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Divergent selection on intramuscular fat in rabbits: Responses to selection and genetic parameters[1]

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ABSTRACT: A divergent selection experiment on intramuscular fat (IMF) was performed in rabbits. The aim of this study is to estimate the response to selection, the correlated responses in carcass and meat quality traits, and their genetic parameters. Selection criterion was the averaged phenotypic value of IMF measured at 9 wk of age in 2 full-sibs of the candidate. Traits considered were IMF, BW, chilled carcass weight, reference carcass weight, scapular and perirenal fat weights, carcass and meat color, pH, protein and fatty acid composition of meat. Total direct response to selection for IMF was 2.6 phenotypic SD of the trait, around 5% of the mean (1.09 g/100 g) per generation, with both lines following a symmetrical trend. Heritability of IMF was high (0.54), and in general, all traits related to carcass fat depots and IMF fatty acid composition showed high heritabilities (dissectible fat of the carcass, 0.70; MUFA percentage, 0.61; PUFA percentage, 0.45; and PUFA:SFA ratio, 0.42), except SFA percentage (0.09). The other carcass and meat quality traits showed moderate to low heritabilities. Intramuscular fat and dissectible fat percentage showed a low genetic correlation (0.34). Intramuscular fat was positively correlated with MUFA percentage (0.95) and negatively correlated with PUFA percentage (−0.89) and PUFA:SFA ratio (−0.98), corroborated with high correlated responses to selection. The rest of the traits did not show any substantial correlated response except protein content, which was greater in the high-IMF line than in the low-IMF line.

Key words: genetic parameters, intramuscular fat, rabbits

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INTRODUCTION

Breeding goals in the meat industry are now changing their focus toward meat quality traits to meet consumer expectations (Hermesch et al., 2000). Intramuscular fat (**IMF**) is a main goal because it has a large effect on the sensory properties of meat (Hocquette et al., 2010). Increasing IMF by selection improves meat quality but can lead to unfavorable consequences in some carcass and meat quality traits, due to undesirable genetic correlations with IMF. For instance, in pigs, IMF and carcass fatness show a positive genetic correlation (Ciobanu et al., 2011), leading to an impairment of carcass quality when selecting for high IMF. Another example is the negative genetic correlation between IMF and major PUFA percentages (reviewed by De Smet et al. [2004]), leading to a lower PUFA:SFA ratio when selecting for high IMF, which is against nutritional recommendations (World Health Organisation, 2008).

Genetic parameters of IMF, particularly genetic correlations, are difficult to obtain because they need to be estimated with a large amount of data. Many genetic parameters of meat quality reported in literature are estimated with a low precision, without giving much information about their actual values (see, for example, Gjerlaug-Enger et al. [2010], in pigs, or Buchanan et al. [2015], in cattle). However, when data come from a selection experiment, heritabilities and genetic correlations, although estimated with a limited precision, can be corroborated by the direct and correlated responses obtained. Selection experiments for IMF are scarce, and none of them have

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been performed in rabbits. Only Sapp et al. (2002), in cattle; Zhao et al. (2007), in chickens; and Schwab et al. (2009), in pigs, performed selection for IMF.

Rabbit is a lean meat having a favorable fatty acid composition compared with beef, veal, and pig meats (Dalle Zotte and Szendrő, 2011). Besides, rabbits are a good model for genetic studies in other livestock species due to their short generation interval and low cost of the carcasses. A divergent selection experiment for IMF is being performed in rabbits (Zomeño et al., 2013). There are no published estimates of IMF heritability in rabbits, apart from that estimated by Zomeño et al. (2013) with the 3 first generations of this experiment, and there are no published genetic correlations among IMF and other meat and carcass quality traits. The aim of this study is to estimate the response to divergent selection for IMF in rabbits, the correlated responses in carcass and meat quality traits, and their genetic parameters.

MATERIAL AND METHODS

Animals

A divergent selection experiment was performed during 7 generations. Animals came from a synthetic rabbit line formerly selected for ovulation rate for 10 generations (Laborda et al., 2011) and selection relaxed the following 2 generations. The base population consisted of 13 males and 83 females. Lines selected for high IMF and low IMF had approximately 8 males and 40 females per generation. Two full-sibs (male and female) of the first parity of each doe were slaughtered and their IMF was measured. All dams were then ranked according to the IMF values obtained by their offspring. The 20% best dams provided all females for the next generation. Each sire was mated with 5 dams, and 1 male of the best dam was selected for the next generation. This selection within male family was performed to reduce inbreeding. Normally, the first parity was used to collect the IMF data and the second parity was used to provide the rabbits for next generation, although, exceptionally, some IMF measurements were made on the second or third parity. A total of 2,365 rabbits were considered in the pedigree file, of which 1,337 were evaluated: 1,101 measurements were made in the first parity, 180 in the second, and 56 in the third. A total of 154 rabbits from the seventh generation were used to study the correlated responses to selection in carcass and meat quality traits: 72 from the high-IMF line and 82 from the low-IMF line.

Rabbits were collectively reared from weaning to slaughter and were fed ad libitum with a commercial diet. Animals were slaughtered at 9 wk using electrical stunning and exsanguination. Before slaughter, the BW was recorded. After slaughter, carcasses were chilled for 24 h at 4°C and the weight of the chilled carcass weight was registered. Commercial rabbit carcass varies among countries; therefore, the World Rabbit Science Association (Toulouse, France) proposed to measure a reference carcass weight (**RCW**; the weight of the carcass without the head, liver, lungs, thymes, esophagus, heart, and kidneys) to allow comparisons between studies (Blasco et al., 1993; Blasco and Ouhayoun, 1996); therefore, RCW was recorded. Scapular and perirenal fat depots were excised and weighed. The dissectible fat percentage was estimated as the sum of scapular and perirenal fat weights divided by RCW. The left leg was dissected to obtain the meat to bone ratio. Color parameters lightness (L*), redness (a*), and yellowness (b*) of the carcass were measured on the surface of the fourth lumbar vertebra, and the color of the meat was measured at the seventh lumbar vertebra transversal section of the longissimus dorsi. Color Euclidean distance Delta E (**ΔE**) was calculated (Sharma, 2002). Muscle pH was measured 24 h postmortem in the longissimus dorsi muscle at the level of the fifth lumbar vertebra. Then, the longissimus dorsi muscle was excised, minced, freeze-dried, and scanned with near-infrared spectroscopy (a technique first proposed for rabbits by Masoero et al. [1992]) to measure IMF, protein content, and fatty acid composition applying the calibration equations previously developed by Zomeño et al. (2012). The potential use of this equation for animal breeding was evaluated by Zomeño et al. (2011). Intramuscular fat and protein content of the longissimus dorsi was expressed as grams per 100 g of muscle on a fresh basis. Saturated fatty acid, MUFA, and PUFA content was expressed as a percentage of total fatty acid. The ratio between PUFA and SFA was calculated.

All experimental procedures involving animals were approved by the Universitat Politècnica de València Research Ethics Committee, according to council directives 98/58/EC (European Economic Community, 1998) and 2010/63/EU (European Commission Directive, 2010).

Statistical Analysis

Descriptive statistics and phenotypic correlations between IMF and carcass and meat quality traits were estimated with data from all generations, after precorrecting data by line–generation–season, parity order, and sex fixed effects.

Direct and correlated responses to selection were calculated 2 different ways. First, they were estimated as the phenotypic differences between the high-IMF and the low-IMF lines at the same generation of selection. Second, they were estimated as the genetic means of each line per generation.

Phenotypic differences between lines were estimated with the model

$$\mathbf{y = Xb + Wc + e.}$$

Data were assumed to be conditionally distributed as

$$\mathbf{y|b, c, \sigma}_e^2 \sim N(\mathbf{Xb + Wc, I\sigma}_e^2),$$

in which **b** is the vector with the fixed effects of line (high IMF and the low IMF), month, sex, and parity order; **c** is the vector of common litter random effect; σ_e^2 is the residual variance; **X** and **W** are the known incidence matrices; and **I** is an identity matrix. Common litter random effect was assumed to be distributed as

$$\mathbf{c} \sim N(\mathbf{0, I\sigma}_c^2),$$

in which σ_c^2 is the common litter variance.

Heritabilities, genetic correlations with IMF, and genetic means per generation were estimated by fitting the following bivariate animal model, with the same effects for all traits:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} + \begin{bmatrix}\mathbf{W}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{W}_2\end{bmatrix}\begin{bmatrix}\mathbf{c}_1\\ \mathbf{c}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}.$$

Data were assumed to be conditionally distributed as

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} | \mathbf{b}_1, \mathbf{b}_2, \mathbf{u}_1, \mathbf{u}_2, \mathbf{c}_1, \mathbf{c}_2, \mathbf{R} \sim \mathrm{N}\left(\mathrm{X}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \mathrm{Z}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} + \mathbf{W}\begin{bmatrix}\mathbf{c}_1\\ \mathbf{c}_2\end{bmatrix}, \mathbf{R}\right),$$

in which $\mathbf{b}_1$ and $\mathbf{b}_2$ are the vectors of fixed effects (month, sex, and parity order); $\mathbf{u}_1$ and $\mathbf{u}_2$ are the vectors of additive genetic effects; $\mathbf{c}_1$ and $\mathbf{c}_2$ are the vectors of common litter effects; **X**, **Z**, and **W** are known incidence matrices; and **R** is the residual co(variance) matrix between the 2 traits

Sorting data by individuals, additive effects were distributed as

$$\mathbf{u} \sim N(\mathbf{0, A} \otimes \mathbf{G}_0),$$

common litter effects were distributed as

$$\mathbf{c} \sim N(\mathbf{0}, \mathbf{I}_m \otimes \mathbf{C}_0),$$

and residuals were distributed as

$$\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}_n \otimes \mathbf{R}_0),$$

in which $\mathbf{G}_0$, $\mathbf{C}_0$, and $\mathbf{R}_0$ are the 2 × 2 genetic additive, common litter, and residual co(variance) matrices between the 2 traits; **A** is the relationship matrix; **I**m is an identity matrix of the same order as the number of levels of common litter effects; and **I**n is an identity matrix of the same order as the number of individuals. All effects were assumed to be independent between them.

Bayesian inference was used, with bounded flat priors for all unknowns. Marginal posterior distributions were estimated using Gibbs sampling. Descriptive statistics and phenotypic differences between lines were computed with the program Rabbit developed by the Institute for Animal Science and Technology (Valencia, Spain). After some exploratory analyses, results were based on Markov chain Monte Carlo chains consisting of 60,000 iterations, with a burn-in period of 10,000, and only 1 of every 10 samples were saved for inferences. Phenotypic correlations and genetic analyses were computed with the software TM (Legarra et al., 2008). In this case, after some exploratory analyses results were based on Markov chain Monte Carlo chains consisting of 1,000,000 iterations, with a burn-in period of 200,000, only 1 of every 100 samples was saved for inferences. In all analyses, convergence was tested using the Z criterion of Geweke and Monte Carlo sampling errors were computed using time-series procedures (Sorensen and Gianola, 2002) included in the Rabbit and TM programs. In all cases, Monte Carlo SE were small and lack of convergence was not detected by the Geweke test.

As Bayesian inference is based in probabilities, this gives great flexibility to construct all kinds of confidence intervals. This allows asking questions that we could not ask within the classical inference approach. It may be important to know how big the phenotypic difference between lines for IMF is, with a chosen probability of, for instance, 80%. Therefore, we can calculate a guaranteed value, that is, the minimum value k that the difference can take with 80% probability. This is the limit of the interval $[k, +\infty)$ with 80% probability. To help in the discussion, we can also calculate the probability of the phenotypic difference between lines being greater than a relevant value. This relevant value is the minimum amount having economical or biological significance; it is normally used in experimental design as the difference to be detected when calculating sample sizes. For some traits, it may be difficult to assess the economical or biological importance for a relevant value; in these cases, it can be taken as relevant around 10% of the phenotypic variance of the trait, or one-third of the phenotypic SD.

The parameters obtained from the marginal posterior distributions of the phenotypic differences between lines were the median of the difference ($\mathbf{D_{H\text{-}L}}$), the SD, the highest posterior density region at 95% of probability ($\mathbf{HPD_{95\%}}$), the probability of the difference being greater than 0 when $D_{H\text{-}L} > 0$ or lower

Table 1. Descriptive statistics of carcass and meat quality traits

Trait[1]	No.	Mean	SD	CV × 100
Carcass quality traits				
BW, g	1,337	1,717	127	7.42
CCW, g	1,335	978	83	8.50
RCW, g	1,336	774	71	9.15
SF, g	1,325	3.92	1.12	28.6
PF, g	1,333	8.44	2.98	35.3
DF, %	1,320	1.57	0.39	24.8
M:B ratio	954	4.44	0.49	10.9
L*	1,336	54.5	2.02	3.71
a*	1,327	3.27	0.86	26.3
b*	1,303	1.26	1.31	NA[2]
Meat quality traits				
IMF, g/100 g	1,337	1.09	0.15	13.9
Protein, g/100 g	1,304	22.0	0.43	1.96
pH	1,329	5.57	0.09	1.58
L*	1,336	53.7	2.27	4.22
a*	1,323	3.60	0.97	27.1
b*	1,335	1.78	0.72	NA
SFA, %	1,298	36.3	1.85	5.10
MUFA, %	1,298	23.3	2.49	10.7
PUFA, %	1,298	39.9	3.71	9.29
PUFA:SFA ratio	1,297	1.10	0.11	9.66

[1]CCW = chilled carcass weight; RCW = reference carcass weight; SF = scapular fat weight; PF = perirenal fat weight; DF = dissectible fat percentage; M:B = meat to bone ratio of the hind leg; L* = lightness, a* = redness, and b* = yellowness measured on the carcass surface (carcass quality traits) or in the longissimus dorsi muscle (meat quality traits); IMF = intramuscular fat. Saturated fatty acids, MUFA, and PUFA are expressed as a percent of total fatty acids.

[2]NA = not applicable, because b* has positive and negative values.

than 0 when $D_{H\text{-}L} < 0$ ($\mathbf{P_0}$), and the guaranteed value of the difference with a probability of 80%, that is, the limit of the interval $[k, +\infty)$ when $D_{H\text{-}L} > 0$ or the limit of the interval $(-\infty, k]$ when $D_{H\text{-}L} < 0$. We considered one-third of the phenotypic SD of a trait as a relevant value (**R**), and we also calculated the probability of relevance (probability of the difference being greater than R when $D_{H\text{-}L} > 0$ or lower than R when $D_{H\text{-}L} < 0$ [$\mathbf{P_R}$]).

Regarding the genetic analyses, we calculated the median and the SD of the marginal posterior distributions of genetic means in each generation. For heritabilities, we estimated the median of each marginal posterior distribution, the $HPD_{95\%}$, and the guaranteed value with probability of 80 or 95%, that is, the limit of the interval $[k, 1]$ with 80 or 95% probability. For genetic and phenotypic correlations, we estimated the median of each marginal posterior distribution, the $HPD_{95\%}$, and the probability of being greater than 0 when the median is positive or lower than 0 when the median is negative (P). A more detailed description of these features can be found in Blasco (2005).

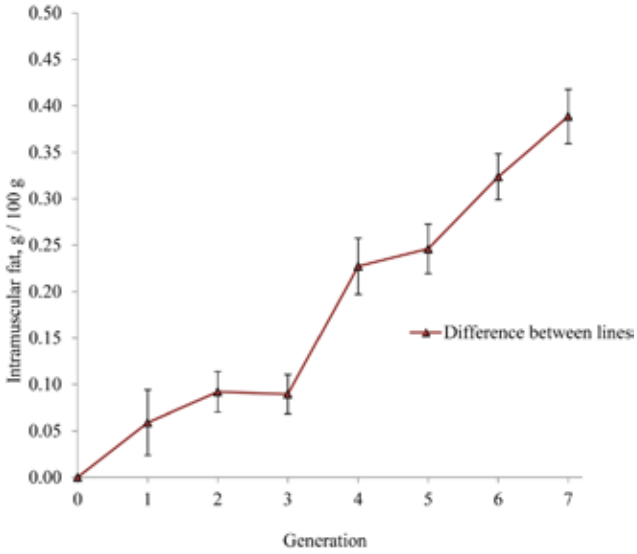

Figure 1. Medians and SD of the estimated marginal posterior distributions of the phenotypic differences for intramuscular fat (IMF) between high-IMF line and low-IMF line.

RESULTS AND DISCUSSION

Descriptive Statistics of the Traits

Table 1 shows descriptive statistics of carcass and meat quality traits. Descriptive statistics for carcass and meat quality traits are in line with those reported by Hernández et al. (2004). Coefficient of variation of yellowness (b*) is not reported because it is not defined, because b* takes positive and negative values.

Scapular and perirenal fat deposits are the 2 main carcass fat depots in rabbits and, on average, account for 65% of carcass dissectible fat (Hernández et al., 2006). Carcass fat percentage of rabbits was very low in comparison with the fat percentage of pig and beef carcasses (Lawrie and Ledward, 2006). Rabbit meat showed a greater percentage of PUFA and a greater PUFA:SFA ratio in comparison with pigs, cattle, and sheep (Dalle Zotte, 2002; Dalle Zotte and Szendrő, 2011). The PUFA:SFA ratio of rabbit meat was greater than 0.60, in line with the nutritional recommendations for adults reported by the World Health Organisation (2008).

Direct Response to Selection for Intramuscular Fat

In our experiment, direct and correlated responses to selection were estimated using 2 independent criteria: the observed phenotypic differences between lines and the estimated genetic means of each line per generation. In divergent selection experiments, assuming that environment affects both lines alike, the genetic progress is the phenotypic difference between lines at the same generation, which is independent on any genetic model. However, to assess whether genetic response is

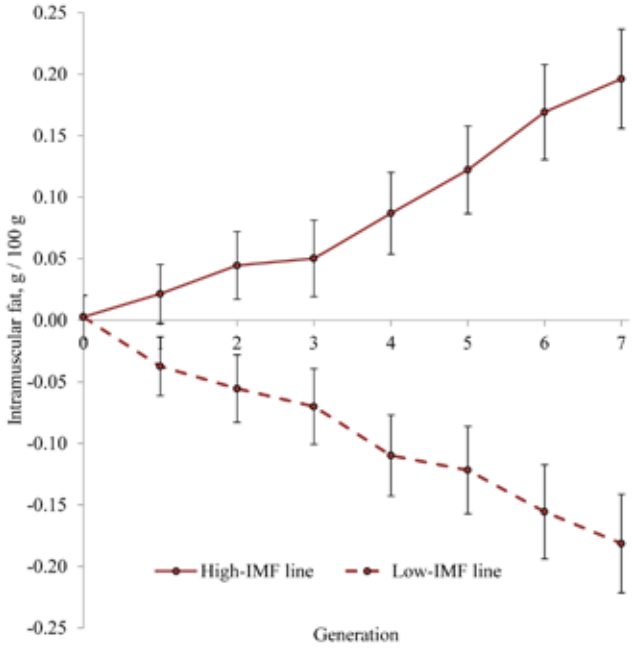

Figure 2. Medians and SD of the marginal posterior distributions of the estimated genetic means for intramuscular fat (IMF) per generation.

symmetrical or not, we need the estimates of the genetic trends that are model dependent (Sorensen and Johansson, 1992); that is, their results depend on the genetic parameters used to estimate them. When the phenotypic observed difference is coincident with the difference observed using genetic trends, this corroborates the model used in the estimation of the genetic values. It is, therefore, interesting to have independent criteria to evaluate the response and correlated responses.

For all the traits, differences between genetic means of the lines were coherent with the phenotypic differences. This corroborates the model used for the genetic analyses. Figure 1 shows the phenotypic differences between lines for IMF in each generation. Comparisons between lines should be done at the same stage of maturity, and our lines were approximately at the same stage (Pascual et al., 2015). Phenotypic difference between lines in the seventh generation was 0.39 g/100 g, around 2.6 SD of the trait, and 5% of the mean per generation. The guaranteed value of the difference with 80% of probability was 0.36 g/100 g.

Figure 2 shows the genetic means of each line per generation. Direct response to selection was symmetrical for both lines. In the seventh generation, direct response was 0.20 g/100 g of IMF in the high-IMF line and −0.18 g/100 g of IMF in the low-IMF line, which is 1.3 and −1.2 SD of the trait in the high-IMF and low-IMF lines, respectively. Environmental trends were the same in both lines and did not show any particular pattern. Similar genetic trends were observed when lines were separately analyzed. Currently, there is no other experiment of selection for IMF in rabbits, and in other species they are scarce (Sapp et al. [2002], in cattle; Zhao et al. [2007], in chickens; and Schwab et al. [2009], in pigs), all of them showing high responses to selection.

Table 2. Features of the marginal posterior distributions of the differences between the high–intramuscular fat (IMF) and low-IMF lines for carcass and meat quality traits in the seventh generation of selection

Trait[1]	D_{H-L}[2]	$HPD_{95\%}$[3]	P_0[4]	R[5]	P_R[6]
Carcass quality traits					
RCW, g	27.9	2.30, 52.3	0.98	23.7	0.63
SF, g	0.28	−0.05, 0.60	0.96	0.37	0.3
PF, g	3.32	2.51, 4.14	1.00	0.99	1.00
DF, %	0.43	0.31, 0.55	1.00	0.13	1.00
M:B ratio	0.23	0.04, 0.42	0.99	0.16	0.76
L*	−0.54	−1.31, 0.22	0.92	0.67	0.37
a*	−0.39	−0.76, 0.01	0.98	0.29	0.71
b*	0.18	−0.36, 0.69	0.76	0.44	0.16
Meat quality traits					
IMF, g/100 g	0.39	0.33, 0.44	1.00	0.05	1.00
Protein, g/100 g	0.38	0.24, 0.53	1.00	0.14	1.00
pH	0.01	−0.02, 0.05	0.82	0.03	0.15
L*	−0.33	−1.48, 0.77	0.72	0.76	0.21
a*	−0.21	−0.60, 0.20	0.85	0.32	0.29
b*	−0.22	−0.57, 0.14	0.88	0.24	0.44
SFA, %	−0.12	−0.87, 0.60	0.61	0.62	0.09
MUFA, %	7.49	6.56, 8.49	1.00	0.83	1.00
PUFA, %	−10.1	−11.5, −8.61	1.00	1.24	1.00
PUFA:SFA ratio	−0.26	−0.30, −0.22	1.00	0.04	1.00

[1]RCW = reference carcass weight; SF = scapular fat weight; PF = perirenal fat weight; DF = dissectible fat percentage; M:B = meat to bone ratio of the hind leg; L* = lightness, a* = redness, and b* = yellowness measured on the carcass surface (carcass quality traits) or in the longissimus dorsi muscle (meat quality traits). Saturated fatty acids, MUFA, and PUFA are expressed as a percent of total fatty acids.

[2]D_{H-L} = the median of the difference (median of the marginal posterior distribution of the difference between the high-IMF line and the low-IMF line).

[3]$HPD_{95\%}$ = the highest posterior density region at 95% of probability.

[4]P_0 = probability of the difference being greater than 0 when $D_{H-L} > 0$ or lower than 0 when $D_{H-L} < 0$.

[5]R = relevant value (proposed as one-third of the SD of the trait).

[6]P_R = probability of the difference being greater than R when $D_{H-L} > 0$ or lower than R when $D_{H-L} < 0$.

Correlated Responses in Carcass Quality Traits

Table 2 shows the correlated responses for carcass and meat quality traits estimated as the phenotypic differences between lines in the seventh generation. Selection for IMF showed a positive correlated response on carcass fat depots. Perirenal fat weight was greater in the high-IMF line than in the low-IMF line (P_0 = 1.00), and this difference was relevant (P_R = 1.00), although considering the low dissectible fat percentage in rabbit, this has no economic importance. Scapular fat was also greater in the high-IMF line than

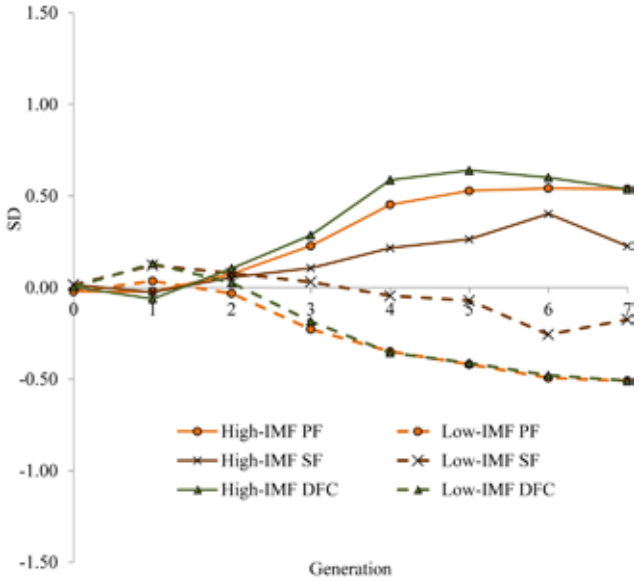

Figure 3. Genetic trends for perirenal fat weight (PF), scapular fat weight (SF), and dissectible fat percentage (DF). High-IMF line = the high-intramuscular fat line; Low-IMF line = the low-intramuscular fat line. Traits are expressed in units of SD of the trait.

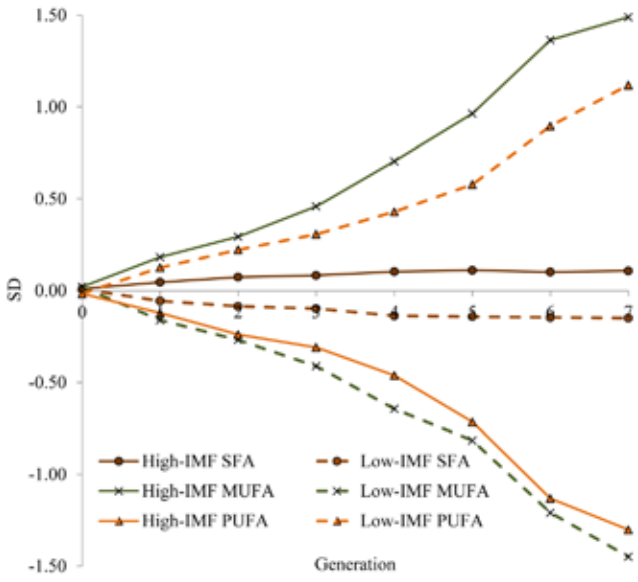

Figure 4. Genetic trends for saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acid percentages. High-IMF line = the high-intramuscular fat line; Low-IMF line = the low-intramuscular fat line. Traits are expressed in units of SD of the trait.

in the low-IMF line, although the difference between lines was not relevant ($P_R = 0.30$). Figure 3 shows the genetic trends for perirenal and scapular fat weights and dissectible fat percentage. To facilitate comparisons, genetic trends of correlated traits are expressed in SD units. Genetic response in both lines was symmetrical, and in the seventh generation, correlated response was ±0.5 SD of perirenal fat weight and dissectible fat percentage. Other experiments of selection for IMF also showed positive correlated responses in the fat content of the carcass (Schwab et al. [2009], in pigs, and Zhao et al. [2007], in chickens). A selection experiment for low backfat thickness restraining IMF was performed in pigs for 1 generation (Ros-Freixedes et al., 2013), reducing backfat thickness with a slight reduction in IMF.

Reference carcass weight was slightly greater in the high-IMF line than in the low-IMF line, but the phenotypic difference between lines was not relevant ($P_R = 0.63$; Table 2). Other experiments of selection for IMF do not show any consistent pattern in the correlated response on carcass weight: Zhao et al. (2007) showed a significant increment in chickens, whereas Sapp et al. (2002), in cattle, and Schwab et al. (2009), in pigs, did not obtain any correlated response.

Meat to bone ratio of the hind leg is an estimator of the meat to bone ratio of the whole carcass in rabbits (Hernández et al., 1996). In the seventh generation, the high-IMF line showed greater meat to bone ratio of the hind leg ($P_0 = 0.99$; Table 2) than the low-IMF line, but the phenotypic difference cannot be considered relevant ($P_R = 0.76$).

Rabbit meat is usually commercialized as a whole carcass and, to a lesser extent, as retail cuts; therefore, carcass color is particularly important for consumers. Selection for IMF produced slight modifications in the color parameters of the carcass in the seventh generation (Table 2): the low-IMF line showed greater lightness (L*) and redness (a*) than the high-IMF line, although phenotypic differences were not relevant, whereas yellowness (b*) of the carcass was not affected by selection. Differences in L*, a*, and b* color parameters have a difficult interpretation. To help the discussion, color distance ΔE was calculated. Lines showed ΔE distance in carcass color of 0.80. Considering a ΔE of 2.3 noticeable for the human eye (Sharma, 2002), selection for IMF did not lead to noticeable changes in carcass color. Color of the carcass was not analyzed in other experiments of selection for IMF in other species. Genetic trends for RCW, meat to bone ratio, and carcass color parameters did not show any clear pattern along the experiment and are not reported.

Correlated Responses in Meat Quality Traits

A side effect of increasing IMF is the decline of the PUFA percentage (De Smet et al., 2004; Sellier et al., 2010; Wood et al., 2008). This leads to unfavorable changes in the PUFA:SFA ratio, which is an indicator of nutritional quality of meat. In the seventh generation of our experiment, the low-IMF line showed relevant greater percentages of PUFA than the high-IMF line ($P_R = 1.00$; Table 2) whereas the SFA percentage was similar in both lines. Consequently, the low-IMF

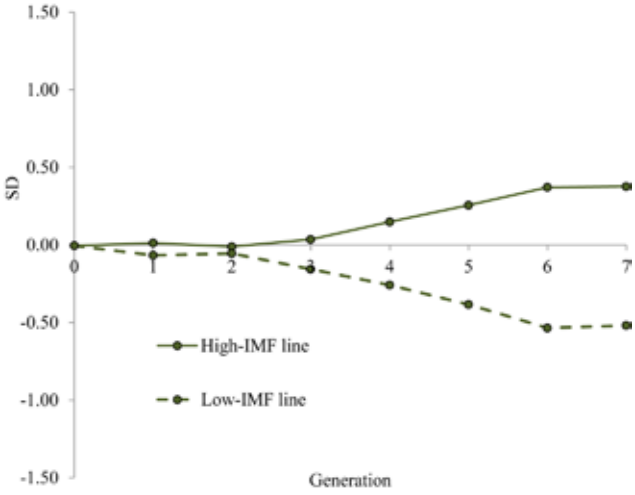

Figure 5. Genetic trends for meat protein content. High-IMF line = the high-intramuscular fat line; Low-IMF line = the low-intramuscular fat line. Traits are expressed in units of SD.

line showed a 0.26 greater PUFA:SFA ratio than the high-IMF line (P_R = 1.00); however, the high-IMF line PUFA:SFA ratio is still above the minimum nutritional recommendations (>0.60, according to the World Health Organisation, 2008). Regarding the MUFA percentage, it was relevantly greater in the high-IMF line than in the low-IMF line (P_R = 1.00; Table 2). Expressing the correlated responses in percentages leads to a decrease in PUFA in the high-IMF line, due to the faster increase of the other fatty acid groups (SFA and MUFA); however, it should be noticed that the amount in absolute terms of all fatty acid groups (PUFA, MUFA, and SFA) was greater in the high-IMF line than in the low-IMF line, because the high-IMF line has more IMF than the low-IMF line. The differences between the high-IMF and low-IMF lines were 58.8 g/100 g of muscle for PUFA, 111 g/100 g for MUFA, and 106 g/100 g for SFA in the seventh generation. Figure 4 shows genetic trends for the fatty acid profile of IMF. Percentages of MUFA and PUFA showed great responses to selection and their genetic trends were similar to those of IMF. In the seventh generation, correlated response in MUFA percentage was 1.5 SD in the high-IMF line and −1.3 SD in the low-IMF line and correlated response in PUFA percentage was −1.1 SD in the high-IMF line and 1.4 in the low-IMF line. Percentage of SFA did not respond to selection. Correlated responses to selection for IMF in the fatty acid profile are innovative results because none of the previous experiments of selection for IMF cited above measured IMF fatty acids. Some studies in rabbit compared the fatty acid composition in several genetic lines differing in their IMF, but they did not show any common pattern (Gašperlin et al., 2006; Polak et al., 2006; Hernández et al., 2008).

In the seventh generation, protein content was relevantly greater in the high-IMF line than in the low-IMF line (P_R = 1.00; Table 2). Genetic trends for protein content are reported in Fig. 5. Protein content was modified by selection for IMF, increasing in the high-IMF line and decreasing in the low-IMF line. Previous selection experiments for IMF did not measure protein content in any species.

The postmortem evolution of pH was not affected by selection, in agreement with the selection experiment for IMF in pigs (Schwab et al., 2009). Meat color was slightly affected by selection for IMF, as observed in the carcass. In the seventh generation of selection, meat redness (a*) and yellowness (b*) were greater in the low-IMF line than in the high-IMF line but differences between lines were irrelevant and lightness was similar in both lines. These differences between lines were not detectable by the human eye, according to Sharma (2002), because the ΔE color distance between lines was 0.62. In other selection experiments for high IMF, lightness of the meat increased (Schwab et al. [2009], in pigs); however, when they measured the color of fresh meat by a sensory panel, they did not detect any effect of selection, in agreement with our results. In the experiment in chickens (Zhao et al., 2007), meat color parameters

Table 3. Heritabilities of carcass and meat quality traits

Trait[1]	Median[2]	$HPD_{95\%}$[3]	$k_{80\%}$[4]	$k_{95\%}$[5]
Carcass quality traits				
RCW	0.18	0.04, 0.35	0.11	0.06
SF	0.32	0.14, 0.53	0.24	0.17
PF	0.54	0.33, 0.74	0.46	0.38
DF	0.70	0.51, 0.90	0.61	0.53
M:B ratio	0.10	0.01, 0.26	0.05	0.02
L*	0.11	0.01, 0.24	0.05	0.03
a*	0.37	0.19, 0.56	0.29	0.22
b*	0.06	0.00, 0.16	0.03	0.01
Meat quality traits				
IMF	0.54	0.37, 0.71	0.47	0.40
Protein	0.25	0.12, 0.42	0.19	0.14
pH	0.08	0.01, 0.20	0.05	0.03
L*	0.19	0.04, 0.35	0.12	0.07
a*	0.25	0.10, 0.43	0.18	0.13
b*	0.14	0.02, 0.29	0.09	0.05
SFA	0.09	0.01, 0.21	0.05	0.02
MUFA	0.61	0.45, 0.77	0.54	0.48
PUFA	0.45	0.31, 0.63	0.39	0.33
PUFA:SFA ratio	0.42	0.26, 0.58	0.35	0.29

[1]RCW = reference carcass weight; SF = scapular fat weight; PF = perirenal fat weight; DF = dissectible fat percentage; M:B = meat to bone ratio of the hind leg; L* = lightness, a* = redness, and b* = yellowness measured on the carcass surface (carcass quality traits) or in the longissimus dorsi muscle (meat quality traits); IMF = intramuscular fat content.

[2]Median is the median of the marginal posterior distribution of the heritability.

[3]$HPD_{95\%}$ = the highest posterior density region at 95% of probability.

[4]$k_{80\%}$ = limit of the interval [k, 1] at 80% of probability.

[5]$k_{95\%}$ = limit of the interval [k, 1] at 95% of probability.

Table 4. Phenotypic and genetic correlations between intramuscular fat and carcass and meat quality traits

	Phenotypic correlation			Genetic correlation		
Trait[1]	Median[2]	$HPD_{95\%}$[3]	P_0[4]	Median	$HPD_{95\%}$	P_0
Carcass quality traits						
RCW	0.26	0.21, 0.31	1.00	0.27	−0.11, 0.63	0.91
SF	0.29	0.24, 0.34	1.00	0.37	0.04, 0.64	0.98
PF	0.35	0.30, 0.39	1.00	0.33	0.05, 0.59	0.98
DF	0.34	0.29, 0.39	1.00	0.34	0.08, 0.60	0.99
M:B ratio	0.17	0.10, 0.23	1.00	0.38	−0.06, 0.93	0.93
Meat quality traits						
Protein	0.32	0.27, 0.37	1.00	0.43	0.10, 0.76	0.99
pH	−0.01	−0.06, 0.05	0.61	0.29	−0.17, 0.71	0.88
SFA	0.12	0.07, 0.18	1.00	0.37	−0.08, 0.88	0.95
MUFA	0.88	0.86, 0.89	1.00	0.95	0.90, 0.99	1.00
PUFA	−0.74	−0.76, −0.71	1.00	−0.89	−0.98, −0.78	1.00
PUFA:SFA ratio	−0.76	−0.79, −0.74	1.00	−0.98	−1.00, −0.91	1.00

[1]RCW = reference carcass weight; SF = scapular fat weight; PF = perirenal fat weight; DF = dissectible fat percentage; M:B = meat to bone ratio of the hind leg.

[2]Median is the median of the marginal posterior distribution of the heritability.

[3]$HPD_{95\%}$ = the highest posterior density region at 95% of probability.

[4]P_0 = probability of the correlation being greater than 0 when positive or lower than 0 when negative.

(L*, a*, and b*) were not affected by selection for IMF. Genetic trends for pH and meat color parameters did not show a clear pattern and are not reported.

Heritabilities of the Traits

Table 3 shows the heritabilities (h^2) of carcass and meat quality traits. Table 4 gives the phenotypic and genetic correlations between IMF and carcass and meat quality traits.

The h^2 of IMF was high (0.54), showing a guaranteed value of 0.47 with 80% probability or 0.40 with 95% probability (Table 3). No other estimates of IMF heritability have been published in rabbits, apart from that estimated by Zomeño et al. (2013) with the 3 first generations of this experiment (0.37). In other species, there is a large range of IMF heritabilities (from 0.26 to 0.86, as reviewed by Ciobanu et al. [2011], in pigs, and from 0.34 to 0.77, as reviewed by Mateescu [2015], in cattle).

In general, all traits related to carcass fat depots presented high h^2 (Table 3), with scapular fat weight showing the lowest estimate. These results are in agreement with previous reports in rabbits (Larzul et al., 2005; Larzul and Rochambeau, 2005; Garreau et al., 2008). Regarding IMF fatty acid composition, MUFA and PUFA percentages and the PUFA:SFA ratio showed high h^2, whereas the SFA percentage showed a low h^2, close to 0. We can corroborate these results with the positive correlated responses in PUFA and MUFA percentages and the PUFA:SFA ratio and a lack of correlated response in SFA percentage (Table 2). There are no previous estimates of fatty acid h^2 in rabbits. In other species, Ros-Freixedes et al. (2014) and Ibáñez-Escriche et al. (2016), in pigs, and Nogi et al. (2011), in cattle, showed high h^2 for MUFA and PUFA and also for SFA percentages.

Protein content had a moderate heritability, in agreement with the study of Al-Saef et al. (2008) in rabbits. Color parameters showed low heritabilities, with the exception of carcass and meat a*, which had a high to moderate h^2 (Table 3), in line with the previous values reported in rabbits by Larzul and Rochambeau (2005). The other carcass and meat quality traits showed a low h^2, in agreement with the estimates reported by Hernández and Gondret (2006) in a rabbit review.

Correlations between Intramuscular Fat and Carcass and Meat Quality Traits

No previous genetic correlations among IMF and carcass and meat quality traits are reported in rabbits. Our results show that, in general, genetic correlations ($\boldsymbol{r_g}$) and phenotypic correlations ($\boldsymbol{r_p}$) were of the same order (Table 4).

The relationships between IMF and the fatty acid profile of meat have interest because both affect organoleptic and nutritional properties of meat (Wood et al., 2004). In our study, strong genetic and phenotypic correlations were found between IMF and MUFA and PUFA percentages and between IMF and the PUFA:SFA ratio. Intramuscular fat was positively correlated with the MUFA percentage (r_g = 0.95 and r_p = 0.88) and negatively correlated with the PUFA percentage and the PUFA:SFA ratio, both genetically (−0.89 and −0.98, respectively) and phenotypically (−0.74 and −0.76, respectively). These genetic correlations

were accurately estimated, as shown by their narrow $HPD_{95\%}$ (Table 4). The great correlated response to selection on these traits (Table 2) corroborates the strong genetic correlations between these traits and IMF. In contrast, genetic correlation between IMF and the SFA percentage had a wide $HPD_{95\%}$, providing scarce information about the actual value of the parameter, but we can state that it was positive with a high probability ($P_0 = 0.95$; Table 4). Phenotypic correlation was also positive but low (Table 4). The possibility of increasing IMF independently of the SFA percentage is beneficial from a nutritional point of view, because it is recommended to reduce the consumption of SFA (World Health Organisation, 2008). To our knowledge, no genetic correlations between IMF and fatty acids have been published in rabbits, although they have been studied in other species, for example in pigs (Ibáñez-Escriche et al., 2016) and beef (Buchanan et al., 2015). Our results showed stronger correlations between IMF and fatty acids than the correlations reported in these studies, except for the SFA percentage.

Improving the eating of quality of meat without impairing carcass quality is a critical point in the meat industry due to the positive genetic correlation between IMF and carcass fat content (Ciobanu et al., 2011). In our experiment, we can state that genetic correlations among IMF and carcass fat content were also positive ($P_0 \geq 0.98$), but the estimate was inaccurate, showing wide $HPD_{95\%}$ (Table 4). However, in Bayesian analysis, we can calculate the maximum value that r_g can take with 80% probability, and in our case, this value was 0.46 for the genetic correlation between IMF and dissectible fat percentage, showing that IMF and carcass fat should have a moderate to low genetic correlation. Phenotypic correlations between IMF and carcass fat content were also positive ($P_0 = 1.00$), with estimates ranging from 0.29 to 0.35 (Table 4).

Genetic and phenotypic correlations between IMF and protein content were positive ($P_0 = 0.99$ and $P_0 = 1.00$, respectively; Table 4), with medians of 0.43 and 0.32, respectively. Although this genetic correlation shows a wide $HPD_{95\%}$, the actual value of this parameter should be substantial, because the high-IMF line showed a relevant higher content of protein than the low-IMF line (Table 2) Our correlations did not agree with those estimated by Gjerlaug-Enger et al. (2010), in pigs, which showed negative genetic and phenotypic correlations.

Our estimates of genetic correlations between IMF and RCW, meat to bone ratio, and pH were inaccurate; nevertheless, we can state that they were positive, with probabilities of 0.91, 0.93, and 0.88, respectively. The phenotypic correlations between IMF and RCW and meat to bone ratio were low but positive, whereas phenotypic correlation between IMF and pH was close to 0 (Table 4). Due to the inaccuracy of the estimates, we cannot make statements about the genetic correlations between IMF and color parameters, and they are not reported. The phenotypic correlations between IMF and color parameters were low or close to 0, ranging from −0.09 to 0.03.

Conclusions

Divergent selection for IMF lead to a difference between the high-IMF and low-IMF lines of 2.6 SD of the trait, with both lines following a symmetrical trend. Heritability of IMF was high, and in general, all traits related to carcass fat depots and IMF fatty acid composition showed high heritabilities, except for SFA percentage. The high-IMF line showed greater carcass dissectible fat percentage than the low-IMF line, although the genetic correlation between both traits was low. Strong genetic correlations were estimated between IMF and fatty acid percentages, positive for MUFA and negative for PUFA, corroborated with high correlated responses to selection, with the high-IMF line showing lower PUFA and greater MUFA percentages than the low-IMF line. Protein content was greater in the high-IMF line than in the low-IMF line, whereas the remaining traits did not show any substantial change due to selection.

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