on the genetic model and by only using the 242 records from those given periods. For the computation of this actual differences 243 between the lines the model should be the same as that previously described but 244 removing the additive genetic effect, we name this as incomplete model (IM). In this 245 case the line effects refer to the real genetic merit of the lines at the time of

comparison as a consequence of selection and genetic drift, but not being dependent on the genetic model. The difference between two lines at a defined period was computed as the difference between the averages of the within line year-season effects for that period. The periods chosen for comparison were arbitrarily defined by the last three year-seasons shared by at least four of the lines under the same management conditions. These periods were from March 1997 to September 1998 for comparisons between the lines A, V, H and R, and from March 2011 to September 2012 for comparisons between the lines A, V, LP and R. It is also possible to predict the actual differences between the lines (those calculated with the IM) at the defined periods using the results of the analysis with the CM model and the complete data set. The difference between two lines in the abovementioned arbitrary periods can be predicted adding to the contrast between the within line average of the solutions of the year-season effects to the differences between the additive values of the animals of each line performing in those particular year-season levels. The estimated differences between lines for the previously indicated arbitrary periods, calculated with IM model, can be compared with the predicted differences obtained using CM model and the whole data set. This comparison could be seem as a way to check the adequacy of the CM model to explain the complete longevity data set. Both for CM and IM parameter estimation was performed by a Bayesian approach, based on statistics computed from samples of the marginal posterior distributions obtained using a Gibbs sampling algorithm. The Gibbs sampler algorithm comprised 200,000 iterations, discarding the first 20,000 in order to allow for the algorithm to reach convergence to the marginal posterior distributions. Afterwards, one sample in each 20 was saved to avoid high correlations between consecutive samples. The

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post-Gibbs analysis used to calculate the parameters of interest of the marginal posterior distributions was implemented with the coda package of the R program (Plummer et al., 2006). Convergence of the chains for the parameters and contrasts of interest was assessed using the Z-criterion of Geweke (Geweke, 1992).

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RESULTS AND DISCUSSION

Comparison between lines at foundation

Monte Carlo standard errors were very small in all cases and they are not showed in the tables. Geweke test did not detect lack of convergence in any case. The comparison among lines at their foundation is shown in Table 2. The contrasts are estimable functions between each pairs of lines through the years-season in which both lines were subjected to the same environmental and management conditions. Using all data and the full pedigree, the additive effects of the animals were considered in the model, the selection response was accounted for by this effect, and consequently, the effects of the lines (included in the line-year-season combination) expressed the values at their foundation. The lines V, H and LP showed a substantial superiority over line A. The line R had higher risk of death or culling with relevant differences when compared to V, H and LP lines. The maximum relative risks were observed between the lines LP and R, and between LP and A. The relative risk describes how much more likely it is that culling or death occurs within one level of a given factor relative to another level of the same factor. For instance, at foundation it was 3.152 times more likely for an A doe to be culled/died than for a LP doe (Table 2). Line LP was created from does that had at least 25 parities (Sánchez et al., 2008). The results presented in Table 2 could seem to show inconsistencies, for example, the difference between lines A and V at their foundation was 0.495 and

between lines A and LP was 1.148. Their difference, (1.148-0.495) is not exactly 0.436, the contrast between lines V and LP. This deviation between the two values is due to the different sets of year-seasons involved in each particular contrast and also to the fact that the model included the interaction line-year-season. The interaction terms involved in the contrasts A-V and A-LP are, obviously, different to that involved in that estimated between V and LP lines, thus the last one cannot be exactly reconstructed from the previous. The longer productive life of LP does could be considered as an indicator of the successful foundation procedure of this line. The line A was created by mating does and bucks of the New Zealand White breed belonged to populations maintaining the standard morphological characteristics of the breed. This line was shown to have a high susceptibility to enterocolitis disease, which was a condition present during some periods shared with the other lines (Ragab and Baselga, 2011). Piles et al. (2006a) also found, in a diallel cross experiment, relevant differences in the genetic effects for functional longevity between maternal rabbit lines A, V and Prat and the crossbred females from them. They stated that a A doe was twice as likely to be replaced than a crossbred Prat x A doe, and in general, the genetic groups with the highest relative risks were those in which the A line participated. All these results, particularly those presented in this study that refer to the situation at the foundation, suggest the hypothesis that founding line A based on morphological aspects of the animals created a genetic load, related with susceptibility to diseases or longevity, that still segregating in the population. We could speculate that if the founder animals would be selected based on any performance criteria, this genetic load would be minimized, since those animals with the putative deleterious alleles would not be selected since their performance phenotypes would be deteriorated.

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In another study comparing lines LP and V, Sánchez et al. (2008) indicated the superiority of the line LP over the line V with respect to survival ability, especially at later cycles. They attributed this result to the foundation procedure in the LP line which was focused on late life survival. In spite this result is the same as the one we have reported in this study, this comparison between LP and V lines was not a comparison at foundation time, because for V line only the closest relationships sibs were considered in the study. In contrast, in the present study all the available pedigree information was used. Line R showed higher risk at foundation compared to the other lines, and the differences between line R and both LP and V lines were relevant. Considering that line R was created by mating animals maintaining the standard morphological characteristics of the Californian breed with animals from another synthetic line created by mating animals from three commercial paternal lines (Estany et al., 1992), the argument considered with regard to A line about the genetic load that was created during the foundation of the line only apply partially. For the case of the R line part of the founders came from populations selected for growth performances. Thus, the lower survival ability of the R line with respect to the other lines could be also linked to a certain genetic antagonism between early growth and length of the reproductive life.

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Comparison between lines at fixed periods

The estimated differences between the lines A, V, H and R from March 1997 to September 1998 and between the lines A, V, LP and R form March 2011 to September 2012 are presented in Table 3. These contracts reflect differences at the foundation of the lines plus the differences generated as a consequence of the

selection process. Lines A and R had a greater risk of death or culling than lines V and H. These overall trends were the same as those observed in the comparison at the foundation time of these lines. The contrasts show the inferiority of the line A for longevity over the other maternal lines during the two periods of comparison. This result is in agreement with those of Ragab et al. (2011) who found that line A was more sensitive to the risk factors compared to V and LP lines. The LP does had a lower risk of death or culling compared to A, V and R lines, this result could be explained, again, as a direct consequence of the foundation process of the LP line. The same result was found by Sánchez et al. (2008) who reported that the LP line had a longer reproductive life than the V line. In general, as the selection process evolves, the differences between the lines were reduced. This may be a consequence of a natural selection process, which is more intense for the lines of lower longevity. For animals with lower longevity, the probability of dying before leaving progeny selected for litter size is higher than for animals having higher longevity. Moreover, the selected progeny of parents with low longevity would have a higher probability of dying before reaching the maturity, thus not leaving offspring for the next generation. This phenomenon can be clearly observed in line A, which had low longevity at its foundation, but it has greatly improved its longevity along many selection generations, thus in the comparisons at fixed times the magnitude of the differences with the other lines are clearly lower than at foundation. Other evidence of these natural selection process in the A line can be seen in the differences between the breeding values of animals of each line involved in the comparison, which seem to favour the line A (Table 4). This progress of the line A is consistent with the genetic trend drawn by its relatively higher additive genetic variance (0.17) (EL Nagar et al., 2020).

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The case of the R line is different to that of the A line. In the comparisons done between March 1997 and September 1998, a certain improvement with respect to the situation at the foundation was observed, but this improvement was less evident than that for the A line, this is compatible with the low additive variance estimated for this line (0.07) (EL Nagar et al., 2020). In the second period of comparison (March 2011 - September 2012) an opposite pattern was observed; for example, with respect to the V line, R line log-hazard was slightly worse than that at foundation, -0.697 and -0.620, respectively. The comparisons involving R line should be considered with caution, since, as it has been previously stated, the reproduction of this line has been organized in a different way to that of the other populations: in the last generations artificial insemination has been used and mating between animals from different generations has been allowed. The change from natural mating to artificial insemination was a management decision adopted to overcome the low fertility observed in the population, this has been a serious handicap to properly generate candidates for the selection. Even after the change to reproduction by artificial insemination these fertility problems remained, probably associated to an excess of body fat in the females. This low fertility issues have had strong consequences in the correct implementation of the selection process for postweaning growth and they are probably also the reason why in the last generations the LPL of the R line seems to be deteriorated. Nonetheless, the genetic trend seems to be favourable, as reported by EL Nagar et al., (2020) and it is also observed when comparing contrasts between breeding value prediction averages in table 4. Thus, the observed deterioration of the LPL in the R line, during the last generations, must be explained by the involvement of the interaction between lines and year-seasons effects. As it has been stated, for R line, the environmental factors could be said to

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be particular unfavourable, associated with the low fertility of the line in the last yearseasons considered in the comparison. The reported responses for LPL in the studied maternal lines are most likely associated, as previously indicated, to natural selection and not to selection for criteria considered in each line, i.e. correlated response. We proposed this idea because EL Nagar (2015) reported that, in the maternal lines under study, the genetic correlation between longevity and prolificacy traits (the selection criteria) were nearly null. For the case of the R line, the hypothesis of the observed response on LPL to be a correlated response cannot be discarded since for this population the correlation between longevity and postweaning growth has not been estimated. The differences between lines at fixed times, obtained using the dataset limited to these times with the CM are presented in Table 4. Comparing these differences with those estimated using the IM; we can see that, for the case of the maternal lines (A, V, H and LP) they are fairly relatively similar. This can be interpreted as an evidence about the suitability of the genetic model to describe this longevity data in order to predict the breeding values and to estimate differences between the lines at their origins. Similar conclusions were obtained by Ragab and Baselga (2011) regarding reproductive traits and by Minguez et al. (2016) in relation to growth traits for the same four lines. For the paternal line R, the differences predicted using CM did not match well those estimated using IM. Thus, according to our previous reasoning for this line it should be concluded that the model is not suitable for fitting the available LPL data. As it has been stated previously, this line presents physiological characteristics very different to that of the other lines considered in this study. These peculiar characteristics get reflected in the statistical model, for example by making the year-season effect to have a completely different meaning than that in the

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maternal lines, and as these interaction terms are also included in the contrasts we have reported they completely alter the results. In any case the output of our study on this regard is that it seems that for the R line the model for fitting LPL should be reviewed.

CONCLUSIONS

By studying functional longevity data from five populations raised partially under the same management and environmental conditions we have observed than the differences between the lines at their foundation clearly respond to the selection criteria used for recruiting the animals for the base population. On this regard, two clear extreme examples have been reported: i) LP line, selected for LPL at its foundation, which clearly favoured the trait. ii) A line, selected not attending to any performance criteria, but according to fulfilling the morphological characteristics of a breed, this procedure seems to have created a genetic load in the population that still segregating and penalizes performances and fitness. Along the generations, at least for the maternal lines under study, it seems to exist a natural selection or unintended artificial selection process that have improved the survival ability of the females reducing the differences between lines with regard to their LPL or risk of being culled. The R line, selected for post-weaning growth, show a clearly different pattern probably associated with the unsuitability of the used model to properly fit the peculiar physiological characteristics of this line that alter its management.

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

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DATA AVAILABILITY STATEMENT

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

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527 TABLES

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Table 1 Number of rabbit does involved in the study

Line	Foundation [†]	First period [‡]	Second period [§]
Α	4986	348	320
V	5275	350	362
Н	1156	317	-
LP	1224	-	333
R	3029	243	266
All lines	15670	1258	1281

[†]Total number of does. ‡Number of does at first period comparison. §Number of does at second period comparison.

Table 2 Differences between the lines at foundation for longevity (log-hazard) estimated with the complete genetic model and all data set

Contrast	PM*	PSD**	RR***	HPD95% [†]	P(%) [‡]
A-V	0.495	0.230	1.640	0.029 , 0.936	99
A-H	0.699	0.280	2.012	0.162 , 1.270	99
A-LP	1.148	0.321	3.152	0.510 , 1.753	100
A-R	-0.125	0.240	0.882	-0.611 , 0.345	77
V-H	0.050	0.192	1.051	-0.333 , 0.418	60
V-LP	0.436	0.192	1.547	0.072, 0.819	99
V-R	-0.620	0.158	0.538	-0.935 , -0.321	100
H-R	-0.344	0.185	0.709	-0.734 , -0.003	97
LP-R	-1.432	0.156	0.239	-1.725 , -1.119	100

^{*}Marginal posterior mean. ** Marginal posterior standard deviation. ***Relative risk = exp(contrast). †Marginal posterior highest density region covering 95% of the density.

[‡]Probability of the difference being >0 when the contrast >0 and probability of the difference being <0 when the contrast <0.

Table 3 Differences between the lines for longevity (log-hazard) at fixed times estimated with the incomplete model and data set of the fixed times

Contrast	PM*	PSD**	RR***	HPD95% [†]	P(%) [‡]
		March 1997 - Septe	ember 1998 (First p	eriod)	
A-V	0.395	0.111	1.484	0.177 , 0.611	99
A-H	0.295	0.119	1.343	0.052, 0.515	99
V-H	-0.099	0.121	0.906	-0.347 , 0.129	79
A-R	0.148	0.115	1.160	-0.078 , 0.374	90
V-R	-0.247	0.121	0.781	-0.488 , -0.012	98
H-R	-0.147	0.128	0.863	-0.400 , 0.102	88
		March 2011 - Septer	nber 2012 (Second	period)	
A-V	0.122	0.120	1.130	-0.121 , 0.365	83
A-LP	0.564	0.156	1.758	0.270, 0.881	99
V-LP	0.442	0.150	1.556	0.145 , 0.735	99
A-R	0.015	0.134	1.015	-0.248, 0.271	54
V-R	-0.107	0.132	0.899	-0.364, 0.149	79
LP-R	-0.550	0.163	0.577	-0.852 , -0.227	100

^{*}Marginal posterior mean. ** Marginal posterior standard deviation. ***Relative risk = exp(contrast). †Marginal posterior highest density region covering 95% of the density.

[‡]Probability of the difference being >0 when the contrast >0 and probability of the difference being <0 when the contrast <0.

Table 4 Differences between the lines for longevity (log-hazard) at fixed times estimated with the complete genetic model and data set of the fixed times

Contrast	PM*	PSD**	RR***	HPD95% [†]	P(%) [‡]	D1§	D2 [¶]
		Ма	rch 1997 - Sept	tember 1998 (First pe	riod)		
A-V	0.314	0.113	1.369	0.087, 0.532	99	0.648	-0.334
A-H	0.251	0.120	1.285	0.008, 0.479	98	0.699	-0.448
V-H	-0.063	0.125	0.939	-0.302, 0.181	69	0.050	-0.113
A-R	-0.073	0.111	0.930	-0.285, 0.143	74	0.355	-0.428
V-R	-0.387	0.114	0.679	-0.622 , -0.179	100	-0.293	-0.094
H-R	-0.324	0.122	0.723	-0.570 , -0.089	100	-0.344	0.020
		Marc	ch 2011 - Septe	mber 2012 (Second p	eriod)		
A-V	0.104	0.127	1.110	-0.152 , 0.345	80	0.655	-0.551
A-LP	0.710	0.157	2.034	0.412 , 1.029	100	1.332	-0.623
V-LP	0.605	0.153	1.831	0.298, 0.896	100	0.677	-0.072
A-R	-0.592	0.127	0.553	-0.835 , -0.341	100	-0.251	-0.342
V-R	-0.697	0.121	0.498	-0.930 , -0.456	100	-0.906	0.209
LP-R	-1.302	0.154	0.272	-1.614 , -1.010	100	-1.583	0.281
LF-K	-1.302	U. 154	0.272	-1.014, -1.010	100	-1.303	

*Marginal posterior mean. **Marginal posterior standard deviation. ***Relative risk = exp(contrast). †Marginal posterior highest density region covering 95% of the density. ‡Probability of the difference being >0 when the contrast >0 and probability of the difference being <0 when the contrast <0. §Part of PM due to differences between lines at foundation. ¶Part of PM due to differences in the additive genetic values of the animals belonged to each line involved in the comparison.