Martinez Alvaro, M.; Hernández, P.; Agha, SA.; Blasco Mateu, A. (2018). Correlated responses to selection for intramuscular fat in several muscles in rabbits. Meat Science. 139:187-191. https://doi.org/10.1016/j.meatsci.2018.01.026

Running head: correlated responses to selection for intramuscular fat

Correlated responses to selection for intramuscular fat in several muscles in rabbits

Marina Martínez-Álvaro[a], Pilar Hernández[a], Saif Agha[a,b] and Agustín Blasco[a]*

[a]Institute for Animal Science and Technology, Universitat Politècnica de València, 46022 València, Spain.

[b]Present address: Animal Production Department, Faculty of Agriculture, Ain Shams University, 11241 Cairo, Egypt.

*Corresponding author.
E-mail adresses: mamaral9@upv.es (M. Martínez-Álvaro), phernan@dca.upv.es (P. Hernández), ablasco@dca.upv.es (A. Blasco).

Abstract

The aim of this study was to evaluate the effect of six generations of selection for intramuscular fat (IMF) in muscle *Longissimus thoracis et lumborum* (LTL) at 9 wk in IMF and fatty acid (FA) composition of muscles with diverse metabolic profile in rabbits. Direct response to selection was 0.33 g of IMF/ 100 g of LTL, around 0.4 SD per generation. A positive correlated response was observed in IMF of *Biceps femoris*, *Supraspinatus* and *Semimembranosus proprius* muscles at 9 wk, representing around 0.2 SD of the trait per generation. Selection affected similarly the FA composition of all muscles at 9 wk, high-IMF line showing greater monounsaturated but lower polyunsaturated FA percentages than low-IMF line, whereas no differences were observed for saturated FA. Traits were also measured at 13 wk and correlated responses were in the same direction. Our results suggest a common genetic background for IMF and FA composition in muscles with different metabolic profile in rabbits.

Key words: intramuscular fat, selection, correlated response, muscles, rabbit.

1. Introduction

Intramuscular fat (IMF) is a main factor in meat quality because affects sensory, nutritional and technologic properties of meat (Wood et al., 2004). This trait can be easily improved by selection due to its high heritability. There are few selection experiments for IMF (Sapp, Bertrand, Pringle, & Wilson, 2002 in cattle; Zhao, Chen, Zheng, Wen, & Zhang, 2007 in chickens and Schwab, Baas, Stalder, & Nettleton, 2009 in pigs). At the Universitat Politècnica de València we are performing a divergent selection experiment for IMF content of *Longissimus thoracis et lumborum* (LTL) muscle in rabbits (Zomeño, Hernández, & Blasco, 2013 and Martínez-Álvaro, Hernández, & Blasco, 2016). Rabbit is a good model for genetic studies in other livestock species due to its short generation interval and the low cost of its carcasses.

There is scarce information about the genetic determination of IMF deposition in muscles with different metabolic profile. Some authors point to some differences in the genetic determinism of muscles with different metabolic type (Quintanilla et al., 2011). According to these authors, selection for IMF of LTL muscle could be affecting differently other muscles with different metabolic profile.

Genetic correlations between muscles involving IMF and other meat quality traits are difficult to obtain because they need a great amount of data to be estimated. The estimates found in literature are often imprecise for this reason (see for example Ros-Freixedes, Reixarch, Bosch, Tor, & Estany, 2014). The study of the correlated responses after selection for IMF is an alternative for examining the genetic relationships between IMF of different muscles, requiring a much lower amount of data, since it only involves the comparison between means. However, none of the selection experiments for IMF cited above studied the correlated responses to selection for IMF in muscles with different metabolic profile. The selection experiment for IMF in chicken breast (Zhao, Chen, Zheng, Wen, & Zhang, 2007) studied the correlated response for IMF in the whole hind leg, but hind leg includes muscles with different metabolic profile. The aim of this work is to study the correlated responses to selection for IMF of LTL, in IMF of other muscles with different metabolic profile in rabbits.

2. Materials and methods

2.1. Animals

This study was performed with rabbits from the sixth generation of a divergent selection experiment for IMF. The base population consisted in 13 males and 83 females coming from a synthetic rabbit line, and the following generations had 8 males and 40 females per line (high-IMF and low-IMF lines). Intramuscular fat was measured in LTL muscle in rabbits slaughtered at 9 wk of age. Two rabbits (a male and a female) from the first parity of each doe were evaluated for IMF, and the average between these two phenotypic values was calculated. Then, all dams were ranked according to this average, and selection of the next generation was performed among rabbits from the second parity. All females of the approximately 20% best dams were selected for next generation. Each sire was mated with five does. To reduce inbreeding, only one male progeny of each sire was selected for the next generation. Lines selected for high-IMF and low-IMF were reared contemporary at the farm of the Universitat Politècnica de València. Controlled ventilation and 16L:8D lighting schedule were applied. Litters were homogenized by performing cross-fostering at birth up to 9 kits per litter. From weaning to slaughter, rabbits were reared collectively in commercial cages of 8 rabbits and fed *ad libitum*. More details of this experiment can be found in Zomeño, Hernández, & Blasco (2013) and Martínez-Álvaro, Hernández, & Blasco (2016).

A total of 134 rabbits from the sixth generation of selection were used to estimate the direct response to selection for IMF in LTL muscle and the correlated responses in carcass weight, fat depots weight, pH and fatty acid composition of LTL at 9 wk of age (68 from the high-IMF line and 66 from the low-IMF line). From those, a subsample of 60 animals was randomly taken to study the correlated responses in IMF, fatty acid composition and pH of muscles with diverse metabolic profile: *Biceps femoris* (BF), *Supraspinatus* (SS) and *Semimembranosus proprius* (SP). Additionally, 51 rabbits (26 from the high-IMF line and 25 from the low-IMF line) were slaughtered at 13 wk of age to study the correlated responses to selection in the traits described above at a later age. Animals were slaughtered at 9 or 13 wk of age by electrical stunning and exsanguination.

All experimental procedures involving animals were approved by the Universitat Politècnica de València Research Ethics Committee, according to Council Directive 2010/63/EU for animal experiments.

2.2. Intramuscular fat, pH and fatty acid measurements

Carcasses were chilled for 24 h at 4 ºC. The reference carcass weight (the weight of the carcass without the head, liver, lungs, thymes, esophagus, heart and kidneys) was recorded according to the World Rabbit Science Association recommendations (Blasco, & Ouhayoun, 1996). Perirenal and scapular fat depots were excised from the carcass and weighed. Dissectible fat percentage (DFP) of the carcass was calculated as the sum of both fat depots weights divided by the reference carcass weight. Muscles LTL, BF, SS and SP were excised from the carcass and muscle pH was measured 24 h *post mortem* with a Crison pH-meter Basic +20 (Crison Instruments, Barcelona, Spain). In LTL, pH was measured at the level of the fifth lumbar vertebra and in BF, SS and SP pH was measured in the central area, always in the left muscles. Muscles LTL, BF and SS were minced, freeze-dried and scanned with Near Infrared Spectrophotometry (model 5000, FOSS NIRSystems INC., Hilleroed, Denmark). Intramuscular fat and saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acid contents were determined in g/100g of muscle on a fresh basis applying the calibration equations previously developed by Zomeño, Hernández, & Blasco (2011) and Zomeño, Juste, & Hernández (2012). Then, fatty acid contents were expressed as a percentage of total fatty acids. As a routine control, around 20% of the total NIRS scanned samples were also chemically analysed for IMF by ether extraction (Soxtec 1043 extraction unit, Tecator, Höganäs, Sweden) to confirm that NIRS predictions are in line with intramuscular fat chemical measurements. Intramuscular fat content of SP muscle was quantified by ether extraction due to its reduced size, and it was expressed in g of IMF/100g of muscle on a fresh basis.

2.3. Statistical analysis

Descriptive statistics of carcass and meat quality traits at 9 and 13 wk were estimated after correcting data by line, sex, and month-season fixed effects. Direct and correlated responses to selection were estimated as the phenotypic differences between high and low-IMF lines at 9 wk and at 13 wk. All the differences within age were estimated with a model including line, sex and month-season fixed effects and common litter random effect. Additionally, differences between lines for IMF and its composition were estimated with the same model including the DFP as a fixed effect (considering different levels each 0.5% of DFP). Phenotypic correlations between IMF of muscles were estimated within age after correcting data by line, sex, and month-season fixed effects.

Bayesian inference was used (Blasco, 2005 and 2017). Common litter effect and residuals of the models were assumed to be independently between them and independently normally distributed. Bounded flat priors were assumed for all fixed effects and variances. Marginal posterior distributions were estimated using Gibbs sampling. Descriptive statistics and differences between lines were performed with the software “Rabbit”, developed by the Institute for Animal Science and Technology (Valencia, Spain). After some exploratory analyses, results were based on Monte Carlo Markov chains runs consisting of 60,000 iterations, with a burn-in period of 10,000, and only one of every 10 samples were saved for inferences. Phenotypic correlations were computed with the software TM (Legarra, Varona, & López de Maturana, 2008). In this case, after some exploratory analyses results were based on Monte Carlo Markov chains runs consisting of 1,000,000 iterations, with a burn-in period of 200,000, and only one of every 100 samples were saved for inferences. Convergence was tested using the Z criterion of Geweke and Monte-Carlo sampling errors were computed using time-series procedures (Blasco, 2017).

The parameters obtained from the marginal posterior distributions of the differences between lines were: the median, the highest posterior density region at 95%

($HPD_{95\%}$) and the probability of the difference being greater than zero when the median is positive or lower than zero when the median is negative (P_0). Additionally, 1/3 of the SD of a trait was considered as a relevant value (r) and the probability of relevance was calculated (probability of the difference between lines being greater than r when the median is positive or lower than r when the median is negative) (Pr). From the marginal posterior distributions of the phenotypic correlations the median, $HPD_{95\%}$ and P_0 were estimated. A more detailed description of these features can be found in Blasco (2005 and 2017).

3. Results and discussion

3.1. Descriptive statistics

Table 1 presents descriptive statistics of carcass traits. Since commercial carcasses of rabbits vary between countries from 9 to 13 wk of age, traits have been evaluated at both ages.

Table 1

Descriptive statistics of carcass traits in rabbits at 9 and 13 wk of age.

	9 wk		13 wk	
[1]Trait	Mean	SD	Mean	SD
RCW, g	766	59.8	1262	91.9
SF, g	3.78	1.22	7.79	2.85
PF, g	7.48	2.32	20.6	7.13
DFP, %	1.45	0.34	2.24	0.65

[1] RCW, reference carcass weight; SF, scapular fat weight; PF, perirenal fat weight; DFP, dissectible fat percentage.

Descriptive statistics are similar than those previously reported by Hernández, Aliaga, Plá, & Blasco (2004) in rabbits at the same ages. Perirenal and scapular fat depots are the greater fat depots in rabbits (Hernández, Ariño, Grimal, & Blasco, 2006). Both depots comprise a dissectible fat percentage of 1.45% at 9 wk, and 2.24% at 13 wk, showing the leanness of rabbit carcass, in comparison to carcasses from other meat species such as pig and beef (Lawrie, & Leward, 2006).

Table 2 presents descriptive statistics of meat quality traits in LTL, BF, SS and SP muscles at 9 and 13 wk of age. These muscles were chosen due to their different physicochemical properties (see their pH in Table 2) and metabolic type, according to Delmas, & Ouhayoun (1990). These authors reported a high glycolytic activity in LTL and a high oxidative activity in SS and SP, whereas BF was intermediate between them. Muscle LTL showed the lowest IMF content in comparison to BF, SS and SP, as observed in previous studies in rabbits (Alasnier, Remington, & Gandemer, 1996 and Gondret, Mourot, & Bonneau, 1998). As expected, IMF increased with age in all muscles, in line with other studies in rabbits (Gondret, Mourot, & Bonneau, 1998).

Table 2

Descriptive statistics of meat quality traits in several muscles of rabbits at 9 and 13 wk of age.

		9 wk		13 wk	
Muscle	[1]Trait	Mean	SD	Mean	SD
Longissimus thoracis et lumborum	pH	5.66	0.11	5.75	0.12
	IMF	1.05	0.14	1.42	0.17
	SFA	36.8	1.28	37.4	1.11
	MUFA	20.8	3.04	26.1	2.25
	PUFA	42.4	3.39	36.5	2.38
Biceps femoris	pH	5.81	0.10	5.86	0.12
	IMF	2.08	0.33	2.55	0.57
	SFA	35.8	1.07	36.3	0.77
	MUFA	29.9	2.17	31.8	1.62
	PUFA	34.2	2.43	31.9	1.73
Supraspinatus	pH	6.22	0.14	6.31	0.18
	IMF	2.13	0.35	2.91	0.58
	SFA	31.2	1.59	31.9	1.31
	MUFA	28.7	2.19	32.1	1.73
	PUFA	40.1	3.39	36.0	2.28
Semimembranosus proprius	pH	6.40	0.11	6.38	0.12
	IMF	2.64	0.51	4.18	0.55

[1] IMF; intramuscular fat expressed as g of IMF/100g muscle; Saturated (SFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) expressed as a percentage of total fatty acids.

The three muscles showed PUFA:SFA ratios near or above nutritional recommendations of 1.00 (World Health Organization, 2008). The ratio between PUFA and SFA was 1.28 for SS, 1.15 for LTL and 0.95 for BF at 9 wk, and 1.13 for SS, 0.98 for LTL and 0.88 for BF at 13 wk. In general, rabbit meat shows greater PUFA:SFA ratio than other species as pig, beef or lamb (Enser, Hallett, Hewitt, Fursey, & Wood, 1996 and Dalle Zotte, 2002).

3.2. Correlated responses to selection for IMF of LTL muscle

3.2.1. Correlated responses in carcass traits

Table 3 shows the differences between high-IMF and low-IMF lines for carcass traits at 9 and 13 wk of age. Comparisons should be made at the same state of maturity. High and low-IMF lines were at the same state of maturity along all their growing period (Pascual, Calle, & Blasco, 2015).

Table 3

Differences between high and low intramuscular fat rabbit lines for carcass traits at 9 and 13 wk of age.

	9 wk					13 wk				
^{1}Trait	^{2}D	^{3}HPD$_{95\%}$	^{4}P$_{0}$	^{5}r	^{6}P$_{r}$	^{2}D	^{3}HPD$_{95\%}$	^{4}P$_{0}$	^{5}r	^{6}P$_{r}$
RCW, g	53.8	29.7, 80.4	1.00	19.9	0.99	23.0	-39.9, 80.8	0.78	30.6	0.40
SF, g	1.00	0.45, 1.50	1.00	0.41	0.99	-0.05	-1.69, 1.65	0.48	0.95	0.14
PF, g	2.89	2.01, 3.90	1.00	0.77	1.00	9.31	5.30, 13.5	1.00	2.38	1.00
DFP, %	0.38	0.25, 0.52	1.00	0.11	1.00	0.68	0.32, 1.06	1.00	0.22	0.99

^{1}RCW, reference carcass weight; SF, scapular fat weight; PF, perirenal fat weight; DFP, dissectible fat percentage; ^{2}D = median of the marginal posterior distribution of the difference between lines; ^{3}HPD$_{95\%}$ = highest posterior density region at 95% of probability; ^{4}P$_{0}$ = probability of the difference being greater than zero when D >0 or lower than zero when D <0; ^{5}r = relevant value, proposed as 1/3 of the standard deviation of the trait; ^{6}P$_{r}$ = probability of relevance (probability of the difference being greater than r when D >0 or lower than r when D <0).

Selection for IMF showed a positive correlated response on carcass fat deposition. High-IMF line showed relevantly greater perirenal fat weight at both ages than low-IMF line (P_r = 1.00), whereas scapular fat weight was relevantly greater only at 9 wk (P_r = 0.99). The apparent lack of a positive correlated response in scapular fat weight at 13 wk was unexpected, but it may be a sampling effect since the HPD$_{95\%}$ of the differences between lines is relatively large (from -1.69 g to 1.65 g). Dissectible fat percentage was relevantly greater in the high-IMF line than in the low-IMF line at 9 and 13 wk of age with a P_r = 1.00. Considering the six generations, DFP showed a mean correlated response of 0.18 SD of the trait per generation at 9 wk, and 0.17 SD at 13 wk. Other experiments of selection for IMF also showed positive correlated responses in the carcass fat content (Zhao, Chen, Zheng, Wen, & Zhang, 2007 in broilers and Schwab, Baas, Stalder, & Nettleton, 2009 in pigs).

3.2.2. Correlated responses in IMF and fatty acid composition of several muscles

Tables 4a and 4b show the differences between high and low-IMF lines for IMF and fatty acid composition of LTL, BF, SS and SP muscles at 9 and 13 wk of age, respectively.

Table 4a

Differences between high and low intramuscular fat rabbit lines for meat traits in several muscles at 9 wk of age.

Muscle	[1]Trait	[2]D	[3]HPD$_{95\%}$	[4]P_0	[5]r	[6]P_r
Longissimus thoracis et lumborum	pH	0.06	0.01, 0.11	0.98	0.04	0.72
	IMF	0.33	0.27, 0.38	1.00	0.05	1.00
	SFA	0.67	0.30, 1.29	1.00	0.43	0.93
	MUFA	7.11	5.76, 8.49	1.00	1.01	1.00
	PUFA	-7.90	-9.41, -6.42	1.00	1.13	1.00
Biceps femoris	pH	0.02	-0.04, 0.08	0.77	0.03	0.62
	IMF	0.39	0.20, 0.60	1.00	0.11	1.00
	SFA	0.38	-0.33, 1.15	0.86	0.36	0.52
	MUFA	2.14	0.96, 3.39	1.00	0.72	0.99
	PUFA	-2.54	-3.95, -0.98	1.00	0.81	0.99
Supraspinatus	pH	0.08	-0.02, 0.18	0.94	0.05	0.72
	IMF	0.45	0.22, 0.68	1.00	0.12	1.00
	SFA	0.52	-0.42, 1.54	0.87	0.53	0.51
	MUFA	3.25	1.95, 4.74	1.00	0.73	1.00
	PUFA	-3.80	-6.02, -1.72	1.00	1.13	0.99
Semimembranosus proprius	pH	-0.05	-0.11, 0.02	0.94	0.04	0.62
	IMF	0.61	0.32, 0.89	1.00	0.17	1.00

[1]IMF; intramuscular fat expressed as g of IMF/100g muscle; Saturated (SFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) expressed as a percentage of total fatty acids. [2]D = median of the marginal posterior distribution of the difference between lines; [3]HPD$_{95\%}$ = highest posterior density region at 95% of probability; [4]P_0 = probability of the difference being greater than zero when D >0 or lower than zero when D <0; [5]r = relevant value, proposed as 1/3 of the standard deviation of the trait; [6]P_r = probability of relevance (probability of the difference being greater than r when D >0 or lower than r when D <0).

Table 4b

Differences between high and low intramuscular fat rabbit lines for meat traits in several muscles at 13 wk of age.

Muscle	[1]Trait	[2]D	[3]$HPD_{95\%}$	[4]P_0	[5]r	[6]P_r
Longissimus thoracis et lumborum	pH	-0.02	-0.10, 0.07	0.70	0.04	0.32
	IMF	0.71	0.61, 0.81	1.00	0.06	1.00
	SFA	0.29	-0.33, 0.98	0.81	0.37	0.40
	MUFA	6.88	5.49, 8.31	1.00	0.75	1.00
	PUFA	-7.17	-8.61, -5.73	1.00	0.79	1.00
Biceps femoris	pH	0.01	-0.08, 0.10	0.62	0.04	0.27
	IMF	0.92	0.60, 1.27	1.00	0.19	1.00
	SFA	0.66	0.12, 1.16	0.99	0.26	0.94
	MUFA	2.39	1.46, 3.32	1.00	0.54	1.00
	PUFA	-3.06	-4.03, -2.02	1.00	0.58	1.00
Supraspinatus	pH	-0.05	-0.15, 0.07	0.78	0.06	0.40
	IMF	0.83	0.45, 1.17	1.00	0.19	1.00
	SFA	0.02	-0.83, 0.83	0.52	0.44	0.16
	MUFA	2.58	1.56, 3.68	1.00	0.58	1.00
	PUFA	-2.62	-4.11, -1.21	1.00	0.76	0.99
Semimembranosus proprius	pH	-0.07	-0.15, 0.01	0.96	0.04	0.79
	IMF	1.76	1.40, 2.10	1.00	0.18	1.00

[1] IMF; intramuscular fat expressed as g of IMF/100g muscle; Saturated (SFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) expressed as a percentage of total fatty acids. [2]D = median of the marginal posterior distribution of the difference between lines; [3]$HPD_{95\%}$ = highest posterior density region at 95% of probability; [4]P_0 = probability of the difference being greater than zero when D >0 or lower than zero when D <0; [5]r = relevant value, proposed as 1/3 of the standard deviation of the trait; [6]P_r = probability of relevance (probability of the difference being greater than r when D >0 or lower than r when D <0).

In the sixth generation, direct response to selection on IMF of LTL at 9 wk was 0.33 g of IMF/100g muscle (P_r = 1.00), representing a 31.4% of the mean and 2.38 SD of the trait. The genetic progress estimated per generation was 0.4 SD of the trait, which is in line with the results obtained with whole data from this selection experiment (Martínez-Álvaro, Hernández, & Blasco, 2016). Other selection experiments for IMF also reported great responses to selection (Sapp, Bertrand, Pringle, & Wilson, 2002 in cattle; Zhao, Chen, Zheng, Wen, & Zhang, 2007 in chickens and Schwab, Baas, Stalder, & Nettleton, 2009 in pigs).

Correlated responses in IMF content of BF, SS and SP muscles at 9 and 13 wk of age were all positive and relevant ($P_r = 1.00$). “In the followings, correlated responses are expressed in units of SD to facilitate comparisons between muscles. Correlated responses at 9 wk were similar (1.18 SD in BF, 1.27 in SS and 1.19 in SP), which are around 0.2 SD of the trait per generation, and they were lower than in LTL. At 13 wk of age, correlated responses to selection in units of SD were greater in muscles LTL (4.12) and SP (3.20), in comparison to BF (1.60) and SS (1.43). Gondret, Mourot, & Bonneau (1998) reported greater rate of intramuscular lipid deposition in rabbits around 14 wk of age, which was particularly large for SP muscle in comparison to *Longissimus lumborun* and BF muscles.

Selection for IMF of LTL affected similarly the fatty acid composition of LTL, BF and SS muscles, regardless of their metabolic profile. Selection for high IMF relevantly increased MUFA and decreased PUFA percentages in all muscles at 9 wk ($P_r \geq 0.99$, Table 4) and 13 wk ($P_r \geq 0.99$, Table 5), in comparison to low-IMF line. Differences between lines at 9 wk were greater in LTL (2.3 SD for MUFA and -2.3 SD PUFA) than in BF (0.99 SD for MUFA and -1.04 for PUFA) and SS (1.48 SD for MUFA and -1.12 SD for PUFA) muscles. Similar conclusions can be obtained at 13 wk of age. We almost did not observe a correlated response to selection in the SFA percentage of muscles, except in LTL at 9 wk and in BF at 13 wk. Result in LTL is likely a sampling effect since SFA percentage of LTL muscle at 9 wk was not affected by selection in a study of whole data from this selection experiment (Martínez-Álvaro, Hernández, & Blasco, 2016). Differences between lines in fatty acid composition are explained by a rapid increase of triglycerides (rich in MUFA and SFA) respect to phospholipids (rich in PUFA) when fat increases (Wood et al., 2008). The lack of a clear positive correlated response in total SFA percentage of muscles may be explained by different richness patterns of the main individual SFA in rabbit meat in the two phases, triglycerols and phospholipids (Alasnier, Rémington, & Gandemer, 1996). The greater differences between lines in MUFA and PUFA observed in LTL in comparison to BF and SS muscles are in line with the greater IMF differences observed in this muscle, at 9 and 13 wk. If correcting by DFP, correlated responses to selection in IMF and fatty acid composition at both ages were approximately the same in all muscles (data not shown).

Our results suggest a common genetic background for the IMF deposition and fatty acid composition in several muscles with different metabolic profile in rabbits. The genetic determinism of IMF deposition and composition in the muscles studied seems to be relatively independent from the determinism of fat deposition in carcass. In this line, Martínez-Álvaro, Hernández, & Blasco (2016) quantified the genetic correlation between IMF of LTL and DFP within animals from this selection experiment and it was low (0.34), although $HPD_{95\%}$ was large (from 0.08 to 0.60). The high correlated response to selection observed in DFP (Table 3) is due to its positive genetic correlation with intramuscular fat, which is the trait being selected, and the high heritabilities of both traits, IMF and DFP (Martínez-Álvaro, Hernández, & Blasco, 2016).

There is not previous information about the correlated responses to selection for IMF in muscles with different metabolic profile. The selection experiment for IMF in chicken breast found a positive correlated response in the IMF content of the whole hind leg, but they do not differentiate between muscles with different metabolic patterns (Zhao, Chen, Zheng, Wen, & Zhang, 2007). In a commercial population of Duroc pigs, Quintanilla et al. (2011) observed that some lipid QTL maps for IMF content and composition of *Longissimus* were different than those from *Gluteus medius,* suggesting that IMF content and composition of these two muscles were partially regulated by different genes. Few studies have reported genetic correlations between muscles, providing results in the same direction as our findings. In pigs, Ros-Freixedes, Reixarch, Bosch, Tor, & Estany (2014) estimated the genetic correlation between IMF in LTL and IMF in *Gluteus medius* muscles and it was 0.68 with $HPD_{95\%}$ [0.48, 0.87]. The genetic correlations between these two muscles for SFA, MUFA and PUFA percentages were also positive and high, ranging from 0.62 to 0.82 (Ros-Freixedes, Reixarch, Bosch, Tor, & Estany, 2014). In the selection experiment for IMF in chickens, Zhao, Wen, Chen, Zheng, & Li (2006) reported a genetic correlation between IMF of breast muscle and IMF of whole hind leg of 0.89.

3.3. Correlations between IMF content of the muscles

Table 5 shows the phenotypic correlations between muscles for IMF at 9 and 13 wk. All the phenotypic correlations between IMF of LTL, BF, SS and SP muscles were positive with P_0 = 0.96 or greater. These positive phenotypic correlations are consistent with the positive correlated responses to selection observed on IMF of different muscles. The medians of the phenotypic correlations ranged between 0.24 and 0.57. However, due to the low amount of data used to estimate these phenotypic correlations, we do not have much information about the actual values (see their large $HPD_{95\%}$).

To our knowledge, there are no previous estimates of correlations between IMF from different muscles of the carcass in rabbits. Phenotypic correlations between IMF of five different muscles in lambs were positive and variable, ranging from 0.30 to 0.75, the strongest correlations found between muscles located within the same region of the carcass (Anderson, Pethick, & Gardner, 2015). In pigs, a positive correlation (0.71) for IMF between muscles *Longissimus* and *Gluteus medius* was reported by Quintanilla et al. (2011).

Table 5

Medians and highest posterior density regions at 95% of probability (within brackets) of the marginal posterior distributions of the phenotypic correlations between intramuscular fat of muscles in rabbits at 9 and 13 wk.

Muscles	*Biceps femoris*	*Supraspinatus*	*Semimembranosus proprius*
Phenotypic correlations at 9 wk			
Longissimus thoracis et lumborum	0.32 [0.06, 0.55]	0.31 [0.04, 0.54]	0.26 [0.00, 0.50]
Biceps femoris		0.54 [0.34, 0.71]	0.28 [0.02, 0.52]
Supraspinatus			0.40 [0.17, 0.62]
Phenotypic correlations at 13 wk			
Longissimus thoracis et lumborum	0.47 [0.27, 0.67]	0.56 [0.36, 0.74]	0.41 [0.14, 0.64]
Biceps femoris		0.52 [0.31, 0.72]	0.24 [-0.02, 0.51]
Supraspinatus			0.57 [0.35, 0.76]

Conclusions

Our results show that there is a common genetic background for the IMF deposition and fatty acid composition in muscles with different metabolic profile in rabbits. Selection for IMF in muscle LTL showed a positive correlated response in IMF of other muscles with different metabolic profile (BF, SS and SP) at 9 and 13 wk of age. Selection for high IMF increased MUFA and decreased PUFA percentage in all muscles at both ages, in comparison with low-IMF line, whereas no differences between lines were observed for SFA.

Acknowledgements

This work was supported by project AGL2014-55921-C2-01-P from the Spanish National Research Plan. M. Martínez-Álvaro acknowledges a FPI grant (BES-2012-052655) from the Economy Ministry of Spain.

References

Alasnier, C., Rémignon, H., & Gandemer, G. (1996). Lipid characteristics associated with oxidative and glycolytic fibres in rabbit muscles. *Meat Science, 43(3-4)*, 213-224. https://doi.org/10.1016/S0309-1740(96)00015-0

Anderson, F., Pethick, D. W., & Gardner, G. E. (2015). The correlation of intramuscular fat between muscles of the lamb carcass and the use of computed tomography to predict intramuscular fat percentage in lambs. *Animal 9(7),* 1239-1249. http://doi.org/10.1017/S175173111500049X

Blasco, A., & Ouhayoun, J. (1996). Harmonization of Criteria and Terminology in Rabbit Meat Research. Revised Proposal. *World Rabbit Science*, *4*(2), 93–99. http://doi.org/10.4995/wrs.1996.278

Blasco, A. (2005). The use of Bayesian statistics in meat quality analyses: A review. *Meat Science 69(1)*, 115-122. https://doi.org/10.1016/j.meatsci.2004.06.012

Blasco, A. (2017). Bayesian data Analysis for Animal Scientists. Springer, NY

Dalle Zotte, A. (2002). Perception of rabbit meat quality and major factors influencing the rabbit carcass and meat quality. *Livestock Production Science 75(1)*, 11–32. http://doi.org/10.1016/S0301-6226(01)00308-6

Delmas, D., & Ouhayoun, J. (1990). Technologie de l`abattage du lapin. I. Etude descriptive de la musculature. *Viandes et Produits Carnés 11(1)*, 11-14.

Enser, M., Hallett, K., Hewitt, B., Fursey A. J., & Wood, J. D. (1996). Fatty acid content and composition of English beef, lamb and pork at retail. *Meat Science 42(4)*, 443-456. http://doi.org/10.1016/0309-1740(95)00037-2

Gondret, F., Mourot, J., & Bonneau, M. (1998). Comparison of intramuscular adipose tissue cellularity in muscles differing in their lipid content and fibre type composition during rabbit growth. *Livestock Production Science 54(1)*, 1-10. http://doi.org/10.1016/S0301-6226(97)00172-3

Hernández, P., Aliaga, S., Plá, M., & Blasco, A. (2004). The effect of selection for growth rate and slaughter age on carcass composition and meat quality traits in rabbits. *Journal of Animal Science 82(11)*, 3138–3143. http://doi.org/ 10.2527/2004.82113138x

Hernández, P., Ariño, B., Grimal, A., & Blasco, A. (2006). Comparison of carcass and meat characteristics of three rabbit lines selected for litter size or growth rate. *Meat Science 73(4)*, 645-650. http://doi.org/10.1016/j.meatsci.2006.03.007

Lawrie, R. A., & Ledward, D. A. (2006). The structure and growth of muscle. In: *Lawrie's Meat Science 7th ed.* (pp. 41-73). Cambrige, England :Woodhead Publising

Legarra, A., Varona, L., & López de Maturana, E. (2008). TM: Thershold model. http://snp.toulouse.inra.fr/~alegarra/manualtm.pdf.

Martínez-Álvaro, M., Hernández, P., & Blasco, A. (2016). Divergent selection on intramuscular fat in rabbits : Responses to selection and genetic parameters. *Journal of Animal Science*, *94*(12), 4993–5003. http://doi.org/10.2527/jas2016-0590

Pascual, M., E., Calle, W., & Blasco, A. (2015). Comparison of degrees of maturity of rabbit lines selected for different traits. *World Rabbit Science, 23(3)*, 155-161. http://dx.doi.org/10.4995/wrs.2015.3964.

Quintanilla, R., Pena, R. N., Gallardo, D., Cánovas, A., Ramírez, O., Díaz, I., …

Amills, M. (2011). Porcine intramuscular fat content and composition are regulated by quantitative trait loci with muscle-specific effects. *Journal of Animal Science*, *89*(10), 2963–2971. http://doi.org/10.2527/jas.2011-3974

Ros-Freixedes, R., Reixarch, J., Bosch, L., Tor, M., & Estany, J. (2014). Genetic correlations of intramuscular fat content and fatty acid composition among muscles and with subcutaneous fat in Duroc pigs. *Journal of Animal Science*, *92(12)*, 5417-5425. http://doi.org// 10.2527/jas.2014-8202.

Sapp, R. L., Bertrand, J. K., Pringle, T. D., & Wilson, D. E. (2002). Effects of selection for ultrasound intramuscular fat percentage in Angus bulls on carcass traits of progeny. *Journal of Animal Science*, *80*(8), 2017–2022. http://doi.org//2002.8082017x

Schwab, C. R., Baas, T. J., Stalder, K. J., & Nettleton, D. (2009). Results from six generations of selection for intramuscular fat in Duroc swine using real-time ultrasound. I. Direct and correlated phenotypic responses to selection. *Journal of Animal Science*, *87*(9), 2774–2780. http://doi.org/10.2527/jas.2008-1335

Wood, J. D., Richardson, R. I., Nute, G. R., Fisher, A. V., Campo, M. M., Kasapidou, E., Sheard, P. R., Enser, M. (2004). Effects of fatty acids on meat quality: A review. *Meat Science*, *66*(1), 21–32.

Wood, J. D., Enser, M., Fisher A. V., Nute, G. R., Sheard, P. R., Richardson, Hughes, S. I., Whittington, F. M. (2008). Fat deposition, fatty acid composition and meat quality: a review. *Meat Science 78(4)*, 343-358.

World Health Organization (2008). Interim summary of conclusions and dietary recommendations on total fat and fatty acids. *Joint FAO/WHO expert consultation on fats and fatty acids in human nutrition*, 10-14.

Zhao, G. P, Wen, J., Chen, J. L., Zheng, M. Q., & Li, X. (2006). Selection response and estimation of the genetic parameters for intramuscular fat in a quality chicken line. *Acta Veterinaria et Zootechnica Sinica 37(9)*, 870-873.

Zhao, G. P., Chen, J. L., Zheng, M. Q., Wen, J., & Zhang, Y. (2007). Correlated Responses to Selection for Increased Intramuscular Fat in a Chinese Quality Chicken Line. *Poultry Science*, *86*(11), 2309–2314.

http://doi.org/10.1093/ps/86.11.2309

Zomeño, C., Hernández, P., & Blasco, A. (2011). Use of near infrared spectroscopy for intramuscular fat selection in rabbits. *World Rabbit Science*, *19*(4), 203–208. http://doi.org/10.4995/vrs.2011.939

Zomeño, C., Juste, V., & Hernández, P. (2012). Application of NIRS for predicting fatty acids in intramuscular fat of rabbit. *Meat Science*, *91*(2), 155–159. http://doi.org/10.1016/j.meatsci.2012.01.009

Zomeño, C., Hernández, P., & Blasco, A. (2013). Divergent selection for intramuscular fat content in rabbits. I. Direct response to selection. *Journal of Animal Science*, *91*(9), 4526-4531.http://doi.org/10.2527/jas.2013-6361