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1 TITLE

2 Genotype by feeding regimen interactions for slaughter traits in

3 rabbit and expected responses under restricted and full feeding

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**Running Head (Short title): GENETIC BY REGIMEN INTERACTION ON
SLAUGHTER TRAITS.**

ABSTRACT

The interaction between the genotype and feeding regimen (GxFR) for slaughter traits was estimated from data corresponding to 2,557 animals under full (FF) and 2,424 with restricted feeding (RF). Expected responses to selection under different scenario regarding feeding regimen were also calculated. Body weight at slaughter (SW), carcass weight (CW) and dressing out percentage (DoP) were analyzed by using linear animal models in which records obtained under different feeding regimes were treated as different traits. Animals belonged to Caldes line, selected for average daily gain (G) under *ad libitum* feeding. The selection process information was included in the analyses. Marginal posterior mean of heritabilities were 0.102 for G, and 0.364, 0.257 and 0.167 for SW, CW and DoP under FF feeding. The corresponding values for animals fed on RF were 0.243, 0.203, and 0.379 for SW, CW and DoP, respectively. Genetic correlations between G and CW were positive and moderate, and those between G and DoP were low. The estimated genetic correlation between SW, CW and DoP under different feeding regimens were: 0.73, 0.69 and 0.87, respectively. These correlations cannot be said to be far enough from one to generate relevant GxFR interaction variance, which were estimated to be only 11.1%, 8.6% and 5.3% of the mean of the phenotypic variance for SW, CW and DoP, respectively. This lack of GxFR interaction variance, jointly with the higher heritability of DoP under RF, explains that the genetic improvement of DoP can be done more efficiently recording traits on animals under RF, even if the interest is on the performances under FF, i.e. by indirect selection.

KEYWORDS: Slaughter traits; Feeding regimen; GxE interaction; Genetic parameters; Indirect selection.

INTRODUCTION

Feed restriction is one widely used practice in livestock species to improve feed efficiency and to reduce the incidence of some diseases (in pig: Pouillet et al. (2019); in cattle: Hoffman et al. (2007) and in poultry: Carneiro et al., 2019). The reduction of mortality is due to a decrease in the flow of nutrients that reach the caecum which turns into a lower proliferation of pathogen bacteria (Romero et al., 2010). In rabbits, restricted feeding at fattening also increases feed efficiency (Tůmová *et al.*, 2004; Dalle Zotte *et al.*, 2005) during the restriction period but especially when this is followed by a full feeding period because of the compensatory growth produced at this last stage (Gidenne et al., 2009). Omitting this final *ad libitum* feeding period would penalize the overall growth during the whole fattening period. This feed restriction leads also to a reduction in dressing out percentage (**DoP**) (Maertens, 1992; Knudsen et al., 2014; Uhlířová et al., 2015) because of changes in the body composition, since growth patterns of organs and tissues are also modified (Dalle Zotte and Ouhayoun, 1998). Currently, the degree of implication of the slaughterhouses in rabbit production schema is steadily increasing, for example in Spain, although there are no official statistics, we can estimate that approximately 10% of the rabbit production follows an integration schema. This figure was obtained after conversations with the manager of one of the most important Spanish rabbit slaughterhouses. A consequence of this implication of the slaughterhouses in the rabbit production sector is that industrial research projects addressing the interests of these companies have been developed (CDTI, 2012).

In most selection nucleus growing rabbits are fed on full feeding (i.e., *ad libitum*). In these conditions, if exists a relevant interaction between the genotype and the feeding regimen (**GxFR**), the genetic improvement achieved in the nucleus of selection might not be observed in commercial farms (Ragab et al., 2015) in which feed restriction is conducted during fattening. This is a common practice, particularly, in production systems slaughtering at high weights, as it could be the case in Italy or France. Despite GxFR effect being well known for growth and feed efficiency (Piles et al., 2017; Piles & Sánchez 2019), there is no published information regarding the existence of GxFR for slaughter traits. Therefore, this research aims at filling this gap, estimating the magnitude of this interaction on slaughter and carcass weights, and dressing out percentage, as well as exploring the consequence of this interaction in selection programs aiming to improve these slaughter characteristics.

MATERIALS AND METHODS

Ethical statement

The housing, husbandry and use of animals for the procedures described in this manuscript were approved by the IRTA welfare committee, following the pertinent Spanish and European legislation.

Animal and management

All animals were housed in the farm belonging to the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) at Caldes de Montbui, Barcelona (Spain). Animals in this experiment came from Caldes line (Gómez et al., 2002) which was founded in 1985, and then selected by an index combining reproductive and post-weaning growth traits until 1992; from this year onward, the selection criterion was solely average daily gain (**G**) during the fattening period (i.e. from 32 to 63 days of age). At weaning, kits from

the same litter were distributed into two groups and housed in collective cages of 8 animals under the same environmental conditions and management, except feeding regimen. One group was fed on full feeding (**FF**) whereas the other one was restricted to 75% of the amount of feed consumed *ad libitum* (**RF**). All of them received the same standard pelleted diet and same management practices. Animals were also distributed according to their weaning weight in two groups, higher or lower than the batch mean, to get a homogeneous animal size within the cage. The fattening period comprised 6 weeks from 28 to 70 days of animal life. Twenty hours before slaughter, animals were kept fasting. Animals were weighed (Slaughter Weight, **SW**) on the farm the hour before transport to a commercial slaughterhouse sited 20 km apart from the farm. After slaughter, chilled carcass weight (**CW**) was also recorded and dressing out percentage was computed as $\text{DoP} = (100 \times \text{CW}) / \text{SW}$. There was a total of 2,424 and 2,557 data of animals on FF and RF, respectively, coming from 1,621 litters in 14 batches of the period comprised from June 2012 to April 2014.

Statistical Model

Records from animals under different feeding regimens were considered to be different traits. Therefore, data were analysed using a multivariate mixed animal lineal model which also included the information of the selection criteria (i.e. average daily growth, G) since the foundation of the line. This was done to avoid biases in the estimates of the genetic parameters.

Model parameters were estimated using a Bayesian MCMC procedure. In this context defining the data probability distribution is required. This distribution can be written for the three sets of traits jointly analysed as:

$$\begin{matrix}
& \mathbf{y}_G \\
& \mathbf{y}_{SW,FF} \\
& \mathbf{y}_{SW,RF} \\
112 \quad \mathbf{p} & \mathbf{y}_{CW,FF} \quad | \boldsymbol{\beta}, \mathbf{l}, \mathbf{a}, \mathbf{R}_0 = \\
& \mathbf{y}_{CW,RF} \\
& \mathbf{y}_{DoP,FF} \\
& \mathbf{y}_{DoP,RF}
\end{matrix}$$

$$\begin{matrix}
& \mathbf{X}_G \boldsymbol{\beta}_G + \mathbf{Z}_{l,G} \mathbf{l}_G + \mathbf{Z}_{a,G} \mathbf{a}_G \\
& \mathbf{X}_{SW,FF} \boldsymbol{\beta}_{SW,FF} + \mathbf{Z}_{l,SW,FF} \mathbf{l}_{SW,FF} + \mathbf{Z}_{a,SW,FF} \mathbf{a}_{SW,FF} \\
& \mathbf{X}_{SW,RF} \boldsymbol{\beta}_{SW,RF} + \mathbf{Z}_{l,SW,RF} \mathbf{l}_{SW,RF} + \mathbf{Z}_{a,SW,RF} \mathbf{a}_{SW,RF} \\
113 \quad MVN & \mathbf{X}_{CW,FF} \boldsymbol{\beta}_{CW,FF} + \mathbf{Z}_{l,CW,FF} \mathbf{l}_{CW,FF} + \mathbf{Z}_{a,CW,FF} \mathbf{a}_{CW,FF} , \mathbf{R} , \\
& \mathbf{X}_{CW,RF} \boldsymbol{\beta}_{CW,RF} + \mathbf{Z}_{l,CW,RF} \mathbf{l}_{CW,RF} + \mathbf{Z}_{a,CW,RF} \mathbf{a}_{CW,RF} \\
& \mathbf{X}_{DoP,FF} \boldsymbol{\beta}_{DoP,FF} + \mathbf{Z}_{l,DoP,FF} \mathbf{l}_{DoP,FF} + \mathbf{Z}_{a,DoP,FF} \mathbf{a}_{DoP,FF} \\
& \mathbf{X}_{DoP,RF} \boldsymbol{\beta}_{DoP,RF} + \mathbf{Z}_{l,DoP,RF} \mathbf{l}_{DoP,RF} + \mathbf{Z}_{a,DoP,RF} \mathbf{a}_{DoP,RF}
\end{matrix}$$

114 where, \mathbf{y}_G is the vector of records, $\boldsymbol{\beta}_G$ is the vector of systematic effects, \mathbf{l}_G is the vector
115 of litter effects and \mathbf{a}_G is the vector of additive genetic effects, all of them corresponding
116 to G. \mathbf{X}_G , $\mathbf{Z}_{l,G}$ and $\mathbf{Z}_{a,G}$ are incidence matrices relating data to the former systematic,
117 litter and additive genetic effects, respectively. The systematic effects included in the
118 model for G were: year-season (280 levels), number of kits born alive (7 levels: <6,
119 6,7,8,9,10 and >10) and parity order (4 levels: 1, 2, 3 and >3) of the litter in which the
120 kit was born.

121 $\mathbf{y}_{i,FF}$ are the vectors of traits recorded under FF for $i = SW, CW$ or DoP ; and $\mathbf{y}_{i,RF}$ are
122 the vectors of traits recorded under RF for $i = SW, CW, DoP$. $\boldsymbol{\beta}_{i,k}$ (for $i = SW, CW$ or
123 DoP and $k = FF$ or RF) are the vectors of systematic effects, $\mathbf{l}_{i,k}$ are the vectors of litter
124 effects and $\mathbf{a}_{i,k}$ are the vectors of additive genetic effects. $\mathbf{X}_{i,k}$, $\mathbf{Z}_{l,i,k}$ and $\mathbf{Z}_{a,i,k}$ are the
125 incidence matrices relating data to the former systematic, litter and additive genetic
126 effects, respectively. The systematic factors included in the model for the slaughter
127 traits were: batch (13 levels), kit size at weaning (2 levels: small and large), number of
128 kits born alive (7 levels as defined for G) and parity order (4 levels as defined for G) of
129 the litter in which the kit was born, and also the number of kits sharing the cage during

130 fattening as a linear covariate (mean=7.4, sd=0.73). Given all the position parameters
 131 the records had the following covariance structure:

$$\begin{aligned}
 132 \quad R = R_0 \quad I = & \begin{pmatrix}
 \sigma_{e_G}^2 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & \sigma_{e_{SW,FF}}^2 & 0 & \sigma_{e_{SW,FF}-e_{CW,FF}} & 0 & \sigma_{e_{SW,FF}-e_{DoP,FF}} & 0 \\
 0 & 0 & \sigma_{e_{SW,RF}}^2 & 0 & \sigma_{e_{SW,RF}-e_{CW,RF}} & 0 & \sigma_{e_{SW,RF}-e_{DoP,RF}} \\
 0 & \sigma_{e_{SW,FF}-e_{CW,FF}} & 0 & \sigma_{e_{CW,FF}}^2 & 0 & \sigma_{e_{CW,FF}-e_{DoP,FF}} & 0 \\
 0 & 0 & \sigma_{e_{SW,RF}-e_{CW,RF}} & 0 & \sigma_{e_{CW,RF}}^2 & 0 & \sigma_{e_{CW,RF}-e_{DoP,RF}} \\
 0 & \sigma_{e_{SW,FF}-e_{DoP,FF}} & 0 & \sigma_{e_{CW,FF}-e_{DoP,FF}} & 0 & \sigma_{e_{DoP,FF}}^2 & 0 \\
 0 & 0 & \sigma_{e_{SW,RF}-e_{DoP,RF}} & 0 & \sigma_{e_{CW,RF}-e_{DoP,RF}} & 0 & \sigma_{e_{DoP,RF}}^2
 \end{pmatrix} I
 \end{aligned}$$

133
 134 Where, $\sigma_{e_G}^2$, $\sigma_{e_{i,k}}^2$ and $\sigma_{e_{i,k}-e_{j,h}}$ (for i,j= SW, CW or DoP and k,h=FF or RF) are the
 135 residual variances and covariance of the seven traits jointly analysed; \otimes denotes the
 136 Kronecker product and I is an identity matrix.
 137 Bayesian analyses also require defining prior distributions for all the model's
 138 unknowns. In our study, the systematic effects (β) were assumed to follow uniform
 139 distributions, and the remaining position parameters were considered to follow
 140 multivariate normal distributions.

141

142

$$\begin{array}{c}
143 \\
p
\end{array}
\begin{array}{c}
\mathbf{l}_G \\
\mathbf{l}_{SW,FF} \\
\mathbf{l}_{SW,RF} \\
\mathbf{l}_{CW,FF} \\
\mathbf{l}_{CW,RF} \\
\mathbf{l}_{DoP,FF} \\
\mathbf{l}_{DoP,RF}
\end{array}
\left| \mathbf{L}_0 \right. \sim \text{MVN}
\begin{array}{c}
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0}
\end{array}
,
\begin{array}{c}
\sigma_{l_G}^2 \\
0 \\
\sigma_{l_{SW,FF}}^2 \\
\sigma_{l_{SW,FF}-l_{SW,RF}} \\
\sigma_{l_{SW,FF}-l_{CW,FF}} \\
\sigma_{l_{SW,FF}-l_{CW,RF}} \\
\sigma_{l_{SW,FF}-l_{DoP,FF}} \\
0
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}}^2 \\
\sigma_{l_{SW,FF}-l_{SW,RF}} \\
\sigma_{l_{SW,RF}-l_{CW,FF}} \\
\sigma_{l_{SW,RF}-l_{CW,RF}} \\
\sigma_{l_{SW,FF}-l_{CW,RF}} \\
\sigma_{l_{SW,RF}-l_{DoP,FF}} \\
\sigma_{l_{SW,FF}-l_{DoP,RF}}
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}}^2 \\
\sigma_{l_{SW,RF}-l_{CW,FF}} \\
\sigma_{l_{SW,RF}-l_{CW,RF}} \\
\sigma_{l_{SW,RF}-l_{CW,RF}} \\
\sigma_{l_{SW,RF}-l_{CW,RF}} \\
\sigma_{l_{SW,RF}-l_{DoP,FF}} \\
\sigma_{l_{SW,RF}-l_{DoP,RF}}
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}-l_{CW,FF}} \\
\sigma_{l_{SW,RF}-l_{CW,FF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{DoP,FF}} \\
\sigma_{l_{CW,FF}-l_{DoP,RF}}
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}-l_{CW,RF}} \\
\sigma_{l_{SW,RF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,FF}-l_{CW,RF}} \\
\sigma_{l_{CW,RF}-l_{DoP,FF}} \\
\sigma_{l_{CW,RF}-l_{DoP,RF}}
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}-l_{DoP,FF}} \\
\sigma_{l_{SW,RF}-l_{DoP,FF}} \\
\sigma_{l_{CW,FF}-l_{DoP,FF}} \\
\sigma_{l_{CW,RF}-l_{DoP,FF}} \\
\sigma_{l_{DoP,FF}}^2 \\
\sigma_{l_{DoP,FF}-l_{DoP,RF}} \\
\sigma_{l_{DoP,FF}-l_{DoP,RF}}
\end{array}
\begin{array}{c}
0 \\
\sigma_{l_{SW,FF}-l_{DoP,RF}} \\
\sigma_{l_{SW,RF}-l_{DoP,RF}} \\
\sigma_{l_{CW,FF}-l_{DoP,RF}} \\
\sigma_{l_{CW,RF}-l_{DoP,RF}} \\
\sigma_{l_{DoP,FF}-l_{DoP,RF}} \\
\sigma_{l_{DoP,FF}-l_{DoP,RF}} \\
\sigma_{l_{DoP,FF}-l_{DoP,RF}}
\end{array}
\mathbf{I}$$

144

$$\begin{array}{c}
145 \\
p
\end{array}
\begin{array}{c}
\mathbf{a}_G \\
\mathbf{a}_{SW,FF} \\
\mathbf{a}_{SW,RF} \\
\mathbf{a}_{CW,FF} \\
\mathbf{a}_{CW,RF} \\
\mathbf{a}_{DoP,FF} \\
\mathbf{a}_{DoP,RF}
\end{array}
\left| \mathbf{G}_0, \mathbf{A} \right. \sim \text{MVN}
\begin{array}{c}
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0} \\
\mathbf{0}
\end{array}
,
\begin{array}{c}
\sigma_{a_G}^2 \\
\sigma_{a_G-a_{SW,FF}} \\
\sigma_{a_G-a_{SW,RF}} \\
\sigma_{a_G-a_{CW,FF}} \\
\sigma_{a_G-a_{CW,RF}} \\
\sigma_{a_G-a_{DoP,FF}} \\
\sigma_{a_G-a_{DoP,RF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}}^2 \\
\sigma_{a_{SW,FF}-a_{SW,RF}} \\
\sigma_{a_{SW,FF}-a_{CW,FF}} \\
\sigma_{a_{SW,FF}-a_{CW,RF}} \\
\sigma_{a_{SW,FF}-a_{DoP,FF}} \\
\sigma_{a_{SW,FF}-a_{DoP,RF}} \\
\sigma_{a_{SW,FF}-a_{DoP,RF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}}^2 \\
\sigma_{a_{SW,RF}-a_{CW,FF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}-a_{CW,FF}} \\
\sigma_{a_{SW,RF}-a_{CW,FF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{CW,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}} \\
\sigma_{a_{SW,RF}-a_{DoP,FF}}
\end{array}
\begin{array}{c}
\sigma_{a_{SW,FF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}} \\
\sigma_{a_{SW,RF}-a_{DoP,RF}}
\end{array}
\mathbf{A}$$

146

Where, \mathbf{l}_G and \mathbf{a}_G are the effects of litter and additive genetic effects for G; and $\mathbf{l}_{i,k}$ and $\mathbf{a}_{i,k}$ (for $i = \text{SW, CW or DoP}$ and $k = \text{FF or RF}$) are the litter and additive genetic effects for the slaughter traits, respectively; \mathbf{L}_0 and \mathbf{G}_0 are the corresponding covariance matrices for the former random effects, whose elements are denoted with the symbols σ^2 and σ for variances and covariances, respectively; \mathbf{A} is the additive genetic relationship matrix, and \mathbf{I} are identity matrices of appropriate dimension.

Unbounded uniform distributions within the valid range domains were assumed for all elements of the matrices of variance components. Note that although not explicit bounds were defined, they were implicitly defined by the computer accuracy.

For the implementation of the Gibbs Sampling, it is necessary to define the fully conditional posterior distribution of all the unknowns. Given the assumed data distribution and the defined prior densities, all the conditional distributions have a known form. Those distributions can be found in Sorensen and Gianola, (2002). The Gibbs sampling algorithm was implemented using Gibbs2f90 program (Misztal *et al.*, 2002). A unique sampling procedure of 500,000 iterations was run. The first 200,000 iterations were discarded as burning after visual inspection of the trace plots and one in 10 samples for each parameter of interest was kept to compute descriptive statistics of its marginal posterior distribution.

Variance of the GxFR interaction

Genotype by environment interaction (GxE) can be defined as the change in the relative performance of one or more genotypes measured in two or more environments. Following this definition, the variance due to GxE interaction can be divided into two parts: one associated with the genetic correlation (r_g) between environments and one associated with the heterogeneity of genetic variance measured

in each environment (Dickerson 1962; Eisen and Saxton, 1983). Thus, samples from the posterior distributions of the GxFR variance ($\sigma_{GxFR,i}^{2,t}$) for a specific slaughter trait i ($i = \text{SW, CW or DoP}$) were obtained from the samples of genetic variances and covariances according to the following formula (Mathur, 2002):

$$\sigma_{GxFR,i}^{2,t} = \frac{1}{2} (\sigma_{a_{FF,i}}^t - \sigma_{a_{RF,i}}^t)^2 + \sigma_{a_{FF,i}}^t \sigma_{a_{RF,i}}^t (1 - r_{a_i}^t)$$

Where for the i^{th} trait and t^{th} iteration, $\sigma_{a_{FF,i}}^t$ and $\sigma_{a_{RF,i}}^t$ are samples of additive genetic standard deviations on FF and RF, respectively, and $r_{a_i}^t$ is a sample of the corresponding additive genetic correlation.

Expected responses to selection using different selection criteria

Based on the marginal posterior mean of the variance components, new records of CW_{FF} , CW_{RF} , DoP_{FF} and DoP_{RF} were generated using the same multiple trait model used for the analysis carried on the real data. The simulations were conducted assuming an infinitesimal model (Fisher, 1918) i.e., breeding values were sampled from a multivariate normal distribution.

For the genetic evaluation, only CW_{FF} and DoP_{FF} or CW_{RF} and DoP_{RF} were considered at the time, using the same models as those used for data simulation. Predictions of breeding values were obtained by solving the mixed model equations with variance components equal to those used in the simulation (best linear unbiased prediction; BLUP). Blupf90 software (Miszta *et al.*, 2002) was used for this purpose.

The simulated datasets mimicked the management of a rabbit selection nucleus of 200 females and 20 bucks, where mating between close relatives, i.e. with common grandparents, was avoided. Reproduction was organized in four batches per generation. Records were generated in the first two batches, and in the last two batches, the candidates were evaluated based on information of carcass traits (CW

and DoP) measured on their sibs in the previous batches and generations. Each batch comprised approximately 1,250 selection candidates (half females) which were distributed in cages of eight animals following the order of the litters they belonged to. Therefore, cages housed animals from more than one litter and less than 25% of the cages were formed by animals from a single litter. The best 100 females from the batch were selected whereas the best 20 males were selected within sire families.

Direct and correlated response to selection were estimated in six alternative scenarios resulting from the combination of feeding regimen (FF or RF) and the economic weights posed on each of the two traits: 100% and 0%, 50% and 50% or 0% and 50% for CW and DoP, respectively.

The simulation was run for five generations and, for each of the 4 traits of interest (i.e., CW_{FF} , CW_{RF} , DoP_{FF} and DoP_{RF}), responses were estimated as the linear regression coefficient of the average phenotype of selection candidates in each generation on generation number. Note that although only two traits were considered in the genetic evaluations records for the four ones were always generated. One hundred replicates were run for each scenario.

The simulation process was implemented in a software pipeline that combined an own Fortran90 code for data generation in each generation, R code to edit the data, compose parameter files needed to run the genetic evaluation programs (blupf90) and create the list of the selected males and females which is read back by the Fortran90 program. The complete software pipeline is available upon request.

RESULTS

Feed Restriction Effect on Performances

Table 1 shows descriptive statistics of the analysed traits including their mean, standard deviation, and minimum and maximum values. As expected, feeding regimen had an important effect on body weight being the means of SW and CW around 20 % higher on FF than on RF. However, the feeding regimen seems not to affect the phenotypic variation of these traits. The coefficient of variation of SW and CW had almost the same value on both feeding regimens: 0.12 and 0.13 for SW and CW, respectively. Despite kits were housed in groups and were not fed individually, the degree of feed restriction would be similar for all animals sharing the cage, since the average, across cages, of the standard deviations of the traits within cage are very similar between feeding regimens. Another important result is that DoP was 1.32 units (~2.29% of the mean) smaller for kits on RF than on FF.

Genetic parameters of slaughter traits in different feeding regimens

Table 2 shows the heritabilities and the ratio of phenotypic variance due to litter effect for G and slaughter traits under FF and RF regimens. Phenotypic variance for SW and CW were higher when kits were full fed than when they were restricted for the whole fattening period, this is a scale effect associated with the higher final weight (table 1) in the animals under FF. Heritabilities of those traits were also bigger on FF than on RF but the ratio of the litter effect variance to the phenotypic variance was higher on RF than on FF. For the case of DoP, the differences between both feeding regimens on the phenotypic variance and on the ratio between the litter variance and the phenotypic variance were weak; but the difference between the heritability estimates across feeding regimen was notorious, the heritability under RF was twice as high as under FF.

Genetic correlations between the studied traits are shown in Table 3. The estimated genetic correlations within a given trait between the two feeding regimens were in the

range between 0.69 and 0.87 (marginal posterior mean). For body and carcass weights the probability of these correlations being lower than 0.9 was higher than 0.95 but for DoP it was only 0.74. Overall, these figures imply that the performances under both feeding conditions have a largely common genetic background, nonetheless it must be stressed that the genetic background overlap between feeding regimes is much higher for SW and CW than for DoP.

Genetically, SW and CW were positively correlated, being the posterior mean of this correlation 0.96 and 0.89 on FF and RF, respectively. Moreover, this parameter ranged between 0.61 to 0.71 when one trait was recorded under FF and the other one under RF. Much lower genetic correlations were estimated between SW or CW and DoP which could not be said to be different from zero in most of the cases. Only the genetic correlation between DoP_{FF} and SW under both feeding regimes reached negative values (-0.34 and -0.28, with SW_{FF} and SW_{RF} , respectively) being statistically different from zero, i.e. the shortest interval containing 95% of the density (Highest Posterior Density, **HPD95**) did not cover zero, and the probability of the correlation being smaller than 0 was greater than 0.95. The estimated genetic correlations between the selection criteria (G) of the line and SW and CW under RF were clearly positives, 0.46 and 0.39, respectively; when the weight traits were recorded under FF the correlations with G were lower, and in the case of SW it could not be said to be statistically different from zero. An opposite pattern was observed for DoP, the statistically positive genetic correlation was estimated under FF (0.30) not under RF.

Regarding the phenotypic correlation estimates, in general, much lower magnitudes were observed, indicating that correlations due to additive genetic and environmental effects might have opposite signs.

Interaction between genotype and feeding regimen

The variance due to GxFR interaction and its ratio with respect to the phenotypic variance of the trait on both feeding regimens are presented in table 4. No trait showed relevant interaction between genotype and feeding regimen. The probability of the ratio of the interaction variance with respect to the phenotypic variance being greater than 0.1 (a quantity that could be considered to be relevant) never was higher than 0.95. The posterior means of these ratios were around 0.111 and 0.086, for SW and CW respectively, while for DoP this parameter was estimated to be just 0.053, being the aforementioned probabilities just 0.62, 0.28 and 0.003, for SW, CW and DoP, respectively.

Responses to selection

Given the estimates of genetic and environmental parameters obtained in our rabbit population, direct and correlated responses to selection obtained from the application of different selection strategies involving CW and DoP, were estimated by conducting a simulation process that mimics the selection process in a rabbit nucleus farm. Six different scenarios were considered according to the feeding regimen of growing rabbits and different weights assigned to CW and DoP. Table 5 includes the expected responses when the records are obtained under FF while Table 6 shows those obtained when records were obtained under RF. In both cases, in a given generation records for genetic evaluations were obtained from half and full sibs of the selection candidates. Regarding DoP the highest genetic responses were observed when phenotypic records were obtained under RF (Table 6). In this scenario when all the weight was assigned to DoP, the expected direct response (on the trait under RF) was 0.884 percent points per generation (%/generation), while that on the trait recorded

under FF was 39% lower (0.536 (%/generation)). When the weight assigned to the two traits (CW and DoP) was the same, the drop in the expected response to selection on DoP from direct (under RF) to indirect (under FF) selection is reduced by 46% (0.708 %/generation vs 0.378 %/generation). Results on CW are different, in the sense that indirect selection is not clear to be more effective than direct selection. For example, when all the weight is assigned to CW the response on this trait under FF is the same as under RF, 33 grams/generation. However, when the selection index assigns the same weight to both traits (CW and DoP) the drop in response from direct to indirect selection was expected to be of around 20%, from 25 grams/generation on CW_{RF} to 15 grams/generation on CW_{FF} .

When the phenotypic records were obtained under FF, if the selection objective was exclusively the improvement of DoP, direct response (0.448 %/generation) was 21 % lower than the indirect response (0.568 %/generation). When the same weight was assigned to both CW and DoP the highest response was obtained for the trait recorded under RF (0.336 %/generation). The situation concerning CW, both for the case in which all the weight is posed on CW or for the case in which the selection intensity is shared between CW and DoP, is partially different from that observed when the phenotypic records are obtained under RF (Table 6), i.e., the highest responses were always observed under direct selection, that is, when performances are recorded under FF. For the case of phenotypes recorded under RF (table 5), no differences between direct and indirect selection were observed if the index only considered CW. When it also considered DoP, the same result was observed as when records were obtained under FF: direct selection outperformed indirect selection.

Comparing results in tables 5 and 6 it can be seen that selection with records obtained under RF yielded responses on DoP under FF even higher, than those obtained when

the phenotypic records are obtained under FF (0.536 vs 0.448 %/generation, respectively). Another relevant result comprises the correlated response on DoP after selection for CW, in the case the records were obtained under FF, some antagonist responses would be expected (Table 5), but if selection is based on RF records, the improvement of CW is expected to be accompanied by also a slightly improvement of DoP (Table 6)

DISCUSSION

Results are compatible with growth performance observed in a much larger set of animals from the same experiment (Piles and Sánchez, 2019). As it could be expected, feed restriction had an important effect on the average slaughter weight. The daily growth of animals under RF was 10 grams lower than that of animals under FF. These differences mean the need of almost two extra weeks to reach the Spanish market slaughter weight of 2 – 2,3 kg (MARM, 2008) and this is the reason why, RF is usually practiced during the first 2-3 weeks of fattening, followed by a period of 1-2 weeks on FF (Gidenne et al., 2009). In this last period, a compensatory growth is observed which is the responsible of a relevant improvement in feed efficiency with respect to that of animals fed entirely on FF. Our data also show a reduction in the DoP of the animals on RF with respect to animals on FF but this reduction was not so clear in other studies (Crespo et al., 2020). When DoP is impaired in animals under RF, this reduction is normally associated with a larger size of the intestinal tract (Gidenne et al., 2009; Knudsen et al., 2017). It has been shown that a minimum length of the restriction period is required to observe an effect on carcass yield (Tumova et al., 2006). Means of slaughter traits of animals on FF were similar to those previously reported from animals

of the same line (Gomez *et al.*, 1998; Piles *et al.*, 2004) or different rabbit sire lines (Hernández *et al.*, 2006) on the same feeding regimen (i.e. FF).

The observed higher heritability of DoP under RF than under FF suggests that selection for increased carcass yield could be more effective under limited feeding.

This result was confirmed by direct and correlated responses obtained from the simulation of a selection process in a nucleus farm. Thus, higher responses were obtained, even for DoP under FF, when traits were recorded under RF than under FF.

Carcass yield is acquiring an increased interest in the last years but improving this trait by genetic selection is difficult because the information to evaluate candidates comes from relatives and also because it is difficult to maintain traceability of the individual records in the slaughterhouse throughout carcass processing. Therefore, it is desirable to define the conditions under which genetic variance is best observed. In this regard, there are no published studies reporting estimates of genetic parameters for carcass traits of growing rabbits on RF. Heritability estimates for carcass traits recorded on animals under FF are also scarce, being their magnitude medium-high (Blasco *et al.*, 2018). It must be noted the difficulty of obtaining the large number of records needed to properly estimate this and other genetic parameters, especially genetic correlations.

INRA's team conducted a selection experiment for growth under feed restriction of animals housed individually for 5 generations. They did not observe any correlated response on carcass yield, either under FF or RF (Molette *et al.*, 2016) despite a clear drop in the carcass yield was observed when animals were raised under RF, as it happened in our experiment. This result is compatible with the null (under RF) or low (0.30 under FF) genetic correlations between DoP and G estimated by us. Other studies reporting correlated responses to selection for growth on FF, also show a nearly null correlated genetic response on DoP (Pascual and Pla, 2007). Note,

however, that if a substantial direct response to selection for growth was observed, carcass traits could be affected because of the lower maturity degree of animals at slaughter as a consequence of the correlated effect on adult body weight which also increases (Piles et al., 2000). Extensive information about the relationship between growth and carcass traits can be found in the review by Blasco et al., (2018).

The presence of GxE is a potential source of reduced efficiency in genetic improvement programs in livestock since it causes a re-ranking of performances across different environments (Nauta *et al.*, 2006; Dominik and Kinghorn, 2008). The existence of G×E interaction has been mainly explained by two complementary results: i) The genetic correlation being different from one between performances on different feed regimens, and ii) An heterogeneous genetic variance of the performances across the feeding regimens. Both suppose that the set of genes involved in the control of the performance across feeding regimens are either different or are expressed differentially. In general, for the analysed slaughter traits we can indicate that both sources are relevant factors: genetic correlations are clearly different from one for SW and CW, not for DoP; and important differences in heritability and genetic variance were observed across feeding regimens. In spite of this differential configuration of the genetic parameters, the estimated G×FR interaction variances cannot be said to be relevant, since they only represent 11.1% and 8.6% of the average phenotypic variances for SW and CW, and 5.3% of the average phenotypic variances for DoP. Thus, the departure from one of the genetic correlations and the genetic heterogeneity across feeding regimes do not seem to be high enough to generate relevant G×FR interaction variance. In these conditions there is still room for indirect selection procedures to be preferable over direct selection methods, particularly for the case of DoP, for which much higher heritability was reported under RF than under FF. As it has been previously stated, the

highest response to selection for DoP would be always achieved using records obtained under RF, even if the objective is to perform under FF. For CW this does not hold, in this case, indirect selection does not yield higher response than direct selection methods, note that for CW the interaction variance estimate is higher, although still limited (around 8.5%), than that for DoP.

CONCLUSIONS

For DoP the GxFR interaction seems to be of low magnitude and heritability estimate under RF is much higher than under FF; thus, it would be advisable to always select animals on RF regardless of the conditions in which they will perform (FF or RF). For the case of CW, since the GxFR interaction variance seems to be slightly higher, and heritability estimates between feeding regimens are similar, direct selection methods are preferable, i.e. to select the animals under the same feeding conditions in which they will perform.

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CONFLICT OF INTERESTS

The authors declare that they have no competing interests.

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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 537

538 **Table 1** Summary statistics for average daily gain (G), and body weight at slaughter
 539 (SW), carcass weight (CW) and dressing-out percentage (DoP) of animals on full
 540 (FF) or restricted (RF) feeding regimen.

541

Trait	N	Mean	SD	Minimum	Maximum	SD Within Cage*
G, g/d	134,419	46.04	8.70	0.25	102.50	-
SW_{FF}, Kg	2,424	2.45	0.29	1.17	3.42	0.23
SW_{RF}, Kg	2,557	2.09	0.26	1.01	3.02	0.19
CW_{FF}, Kg	2,424	1.43	0.19	0.56	2.08	0.15
CW_{RF}, Kg	2,557	1.19	0.17	0.55	1.78	0.13
DoP_{FF}, %	2,424	58.37	2.33	43.36	69.30	1.91
DoP_{RF}, %	2,557	57.05	2.27	42.63	71.56	1.91

542 *Average, across cages, of the within-cage standard deviation.

543 **Table 2** Means (HPD^a, HPD^b) of the marginal posterior distribution of the phenotypic variance (σ_p^2), the heritability (h^2) and the ratio
544 of the litter effect variance to the phenotypic variance (l^2) for slaughter traits of animals on full or restricted feeding

Trait	Full feeding			Restricted feeding		
	σ_p^2	h^2	l^2	σ_p^2	h^2	l^2
G	54.83(54.18,55.52)	0.102(0.086,0.121)	0.314(0.305,0.323)*	-	-	-
SW	0.074(0.067,0.084)	0.364(0.243,0.499)*	0.189(0.139,0.237)*	0.047(0.043,0.051)	0.243(0.132,0.375)*	0.204(0.154,0.254)*
CW	0.031(0.029,0.034)	0.257(0.154,0.357)*	0.199(0.148,0.249)*	0.020(0.018,0.021)	0.203(0.082,0.338)*	0.211(0.157,0.264)*
DoP	5.406(5.043,5.758)	0.167(0.101,0.235)*	0.161(0.109,0.209)*	5.159(4.764,5.55)	0.379(0.279,0.483)*	0.141(0.098,0.188)*

545 HPD^a: lower bound of the 95% highest posterior density interval; HPD^b: upper bound of the 95% highest posterior density interval

546 ¹**G**: Average daily gain; **SW**: live body weight at slaughter; **CW**: Carcass weight; **DoP**: Dressing out percentage.

547 * The probability of the ratio being greater than 0.1 is higher than 0.95

548

549 **Table 3** Means (HPD^a, HPD^b) of the marginal posterior distribution of the genetic (upper triangular) and phenotypic (lower triangular)
550 correlations between the studies traits in animals on full (FF) and restricted (RF) feeding.

Trait	G	SW _{FF}	SW _{RF}	CW _{FF}	CW _{RF}	DoP _{FF}	DoP _{RF}
G	-	0.16(-0.14,0.55)	0.46(0.22,0.67)*	0.29(0.02,0.64)*	0.39(0.10,0.62)*	0.30(0.09,0.51)*	-0.05(-0.31,0.22)
SW_{FF}	0.03(-0.03,0.10)	-	0.73(0.56,0.84) [#]	0.96(0.94,0.98)*	0.61(0.41,0.81)*	-0.34(-0.62,-0.07)*	-0.26(-0.63,0.03)
SW_{RF}	0.07(0.03,0.11)*	0.37(0.30,0.46) [#]	-	0.71(0.55,0.86)*	0.89(0.82,0.94)*	-0.28(-0.51,-0.04)*	-0.21(-0.53,0.09)
CW_{FF}	0.05(0.00,0.10)*	0.95(0.95,0.96)*	0.33(0.27,0.41)*	-	0.69(0.49,0.88) [#]	-0.09(-0.37,0.17)	-0.07(-0.40,0.25)
CW_{RF}	0.05(0.01,0.10)*	0.32(0.23,0.40)*	0.95(0.94,0.96)*	0.32(0.24,0.39) [#]	-	0.10(-0.16,0.36)	0.25(-0.06,0.50)
DoP_{FF}	0.04(0.01,0.07)*	0.26(0.20,0.31)*	-0.01(-0.07,0.05)	0.53(0.48,0.57)*	0.08(0.03,0.14)*	-	0.87(0.78,0.93)
DoP_{RF}	-0.01(-0.06,0.04)	-0.04(-0.15,0.07)	0.26(0.21,0.31)*	0.05(-0.03,0.15)	0.54(0.50,0.58)*	0.30(0.23,0.38) [#]	-

551 HPD^a: lower bound of the 95% highest posterior density interval; HPD^b: upper bound of the 95% highest posterior density interval; G:
552 Average daily gain (g/d); SW: Live body weight at slaughter (kg); CW: Carcass weight (kg); DoP: Dressing-out percentage (%).

553 * The probability of the correlation being greater than 0 is higher than 0.95 or smaller than 0.05.

554 [#] The probability of the correlation being smaller than 0.9 is higher than 0.95 – only applies to the correlation within the same trait
555 between the two alternative feeding regimes, these parameter estimates are presented in italic.

556

557 **Table 4** Marginal posterior means (PM) and 95% highest posterior density interval
 558 (HPD95) for the variance due to genotype by feeding regimen interaction and for the
 559 ratio of this variance to the average phenotypic variance (σ_P^2) of the two carcass traits
 560 involved, under full (FF) or restricted (RF) feeding.

Trait ¹	Interaction Variance		Ratio of Interaction Variance to σ_P^2	
	PM	HPD95	PM	HPD95
SW	0.007	0.004 , 0.011	0.111	0.054 , 0.168
CW	0.002	0.001 , 0.004	0.086	0.040 , 0.138
DoP	0.282	0.122 , 0.442	0.053	0.023 , 0.083

561 ¹SW: Live body weight at slaughter; CW: Carcass weight; DoP: Dressing-out
 562 percentage.
 563

564 **Table 5** Responses (units per generation) to selection under full feeding, assigning
565 alternative weights to breeding value predictions for CW_{FF} and DoP_{FF} . Mean and SD
566 over 100 replicates.

Trait	0%-100%*	50%-50%	100%-0%
CW_{FF} (Kg/gen.)	-0.014(0.008)	0.027(0.008)	0.046(0.007)
CW_{RF} (Kg/gen.)	-0.002(0.005)	0.015(0.006)	0.020(0.006)
DoP_{FF} (%/gen.)	0.448(0.065)	0.255(0.076)	-0.146(0.082)
DoP_{RF} (%/gen.)	0.568(0.102)	0.336(0.112)	-0.176(0.120)

567 * Weights posed on CW_{FF} and DoP_{FF} were 0% and 100%, respectively.

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570 **Table 6** Responses (units per generation) to selection under restricted feeding,
571 assigning alternative weights to breeding value predictions for CW_{RF} and DoP_{RF} . Mean
572 and SD over 100 replicates.

Trait	0%-100%*	50%-50%	100%-0%
CW_{FF} (Kg/gen.)	-0.010(0.010)	0.015(0.009)	0.033(0.009)
CW_{RF} (Kg/gen.)	0.004(0.007)	0.025(0.005)	0.033(0.006)
DoP_{FF} (%/gen.)	0.536(0.085)	0.378(0.084)	0.006(0.100)
DoP_{RF} (%/gen.)	0.884(0.114)	0.708(0.108)	0.128(0.147)

573 * Weights posed on CW_{RF} and DoP_{RF} were 0% and 100%, respectively

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