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Additional Information

1 **Genetic analysis of meat quality traits in maternal lines of rabbit and their diallel**

2 **cross.[1]**

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ABSTRACT: Young rabbits, the dams of which came from a full diallel cross among four maternal lines (A, V, H and LP) and the sires from a single paternal line (R), that produce sixteen genetic groups, was carried out to evaluate the genetic groups and to estimate the crossbreeding genetic parameters of meat quality. The meat quality traits were recorded by NIRS from a sample of 285 *longissimus lumborum* muscles. Crossbreeding parameters were estimated according to Dickerson model. No differences in protein were found. The line A had significant differences with V line for intramuscular fat, and fatty acids groups. Significant differences for these traits appeared between the crossbred AH and VV (in favour of AH). As conclusion, in crossbreeding parameters for quality meat traits in rabbits, the significant contrasts are mainly consequence of direct-maternal genetic effects, however grandmaternal and maternal heterosis effects were not significant.

KEYWORDS: Crossbreeding parameters, diallel cross, meat quality, maternal lines, rabbit.

CHEMICAL COMPOUNDS STUDIED IN THIS ARTICLE:

Myristic Acid (PubChem CID: 11005); Palmitic Acid (PubChem CID: 985); Palmitoleic Acid (PubChem CID: 445638); Stearic Acid (PubChem CID: 5281); Vaccenic Acid (PubChem CID: 5281127); Oleic Acid (PubChem CID: 445639); Linoleic Acid (PubChem CID: 5280450); Arachidomic Acid (PubChem CID: 444899); Docosatetraenoic Acid (PubChem CID: 5282844); Docosahexanoic Acid (PubChem CID: 445580)

INTRODUCTION

Meat rabbit selection programmes improves, between other traits, litter size in dam lines and growth rate in sire lines (Rochambeau, 1988; Baselga, 2004). Maximizing growth potential of sire lines is important to ensure the economic viability of rabbits producers (Cartuche, L., Pascual, M., Gómez, E., & Blasco, A. (2014)); however, it can produce an undesirable effect on meat and carcass qualities because the degree of maturity at market weight is reduced (Pascual, 2007). Meat quality is a generic term used to describe properties and perceptions of meat: sensory characteristics, nutritional properties, healthiness, technological factors, microbiological and chemical safety and ethical and environment aspects. Rabbit meat has good nutritive properties because it has lower fat and higher polyunsaturated fatty acid (**PUFA**) content than other meats (Hernández & Gondret, 2006). The most ubiquitous fatty acids (**FA**) are palmitic (C16:0), oleic (C18:1 n-9) and linoleic (C18:2 n-6) acids, showing percentages higher than 20% of total FA. Rabbit meat also contains high protein content and high levels of essential amino acids (Hernández & Dalle Zote, 2010).

Traditional methods used to determine meat chemical composition are laborious, expensive, time-consuming and destructive. New methods for meat quality evaluation were used by researchers, as e.g. ultrasound, electric nose, tastes sensing, NIRS, TOBEC and Video Image Analysis (Cross & Belk, 1992). NIRS (near infrared reflectance spectroscopy) is a fast, accurate and cheap analytical technique and rabbit is a good experimental model to measure meat quality. For these reasons, NIRS had been used in some studies in meat quality traits in rabbits, for example Pla et al. (2007) to discriminate between conventional and organic production, Pascual, M., & Pla, M. (2007) to evaluate changes in meat quality when selecting rabbits for growth rate or

58 Zomeño, C., Juste, V., & Hernández, P. (2012) to predict fatty acid content in rabbit

59 selection programs.

60 Some studies were made to describe the effects of genotype and crossbreeding

61 parameters on meat quality in other species as in pigs (Sellier, P., & Monin, G. (1994);

62 Larzul, C., Lefaucheur, L., Ecolan, P., Gogue, J., Talmant, A., Sellier, P., Le Roy, P. &

63 Monin, G. (1997)), beef cattle (Gregory, K. E., Cundiff, L. V., Koch, R. M., Dikeman,

64 M. E., & Koohmaraie, M. (1994)), sheep (Hopkins, D. L., Fogarty, N. M., & Mortimer,

65 S. I. (2011)), chicken (Liu, G., Dunnington, E. A., & Siegel, P. B. (1993)) or ducks

66 (Wołoszyn, J., Okruszek, A., Orkusz, A., Wereńska, M., Książkiewicz, J., & Grajeta, H.

67 (2011)), but in rabbits, there are few studies on these topics.

68 The objective of this work was to estimate differences and crossbreeding parameters for

69 some meat chemical composition based on NIRS measurements in rabbits, the dams of

70 which come from a full diallel-cross among four maternal lines and the sires from a

71 paternal line; trying to evaluate the impact of a large genetic improvement program in

72 meat rabbit on meat quality.

73 **MATERIAL AND METHODS**

74 *Animals*

75 The rabbit lines and the animals used for this study were the same rabbits used in

76 Mínguez, C., Sánchez, J., Brun, J., Ragab, M., El Nagar, A., & Baselga, M. (2015a) and

77 Mínguez, C., Sánchez, J., Ragab, M., El Nagar, A., & Baselga, M. (2015b) to measure

78 growth and carcass traits, respectively. The genetic groups involved in the study were

79 four pure lines (AA, VV, HH and LL) and 12 single crosses: AV, VA, AH, HA, AL,

80 LA, VH, HV, VL, LV, HL and LH (a total of 16 genetic groups) and involved four

81 different farms, located in Altura (Castellón, Spain), Rioseco de Tapia (León, Spain),

82 Valencia (Spain) and Sant Carles de la Rápita (Tarragona, Spain). The genetic group

83 VV was present on all farms allowing data connection between farms. The pure line HH

84 was only presented in Tarragona. For this reason, pure line HH do not share the farm

85 with the A and LP lines.

Crossbreeding Design and Management

87 The crossbreeding design and the procedure of slaughter were described in Minguez et

88 al. (2015a,b)

89 After slaughtering, the carcasses were stored at 4º C during 24 hours and then, in the

90 meat laboratory of the Department of Animal Science of the Universidad Politécnica de

91 Valencia (UPV), the *longissimus lumborum* muscles (LL) were excised from the

92 carcasses.

Meat quality traits

94 Muscle pH at 24 h. *post mortem* was obtained in the LL muscle at the level of the fifth

95 lumbar vertebra of the left side and recorded with a Crison pH-meter Basic 20+ (Crison

96 Instruments, Barcelona, Spain). Meat colour (lightness, L*; redness, a*; and yellowness,

97 b*) was measured at the seventh lumbar vertebra in a transversal section of the right LL.

98 Meat obtained from the LL was ground, freeze-dried and stored at -80º C until analyses.

99 Meat was scanned with near infrared reflectance spectroscopy (NIRS) (model 5000,

100 FOSS NIRSystems INC., Hilleroed, Denmark). Protein content and fatty acid (FA)

101 composition of the LL were determined applying calibration equations previously

102 developed (Zomeño, C., Juste, V., & Hernández, P. (2012).).

Data Recording and Statistical Model

104 The pH was measured in a total of 950 LL which came from carcasses that were used

105 by Minguez et al. (2015b) and the other meat quality traits were recorded in a sample of

106 285 LL of these animals.

107 The model used in the analysis was:

108

$$Y_{jkl} = GG_j + F_k + S_l + e_{jkl}$$

109

110 Where: Y_{jkl} is a record of the trait; GG_j is the effect of genetic group (16 levels); F_k is

111 the effect of the farm (4 levels, one level for each farm); S_l is the effect of the sex and

112 e_{jkl} is the residual effect.

113 Estimates of the differences between all the genetics groups and VV animals,

114 crossbreeding parameters (proposed by Dickerson (1969)) and the estimable functions

115 of the crossbreeding parameters were calculate according to Minguez et al. (2015a).

116 **RESULTS AND DISCUSSION**

117 *Descriptive Statistics*

118 Table 1 and 2 show descriptive for the traits measured. The value for pH was similar to

119 those obtained in previous studies (Hernández, P., Aliaga, S., Pla, M., & Blasco, A.

120 (2004); Hernández & Gondret, 2006; Zomeño, 2013) and is in the optimum range to

121 avoid potentials problems related with meat pH. In rabbit, pH ranges between 5.4 and

122 6.4 depending on muscle location (Hulot & Ouhayoun, 1999) and it does not look like a

123 potential problem for meat quality. To date, the literature has not reported any abnormal

124 port-mortem acidification kinetics characteristics or pale, soft and exudative (PSE) or

125 acid meat in rabbit meat (Hernández & Dalle Zotte, 2010).. Color variables were also in

126 the range of that reported by Hernández et al. (2004), Combes & Dalle Zotte (2005),

127 Hernández & Gondret (2006) and Zomeño (2013). Rabbit meat has a high lightness

128 (L*) because it has a high capacity to reflect the light and due to its low myoglobin

129 content it has a low red index (a*).

130 Intramuscular fat (IMF) showed a low value because LL is the leanest muscle of the

131 carcass (Pla, M., Pascual, M., & Ariño, B. (2004)). Fat and protein values are in the

132 ranges already reported by Metzger, Sz., Kustos, K., Szendrõ, Zs., Szabó, A., Eiben,

133 Cs., Nagy, I. (2003), Pla et al. (2004), Hernández & Dalle Zotte (2010) and Zomeño

134 (2013). The main FA groups in rabbit LL were polyunsaturated (PUFA) and saturated

135 (SFA), with percentages around 37% and 36% of total FA, respectively.

136 Monounsaturated (MUFA) FA represented a lower percentage (27%). Among PUFA, n-

137 6 was the most abundant with percentage of 32%, while n-3 had a percentage of 6%.

138 These values are in the same magnitude of those by Hernandez & Dalle Zotte (2010),

139 Dalle Zotte & Szendro (2011) and Zomeño et al. (2012). PUFA/SFA and n-6/n-3 ratios,

140 used to evaluate quality of fat, showed values close to the nutritional recommendations

141 (reviewed by Hernández and Dalle Zotte, 2010).

142 In Table 2 is shown that the most abundant FA in LL were palmitic (C16:0), oleic

143 (C18:1 n-9) and linoleic (C18:2 n-6) acids, showing percentages of 24%, 23% and 23%,

144 respectively. Stearic (C18:0) and arachidonic acids (C20:4 n-6) were also important

145 with percentages around 8% and 5%, respectively. Linolenic acid (C18:3 n-3) and some

146 long chain PUFA (i.e. C20:5 n-3, C22:4 n-6 and C22:6 n-3) were also present in rabbit

147 meat although at a lower content. The FA composition in LL observed was similar to

148 that reported in previous studies (reviewed by Hernández & Gondret, 2006; Zomeño et

149 al., 2012).

150 *Differences between genetic groups*

151 In Table 3 the contrasts between the dam effects of the lines for pH, colour,

152 intramuscular fat (IMF, g./100g muscle), protein (g./100g muscle), fatty acid groups

153 (mg/100 g muscle) and fatty acid ratios of the LL can be observed. Table 4 shows the

154 same contrasts for individual fatty acid composition (mg/100 g muscle). Notice that,

155 when the lines involved in the contrast do not share the farm (H line with A and LP

156 lines) have higher standard errors. Muscle pH exerts a high influence on the

technological and eating quality of meat. The post-mortem evolution of pH and the pH

measured at 24 h post-mortem affect the brightness of meat, its water holding capacity

and toughness (Lawrie, 1998) and an abnormal postmortem acidification can produce

PSE or DFD meat. A significant difference was observed between A and LP lines.

However, this difference was not relevant, and all lines were in the range of an

appropriate pH. Hernández & Gondret (2006) studied pH differences between A and V

lines and did not observe differences between them. Meat color affects consumer

acceptance and purchasing decisions (Hernández & Dalle Zotte, 2010). Significant

differences were not observed in the contrasts between lines for L*, a* and b*.. IMF

plays an essential role in meat quality, largely determining eating quality and the

nutritional value of the meat (Wood, J. D., Enser, M., Fisher, A. V., Nute, G. R.,

Sheard, P.R., Richardson, R. I., Hughes, S. I., & Whittington, F. M. (2008)). Regarding

IMF, the line A had the higher content, being significant the difference with respect to

line V. Rabbit meat is rich in proteins compared to other meats, and also contains high

levels of essential amino acids with an easy digestibility (Hernández & Dalle Zotte,

2010). Non-significant differences were found for the content of protein between the

lines. One of the main aims of meat researchers is to produce dietetic and healthy meat

to reduce the SFA and increase the unsaturated FA (Dalle Zotte, 2002). Thus, it is

important to measure the possible differences between lines for these traits. Significant

differences in the contrast A-V were found for all fatty acid groups (in favor of the A

line), and despite non-significant differences with the other lines, it seems that the line

A had the highest content for fatty acid groups (SFA, MUFA and PUFA)in agreement

with its highest value for IMF. Among PUFA, significant differences were shown

between A-V for n-3 PUFA and between A-V and A-LP for n-6 PUFA (in favor of the

A line). Although, no other contrasts for fatty acid groups content involving line A were

significant, it seems that this line has the highest values. The Department of Health and

Social Security (1994) recommended a ratio of 0.45 or higher for PUFA/SFA and a

maximum of 4.0 for the n-6/n-3 ratio. However, diets in developed countries seem to

have much higher n-6/n-3 ratios fatty acids than in n-3 fatty acids, and the PUFA/SFA

ratios are far from the recommended value. For ratios n-6/n-3 and PUFA/SFA no

significant differences were found between the lines, and the four lines have correct

values for the first ratio and a light excess of n-6 in the second (Table 1). Table 4 shows

significant differences in the contrast A-V, in favor of the A line, for SFA (C14:0,

C15:0, C16:0, C17:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:2 n-

6, C18:3 n-3 and C20:2 n-6. Significant differences were not found between the A line

and the other lines, but it seems that this line had the highest values for all traits, as

commented before for IMF, and fatty acid groups (Table 3).

In commercial farms, crossbred does are the most common type of females and,

consequently, some differences in meat quality traits in dam effects might have

importance. As Mínguez et al. (2015b) and Mínguez et al. (2015a) made for growth

traits and carcass traits, respectively; we consider first the different crossbred groups

(the average of a cross and its reciprocal) with respect to the V line. In Table 5 the

contrasts between the dam effects of the lines for pH, colour, intramuscular fat (IMF,

g/100g muscle), protein (g/100g muscle), fatty acid groups (mg/100 g muscle) and fatty

acid ratios of the LL can be observed. In general, no significant differences were found

in the contrast All-VV. Only for a*, this contrast was significant in favor of V line. Also

for a*, the contrasts AH-VV and AL-VV were significantly superior for the line V.

Table 5 shows that the crossbreds involving A line had the higher content for IMF,

SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA respect to purebred V animals (significant

differences between AH and VV). This agrees with the result commented before in the

Table 3. Table 6 shows no significant differences for individual fatty acids in the contrast All-VV. In agreement with Table 5 and Table 4, Table 6 indicated that the contrast AH-VV was significant for SFA (C14:0, C15:0, C16:0 and C18:0), MUFA (C16:1, C18:1n-9 and C18:1n-7) and C18:3 n-3 in favor of the crossbred AH. However, C22:4 n-6 was higher for animals from purebred V dams than for animals from AH dams.

The importance of using a particular line either as sire or dam in a cross was assessed by testing the differences between a particular cross and its reciprocal (Table 7 and 8). In Table 7, a significant difference was found in the contrast HV-VV for a* in favor of the line V as sire. For the contrast AV-VA the significant difference in SFA was favorable to the A acting as sire, because the crossbred AV had lower value of SFA than VA animals, and, as commented before, one desirable feature would be to reduce the level of SFA.

Table 8 shows significant differences for C16:0 and C16:1 in the contrast AV-VA (higher values for VA). The higher value of C16:0 in the cross VA fully agree the results in Table 7 of this cross having higher level of SFA. In addition to this, Table 8 also shows significant differences in the contrast AH-HA for C20:5n-3 (in favor of H as sire) and for C22:5n-3 (in favor of A as sire). These results and the rest of the contrasts between the reciprocal crosses, the situation is not clear to decide if one cross or its reciprocal is the best because, in general, the reciprocal effects are infrequent, do not follow neither pattern and made difficult to decide which crossbred is optimal.

Direct-maternal effects

Differences between direct-maternal effects are shown in Table 9 and 10. The results of the contrasts between lines (Table 2 and 3) are in close agreement with the results for direct-maternal differences between lines. For pH, significant differences were found

232 for G^I_{A-V}, G^I_{L-H} and G^I_{L-V} (negative values). These indicate direct-maternal effects of the

233 LP line are the lowest.

234 The concordance for the significant differences between Table 3 and 9 is complete for

235 IMF, SFA, MUFA, PUFA, n-3 PUFA and n-6 PUFA. Thus, G^I_{A-V} was significant for

236 these traits. According to the Table 3, here G^I_{A-H} and G^I_{A-L} had positive values (no

237 significant difference) and there were indications that the direct-maternal effects of the

238 A line were the highest. In Table 10, significant differences were found in G^I_{A-V} for

239 C14:0, C15:0, C16:1, C17:0, C18:0 C18:1n-7, C18:1n-9, C18:2n-6 and C18:3 n-3 in

240 favor of the A line. These agree with the results commented from Table 4. For C16:0,

241 C17:0, C18:1n-7 and C20:2n-6, no significant differences were found regarding G^I_{A-V},

242 these results do not agree with those from Table 4 but they show the same pattern. For

243 G^I_{A-H} and G^I_{A-L}, there are not significant differences but, as happened before in Table 4,

244 there are indications that the direct-maternal effects of the A line were the highest.

245 *Grand-maternal effects*

246 Tables 11 and 12 show grand-maternal effect differences between lines. As Mínguez et

247 al. (2015a) and Mínguez et al. (2015b) reported, it can be observed that the errors for

248 the latter are smaller than those for the former, showing that our data structure is better

249 suited to estimate grand-maternal effects than direct-maternal effects. Contrary for

250 direct-maternal effects, no significant contrast were found for grand maternal effects,

251 clearly indicating that the importance of the latter should be lower than the importance

252 of the former.

253 *Maternal heterosis.*

254 Estimates of maternal heterosis effects are shown in Table 13 and 14. No significant

255 differences were found. Many results of positive heterosis, regarding litter size, have

256 been reported (Brun & Saleil, 1994; Khalil & Afifi, 2000; Baselga, M., Garcia, M.L.,

257 Sanchez, J.P., Vicente, J. S., & Lavara, R., 2003; Brun & Baselga, 2005; Youssef, Y.

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259 M. 2008). Minguez et al. (2015a) and Mínguez et al. (2015b) reported that maternal

260 heterosis estimates on the majority of growth and carcass traits in crosses involving

261 lines with high prolificacy (H and LP lines) were significantly negative. However, our

262 results did not found this negative heterosis estimates in meat quality traits, perhaps

263 because these traits are less dependent on litter size that growth and carcass traits. Also,

264 Sellier (1988) indicated that heterosis for quality of pork does not exist in most breed

265 crosses.

266 **CONCLUSIONS**

267 Significant differences regarding both direct-maternal effects and differences between

268 purebred lines have been found between A and V lines for SFA, MUFA, PUFA, n-3

269 PUFA, n-6 PUFA and for the majority of individual fatty acids, resulting meat from A

270 line as the fattiest. No significant differences were found for contrasts involving other

271 lines and the A line but there were indications that the A line had the highest contents of

272 the different fatty acids. Regarding the comparisons between the crosses and V line, the

273 crossbred AH was superior for IMF, SFA, MUFA, PUFA, n-3 PUFA, n-6 PUFA and

274 for some of individual fatty acids. Again, the results pointed out that those contrast

275 involving the A line were the fattiest, and probably those involving the line V the

276 leanest. However, no significant differences were found for the contrasts All-V, which

277 is an indication of the lack of overall heterotic effects. In general, the reciprocal cross

278 effects were not significant. After decomposing the estimates of the genetic group

279 effects into direct-maternal, grand-maternal and maternal heterosis effects, following

280 Dickerson's model, similar patterns of effects to those obtained in the comparison

281 between lines and crosses were obtained for the direct-maternal effects. No significant

282 differences were found for the grand-maternal effects, and in general were of lower

283 magnitude than the direct-maternal effects. No significant values of maternal heterosis

284 were found and were explained by the relative independence of   meat quality traits

285 from litter size.

286 It can be concluded that the observed significant contrasts are mainly consequence of

287 direct-maternal genetic effects, playing grand-maternal and heterotic effects a much

288 lower role in the control of the meat quality traits in rabbit

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TABLES

Table 1. Descriptive statistics of pH, colour, intramuscular fat (IMF), protein, fatty acid groups and fatty acid ratios of the *Longissimus lumborum* muscle (LL).

Trait	N[1]	Mean	SD[2]	Minimum	Maximum
pH	950	5.66	0.17	5.05	6.20
L*	285	51.52	3.37	39.07	59.89
a*	285	4.69	1.44	1.97	9.72
b*	285	1.61	1.44	-1.80	6.97
Groups (g/100g muscle)					
IMF	285	1.21	0.22	0.80	2.09
Protein	285	22	0.40	20	23
Groups (mg/100g muscle)					
SFA	285	308	66	173	546
MUFA	285	232	70	99	491
PUFA	285	331	36	243	449
n-3 PUFA	285	54	3	47	66
n-6 PUFA	285	277	35	208	409
Ratios					
n-6/n-3	285	5.10	0.47	3.94	7.95
PUFA/SFA	285	1.09	0.08	0.84	1.29

..
[1] N= number of LL. [2] SD= standard deviation

401   **Table 2.** Descriptive statistics of individual fatty acid composition (mg/100 g muscle)

402   of the *Longissimus lumborum* muscle(LL).

Trait	N[1]	Mean	SD[2]	Min[3]	Max[4]
C14:0	285	14.2	5.2	1.0	32.0
C15:0	285	4.3	0.9	2.6	7.8
C16:0	285	200	45	119	387
C16:1	285	15.8	9.7	3.3	56.7
C17:0	285	6.0	1.1	3.6	10.5
C18:0	285	70	9	52	108
C18:1 n-7	285	14.1	2.3	9.4	23.4
C18:1 n-9	285	192	54	90	402
C18:2 n-6	285	196	36	124	326
C18:3 n-3	285	14.0	4.4	4.6	30.1
C20:2 n-6	285	2.6	0.6	1.9	4.2
C20:3 n-6	285	4.2	0.4	3.3	7.7
C20:4 n-6	285	45.9	2.5	29.3	51.7
C20:5 n-3	285	12.4	1.5	7.4	16.2
C22:4 n-6	285	16.5	0.4	15.4	19.3
C22:5 n-3	285	6.4	0.8	1.8	10.0
C22:6 n-3	285	21.0	2.5	4.6	27.5

403   [1]. N= number of LL. [2]. SD= standard deviation [3]. Min= minimum [4]. Max= maximum

404   **Table 3**. Contrasts (standard error) between the lines for pH, colour, intramuscular fat (IMF, g/100g muscle), protein (g/100g muscle), fatty acid

405   groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum* muscle.

Trait	A-H	A-LP	A-V	H-V	LP-H	LP-V
pH	0(0.03)	0.05(0.02)*	0.04(0.02)	0.04(0.02)	-0.06(0.03)	-0.02(0.02)
L*	-0.78(1.50)	-0.44(1.07)	-0.14(1.09)	0.64(1.03)	-0.34(1.47)	0.30(1.05)
a*	0.79(0.66)	0(0.47)	-0.20(0.48)	-1.00(0.45)	0.78(0.65)	-0.21(0.46)
b*	0.03(0.55)	-0.12(0.40)	0.08(0.41)	0.05(0.40)	0.15(0.56)	0.20(0.40)
IMF	0.15(0.11)	0.14(0.08)	0.23(0.08)*	0.08(0.08)	0.01(0.11)	0.09(0.08)
Protein	-0.10(0.20)	0.05(0.14)	0.17(0.15)	0.27(0.14)	-0.15(0.20)	0.13(0.15)
SFA	49(33)	38(23)	67(24)*	19(23)	10(33)	29(24)
MUFA	58(33)	41(23)	66(24)*	8(23)	17(33)	25(24)
PUFA	26(18)	24(13)	34(13)*	7(13)	3(18)	10(13)
n-3 PUFA	2.4(1.6)	2.1(1.1)	3.1(1.1)*	0.7(1.1)	0.2(1.6)	0.9(1.1)
n-6 PUFA	26(18)	25(13)*	31(13)*	4(12)	1(13)	5(12)

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n-6/n-3	0.41(0.24)	0.22(0.16)	0.25(0.16)	-0.16(0.16)	0.19(0.24)	0.03(0.16)
PUFA/SFA	-0.05(0.04)	-0.02(0.02)	-0.05(0.03)	0(0.02)	-0.02(0.04)	-0.02(0.03)

406   . *P < 0.05 (significant difference at α = 0.05).

407

409 **Table 4**. Contrasts (standard error) between the lines for individual fatty acid composition (mg/ 100 g muscle) of the *Longissimus lumborum*

410 muscle).

Trait	A-H	A-LP	A-V	H-V	LP-H	LP-V
C14:0	3.0(2.6)	2.5(1.8)	5.6(1.9)*	2.5(1.8)	0.5(2.6)	3.1(1.9)
C15:0	0.7(0.4)	0.5(0.3)	0.9(0.3)*	0.2(0.3)	0.1(0.4)	0.3(0.3)
C16:0	31(22)	22(15)	41(16)*	10(15)	9(22)	19(16)
C16:1	7.1(4.7)	7.4(3.2)	10.0(3.3)*	2.7(3.2)	2.6(4.7)	5.4(3.3)
C17:0	0.9(0.6)	0.7(0.4)	0.9(0.4)*	0.0(0.4)	0.3(0.6)	0.2(0.4)
C18:0	6.9(4.7)	6.2(3.3)	9.4(3.4)*	2.6(3.3)	0.7(4.7)	3.3(3.4)
C18:1 n-7	1.6(1.2)	1.5(0.8)	2.3(0.8)*	0.6(0.8)	0.2(1.2)	0.8(0.8)
C18:1 n-9	47(27)	33(19)	53(19)*	6(19)	13(27)	19(19)

C18:2 n-6	33(18)	24(13)	32(13)*	-1(13)	9(18)	8(13)
C18:3 n-3	4.3(2.2)	2.7(1.5)	4.0(1.6)*	-0.3(1.5)	1.6(2.2)	1.3(1.6)
C20:2 n-6	0.3(0.2)	0.2(0.1)	0.3(0.1)*	0.0(0.1)	0.1(0.2)	0.1(0.1)
C20:3 n-6	0.2(0.2)	0(0.1)	0(0.1)	-0.2(0.1)	0.2(0.2)	0.1(0.1)
C20:4 n-6	-1(1)	0.7(1)	0(1)	1(1)	-1(1)	0(1)
C20:5 n-3	-0.3(0.6)	-0.3(0.4)	-0.1(0.4)	0.2(0.4)	0.0(0.6)	0.2(0.4)
C22:4 n-6	-0.1(0.2)	-0.1(0.1)	-0.2(0.1)	0.2(0.1)	0(0.2)	0.2(0.1)
C22:5 n-3	0.0(0.4)	0.5(0.3)	0.1(0.3)	0.2(0.3)	-0.1(0.4)	0.1(0.3)
C22:6 n-3	-1.6(1.5)	0.1(1.0)	0.3(1.0)	1.9(1.1)	-1.7(1.5)	0.2(1.0)

411   [1].. *P < 0.05 (significant difference at $\alpha = 0.05$).

412   **Table 5**. Contrasts (standard error) between crossbred genetic groups[1] and V line for pH, colour, intramuscular fat (IMF, g/100g muscle), protein
413   (g/100g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum* muscle.

Trait	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
pH	0.04(0.02)	0.03(0.02)	0(0.02)	0(0.02)	0(0.02)	0(0.02)	0.01(0.01)
L*	0.41(0.69)	-0.31(0.70)	0.44(0.70)	0.14(0.71)	-0.52(0.71)	-0.32(0.70)	-0.02(0.53)
a*	-0.64(0.30)*	-0.61(0.31)*	-0.44(0.31)	-0.55(0.31)	-0.40(0.31)	-0.19(0.31)	-0.47(0.23)*
b*	-0.40(0.26)	-0.58(0.27)	-0.21(0.27)	-0.03(0.27)	-0.26(0.27)	-0.18(0.27)	-0.27(0.20)
IMF	0.15(0.05)*	0.05(0.05)	0.2(0.05)	0.06(0.05)	0.07(0.05)	-0.06(0.05)	0.05(0.04)
Protein	0.1(0.1)	0(0.1)	0(0.1)	0(0.1)	0(0.1)	0.1(0.1)	0(0.1)
SFA	47(16)*	17(16)	8(16)	19(16)	24(16)	-18(16)	16(12)
MUFA	40(16)*	13(16)	2(16)	16(16)	16(16)	-18(16)	11(12)
PUFA	20(9)*	4(9)	0(9)	7(9)	6(9)	-10(9)	4(6)
n-3 PUFA	2.1(0.8)*	0.7(0.8)	0.2(0.8)	0.7(0.8)	1.0(0.8)	-0.8(0.8)	0.6(0.6)
n-6 PUFA	19(9)*	6(9)	-1(9)	10(9)	12(9)	-4(9)	6(7)
n-6/n-3	0.1(0.1)	0(0.1)	-0.1(0.1)	0(0.1)	0(0.1)	-0.1(0.1)	0(0.1)

PUFA/SFA	-0.03(0.02)	0(0.02)	-0.02(0.02)	-0.01(0.02)	-0.01(0.02)	0.02(0.02)	-0.01(0.01)

414   [1]. One cross and its reciprocal are considered together. . *P < 0.05 (significant difference at $\alpha = 0.05$).

415

416 **Table 6**. Contrasts (standard error) between crossbred genetic groups[1] and V line for individual fatty acid composition (mg/ 100 g muscle) of the

417 *Longissimus lumborum* muscle.

Trait	AH-VV	AL-VV	AV-VV	HV-VV	LH-VV	LV-VV	All-VV
C14:0	3.71(1.28)*	1.74(1.29)	0.29(1.29)	1.36(1.30)	1.86(1.31)	-1.21(1.30)	1.28(0.99)
C15:0	0.51(0.21)*	0.14(0.21)	0.03(0.21)	0.23(0.21)	0.20(0.21)	-0.23(0.21)	0.15(0.16)
C16:0	26(10)*	11(10)	8(10)	13(10)	19(10)	-12(10)	11(8)
C16:1	6.7(2.3)*	2.9(2.3)	1.1(2.3)	3.2(2.3)	4.1(2.3)	-2.0(2.3)	2.6(1.7)
C17:0	0.4(0.3)	0.1(0.3)	-0.1(0.3)	0.1(0.3)	0.2(0.3)	-0.3(0.3)	0.1(0.2)
C18:0	5.6(2.3)*	1.5(2.3)	0.0(2.3)	1.7(2.3)	2.0(2.3)	-2.6(2.3)	1.5(1.7)
C18:1 n-7	1.4(0.6)*	0.4(0.6)	0.0(0.6)	0.7(0.6)	0.5(0.6)	-0.6(0.6)	0.4(0.4)
C18:1 n-9	32(13)*	10(13)	1(13)	12(13)	13(13)	-15(13)	9(10)

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C18:2 n-6	16(9)	7(9)	-1(9)	6(9)	11(9)	-7(9)	5(7)
C18:3 n-3	2.1(1.1)*	1.0(1.1)	0.1(1.1)	0.9(1.1)	1.5(1.1)	-0.8(1.1)	0.8(0.8)
C20:2 n-6	0.1(0.1)	0.1(0.1)	0.0(0.1)	0.0(0.1)	0.1(0.1)	-0.1(0.1)	0.1(0.1)
C20:3 n-6	0.0(0.1)	0.1(0.1)	-0.1(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)	0.0(0.1)
C20:4 n-6	0.3(0.6)	-0.2(0.6)	-0.2(0.6)	-0.8(0.6)	-0.3(0.6)	-1.0(0.6)	0.3(0.4)
C20:5 n-3	0.0(0.3)	-0.1(0.3)	0.0(0.3)	0.1(0.3)	-0.1(0.3)	0.2(0.3)	0.1(0.2)
C22:4 n-6	-0.3(0.1)*	-0.2(0.1)	-0.1(0.1)	-0.1(0.1)	-0.3(0.1)*	-0.1(0.1)	-0.2(0.1)
C22:5 n-3	-0.1(0.2)	-0.1(0.2)	0.1(0.2)	-0.1(0.2)	-0.2(0.2)	-0.3(0.2)	-0.1(0.2)
C22:6 n-3	-0.2(0.7)	-0.5(0.7)	-0.1(0.7)	-0.8(0.7)	-1.0(0.7)	-1.0(0.7)	-0.6(0.6)

418   [1]. One cross and its reciprocal are considered together. *P < 0.05 (significant difference at $\alpha = 0.05$).

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Table 7. Contrasts (standard error) between reciprocal crosses for pH, colour, intramuscular fat (IMF, g/100g muscle), protein (g/100g muscle),

fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *Longissimus lumborum*muscle.

Trait[1]	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
pH	0.04(0.03)	-0.02(0.03)	-0.01(0.03)	-0.02(0.03)	-0.06(0.03)	-0.04(0.03)
L*	-1.6(1.4)	1.4(1.4)	0.4(1.4)	2.0(1.4)	2.4(1.4)	0.3(1.4)
a*	-0.2(0.6)	0.2(0.6)	0.1(0.6)	-1.3(0.6)*	-0.4(0.6)	0.5(0.6)
b*	-0.8(0.05)	0.5(0.05)	0.4(0.05)	0.5(0.05)	-0.3(0.05)	0.3(0.05)
IMF	0.1(0.1)	-0.1(0.1)	-0.2(0.1)	0.1(0.1)	0.1(0.1)	0.0(0.1)
Protein	0.1(0.2)	0.1(0.2)	0(0.2)	-0.2(0.2)	0.2(0.2)	0.1(0.2)
SFA	46(32)	-18(32)	-70(32)*	41(32)	25(32)	-8(32)
MUFA	40(33)	-17(33)	-58(33)	32(33)	22(33)	-3(33)
PUFA	17(18)	-8(18)	-29(18)	15(18)	10(18)	-3(18)
n-3 PUFA	2.5(1.6)	-1.3(1.6)	-2.9(1.6)	1.4(1.6)	1.1(1.6)	-1.0(1.6)

n-6 PUFA	15(17)	0(17)	-25(17)	19(17)	6(17)	-1(17)
n-6/n-3	0(0.2)	0(0.2)	-0.1(0.2)	0.1(0.2)	0.1(0.2)	0.2(0.2)
PUFA/SFA	-0.06(0.04)	0.03(0.04)	0.06(0.04)	-0.03(0.04)	-0.02(0.04)	0.00(0.04)

422 . *$P < 0.05$ (significant difference at $\alpha = 0.05$).

423

424 **Table 8.** Contrasts (standard error) between reciprocal crosses for individual fatty acid composition (mg/ 100 g muscle) of the *longissimus*

425 *lumborum* muscle.

Trait	AH-HA	AL-LA	AV-VA	HV-VH	LH-HL	LV-VL
C14:0	2.9(2.6)	-1.5(2.6)	-4.9(2.6)	2.5(2.6)	1.8(2.6)	0.0(2.6)
C15:0	0.5(0.4)	-0.2(0.4)	-0.7(0.4)	0.4(0.4)	0.6(0.4)	-0.3(0.4)
C16:0	32(21)	-13(21)	-45(21)*	26(21)	8(21)	-9(21)
C16:1	6.8(4.6)	-3.3(4.6)	-9.7(4.6)*	4.3(4.6)	3.0(4.6)	-3.1(4.6)
C17:0	0.6(0.6)	-0.2(0.6)	-0.8(0.6)	0.7(0.6)	0.2(0.6)	0.0(0.6)
C18:0	5.0(4.6)	-2.5(4.6)	-8.0(4.6)	4.5(4.6)	2.7(4.6)	-0.6(4.6)
C18:1 n-7	1.0(1.2)	-0.5(1.2)	-1.9(1.2)	1.1(1.2)	0.6(1.2)	-0.3(1.2)
C18:1 n-9	-33(26)	-14(26)	-48(26)	27(26)	18(26)	-2(26)

C18:2 n-6	15(18)	-3(18)	-25(18)	18(18)	5(18)	-2(18)
C18:3 n-3	2.0(2.2)	-0.4(2.2)	-3.3(2.2)	2.3(2.2)	0.7(2.2)	-0.6(2.2)
C20:2 n-6	0.1(0.2)	0.1(0.2)	-0.2(0.2)	0.1(0.2)	-0.1(0.2)	-0.1(0.2)
C20:3 n-6	-0.2(0.2)	0.2(0.2)	0.0(0.2)	0.1(0.2)	-0.1(0.2)	0.3(0.2)
C20:4 n-6	2.2(1.2)	-1.6(1.2)	-1.3(1.2)	-0.1(1.2)	0.6(1.2)	-0.3(1.2)
C20:5 n-3	-1.6(0.5)*	0.4(0.5)	0.3(0.5)	0.0(0.5)	0.2(0.5)	0.0(0.5)
C22:4 n-6	0.1(0.2)	-0.2(0.2)	0.1(0.2)	0.1(0.2)	0.1(0.2)	0.0(0.2)
C22:5 n-3	1.00(0.4)*	-0.2(0.4)	-0.5(0.4)	0.0(0.4)	0.3(0.4)	-0.6(0.4)
C22:6 n-3	1.0(1.5)	-1.0(1.5)	0.0(1.5)	-0.2(1.5)	-0.1(1.5)	-0.4(1.5)

426   *$P < 0.05$ (significant difference at $\alpha = 0.05$).

427   **Table 9**. Direct-maternal effect differences between lines[1] (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle), protein
428   (g/100g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	$^{1}\,G^{I}_{A-H}$	G^{I}_{A-L}	G^{I}_{A-V}	G^{I}_{H-V}	G^{I}_{L-H}	G^{I}_{L-V}
pH	0.00(0.04)	0.08(0.03)*	0.02(0.03)	0.02(0.03)	-0.08(0.04)*	-0.06(0.03)*
L*	-1.35(1.6)	-0.82(1.3)	0.22(1.3)	1.58(1.3)	-0.53(1.6)	1.05(1.3)
a*	1.20(0.72)	-0.06(0.56)	-0.19(0.56)	-1.39(0.56)*	1.26(0.72)	-0.13(0.56)
b*	-0.39(0.63)	-0.10(0.48)	0.31(0.48)	0.71(0.48)	-0.29(0.63)	0.41(0.48)
IMF	0.14(0.12)	0.11(0.10)	0.20(0.10)*	0.06(0.10)	0.03(0.12)	0.09(0.10)
Protein	-0.01(0.23)	-0.05(0.18)	0.11(0.18)	0.13(0.18)	-0.04(0.23)	0.17(0.18)
SFA	45(37)	33(29)	63(29)*	17(29)	12(37)	30(29)
MUFA	56(37)	34(29)	61(29)*	4(29)	22(37)	26(29)
PUFA	24(20)	20(16)	33(16)*	5(16)	4(20)	9(16)
n-3 PUFA	2.4(1.8)	2.2(1.4)	2.9(1.4)*	0.2(1.4)	0.4(1.8)	0.6(1.4)
n-6 PUFA	24(20)	26(15)	31(15)*	7(15)	-2(20)	5(15)
n-6/n-3	0.4(0.3)	0.1(0.2)	0.3(0.2)	-0.1(0.2)	0.3(0.3)	0.2(0.2)

| | PUFA/SFA | -0.06(0.04) | -0.02(0.03) | -0.05(0.03) | 0.00(0.03) | -0.04(0.04) | -0.03(0.03) |

429   [1]. G^I_{i-j} = direct-maternal differences between lines i and j (see text for a complete explanation. *P < 0.05 (significant difference at α = 0.05).

430

431

432 **Table 10**. Direct-maternal effect differences between lines[1] (standard error) for individual fatty acid composition (mg/ 100 g muscle) of the

433 *longissimus lumborum* muscle .

Trait	[1] G^I_{A-H}	G^I_{A-L}	G^I_{A-V}	G^I_{H-V}	G^I_{L-H}	G^I_{L-V}
C14:0	2.7(2.9)	1.6(2.3)	5.0(2.3)*	2.3(2.3)	1.0(2.9)	3.3(2.3)
C15:0	0.6(0.5)	0.5(0.4)	0.8(0.4)*	0.1(0.4)	0.1(0.5)	0.3(0.4)
C16:0	28(25)	22(20)	37(20)	9(20)	6(25)	15(20)
C16:1	6.9(5.2)	4.1(4.1)	8.2(4.1)*	1.3(4.1)	2.7(5.2)	4.1(4.1)
C17:0	0.8(0.6)	0.6(0.5)	0.9(0.5)	0.1(0.5)	0.2(0.6)	0.3(0.5)
C18:0	6.2(5.2)	5.1(4.1)	8.6(4.1)*	2.3(4.1)	1.1(5.2)	3.4(4.1)
C18:1 n-7	1.3(1.3)	1.2(1.0)	1.9(1.0)	0.6(1.0)	0.1(1.3)	0.7(1.0)
C18:1 n-9	46(30)	28(24)	50(24)*	3(24)	17(30)	21(24)

C18:2 n-6	30(20)	24(16)	32(16)*	1(16)	6(20)	7(16)
C18:3 n-3	4.0(2.5)	2.8(1.9)	3.9(1.9)*	-0.1(1.9)	1.2(2.5)	1.1(1.9)
C20:2 n-6	0.2(0.3)	0.3(0.2)	0.3(0.2)	0.0(0.2)	-0.1(0.2)	0(0.2)
C20:3 n-6	0.1(0.2)	-0.1(0.2)	0.1(0.2)	0.0(0.2)	0.2(0.2)	0.2(0.2)
C20:4 n-6	0.4(1.3)	0.3(1.0)	-0.1(1.0)	-0.4(1.0)	0.7(1.3)	-0.2(1.0)
C20:5 n-3	-0.7(0.6)	-0.5(0.5)	-0.2(0.5)	0.4(0.5)	-0.1(0.6)	0.3(0.5)
C22:4 n-6	-0.1(0.3)	-0.2(0.2)	-0.2(0.2)	-0.1(0.2)	0.1(0.3)	-0.1(0.2)
C22:5 n-3	0.4(0.5)	0.3(0.4)	0.1(0.4)	-0.3(0.4)	0.0(0.5)	-0.2(0.4)
C22:6 n-3	-1.1(1.6)	0.2(1.3)	0.4(1.3)	1.6(1.3)	-1.4(1.6)	0.2(1.3)

434   [1]. G_{i-j}^{I} = direct-maternal differences between lines i and j (see text for a complete explanation). *P < 0.05 (significant difference at α = 0.05).

435

436 **Table 11**. [1]Grand-maternal effect differences between lines (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle), protein

437 (g/100g muscle), fatty acid groups (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	[1] $G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
pH	0.03(0.02)	0.01(0.02)	0.02(0.02)	-0.02(0.02)	0.02(0.02)	0.00(0.02)
L*	-0.99(0.88)	-0.59(1.10)	-0.44(1.16)	0.55(0.88)	-0.40(0.88)	0.15(1.02)
a*	-0.05(0.39)	-0.35(0.44)	-0.42(0.51)	-0.37(0.39)	0.31(0.39)	-0.06(0.45)
b*	-0.48(0.33)	-0.27(0.38)	-0.74(0.44)	-0.26(0.33)	-0.21(0.33)	-0.47(0.39)
IMF	-0.02(0.07)	-0.10(0.08)	-0.11(0.09)	-0.09(0.07)	-0.09(0.07)	0.00(0.08)
Protein	0.08(0.12)	0.05(0.14)	-0.17(0.16)	-0.09(0.12)	0.03(0.12)	-0.12(0.14)
SFA	-5(20)	-34(23)	-30(26)	-25(20)	28(20)	2(23)
MUFA	-1(20)	-35(23)	-32(26)	-30(20)	34(20)	3(23)
PUFA	-1(11)	-17(12)	-17(14)	-16(11)	16(11)	0(12)
n-3 PUFA	0.0(1.0)	-1.5(1.1)	-1.2(1.2)	-1.3(1.0)	1.5(1.0)	0.2(1.1)

n-6 PUFA	4(10)	-10(12)	-11(14)	-15(10)	15(10)	0(12)
n-6/n-3	0.07(0.15)	-0.19(0.17)	-0.13(0.19)	-0.20(0.15)	0.03(0.15)	0.05(0.17)
PUFA/SFA	0.03(0.02)	0.04(0.03)	0.03(0.03)	0.00(0.02)	-0.01(0.02)	0.00(0.03)

438 [1]. $G_{i-j}^{M'}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). *P < 0.05 (significant difference at α =

439 0.05).

440

441 **Table 12**. [1]Grand-maternal effect differences between lines (standard error) for individual fatty acid composition (mg/ 100 g muscle) of the
442 l*ongissimus lumborum* muscle .

Trait	$^1 G_{A-H}^{M'}$	$G_{A-L}^{M'}$	$G_{A-V}^{M'}$	$G_{H-V}^{M'}$	$G_{L-H}^{M'}$	$G_{L-V}^{M'}$
C14:0	-0.1(1.6)	-2.1(1.8)	-2.6(2.1)	-2.5(1.6)	2.1(1.6)	-0.4(1.8)
C15:0	0.0(0.3)	-0.4(0.3)	-0.4(0.3)	-0.4(0.3)	0.4(0.3)	0.0(0.3)
C16:0	-6(13)	-19(15)	-18(17)	-12(13)	12(13)	1(15)
C16:1	-1.0(2.8)	-5.1(3.2)	-4.7(3.7)	-3.7(2.8)	4.1(2.8)	0.4(3.2)
C17:0	0.0(0.3)	-0.4(0.4)	-0.5(0.5)	-0.5(0.3)	0.4(0.3)	-0.1(0.4)
C18:0	-0.1(2.9)	-4.4(3.3)	-4.8(3.7)	-4.6(2.9)	4.2(2.9)	-0.4(3.3)
C18:1 n-7	0.1(0.7)	-1.0(0.8)	-1.1(0.9)	-1.1(0.7)	1.1(0.7)	0.0(0.8)
C18:1 n-9	-1(16)	-28(18)	-26(21)	-25(16)	27(16)	2(18)

C18:2 n-6	4(11)	-13(12)	-13(14)	-17(11)	17(11)	0(12)
C18:3 n-3	0.2(1.3)	-1.8(1.5)	-1.6(1.7)	1.8(1.3)	2.1(1.3)	0.2(1.5)
C20:2 n-6	0.05(0.10)	-0.05(0.10)	-0.01(0.10)	-0.14(0.10)	0.10(0.10)	0.00(0.10)
C20:3 n-6	0.10(0.10)	-0.01(0.12)	0.02(0.14)	-0.08(0.10)	0.12(0.10)	0.04(0.12)
C20:4 n-6	0.17(0.73)	0.31(0.83)	-0.17(0.96)	-0.34(0.73)	-0.14(0.73)	-0.48(0.83)
C20:5 n-3	-0.19(0.33)	-0.09(0.38)	-0.13(0.44)	0.06(0.33)	-0.10(0.33)	-0.04(0.38)
C22:4 n-6	0.01(0.12)	0.04(0.14)	0.03(0.16)	0.02(0.12)	0.03(0.12)	-0.01(0.14)
C22:5 n-3	-0.28(0.25)	0.03(0.28)	-0.20(0.32)	0.08(0.25)	-0.31(0.25)	-0.23(0.28)
C22:6 n-3	-0.5(0.9)	0.5(1.0)	-0.8(1.2)	-0.2(0.9)	-1.1(0.9)	-1.3(1.0)

443   [1]. $G_{i-j}^{M'}$ = grand-maternal differences between lines i and j (see text for a more complete explanation). *P < 0.05 (significant difference at α =

444   0.05).

445

447 **Table 13**. [1]Maternal heterosis (standard error) for pH, colour, intramuscular fat (IMF, g/100g muscle), protein (g/100g muscle), fatty acid groups

448 (mg/100 g muscle) and fatty acid ratios of the *longissimus lumborum* muscle.

Trait	$^{1}H_{AH}^{M}$	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
pH	0.00(0.02)	0.00(0.02)	-0.01(0.02)	0.01(0.02)	0.01(0.02)	0.04(0.02)
L*	-0.44(0.87)	-0.86(1.02)	-0.12(0.87)	-0.92(0.72)	-0.37(0.72)	-0.74(0.72)
a*	-0.10(0.38)	0.16(0.44)	-0.09(0.38)	0.39(0.32)	0.00(0.32)	-0.08(0.32)
b*	-0.29(0.33)	-0.38(0.38)	-0.06(33)	-0.26(0.27)	-0.23(0.27)	-0.21(0.27)
IMF	-0.11(0.07)	-0.02(0.07)	0.02(0.07)	0.02(0.05)	0.03(0.05)	0.01(0.05)
Protein	0.02(0.12)	-0.18(0.14)	-0.08(0.12)	-0.05(0.10)	-0.04(0.10)	-0.12(0.10)
SFA	-32(20)	0(23)	9(20)	2(17)	4(17)	0(17)
MUFA	-30(20)	0(23)	12(19)	3(16)	5(16)	-1(16)
PUFA	-15(11)	-2(12)	4(11)	1(9)	3(9)	0(9)

n-3 PUFA	1.2(1.0)	0.2(1.1)	0.4(1.0)	0.4(0.8)	0.4(0.8)	0.3(0.8)
n-6 PUFA	-7(10)	7(12)	7(10)	-2(9)	-1(9)	1(9)
n-6/n-3	-0.09(0.14)	0.04(0.17)	0.06(0.14)	-0.05(0.12)	-0.04(0.12)	-0.12(0.12)
PUFA/SFA	0.03(0.02)	0.00(0.02)	0.00(0.02)	-0.01(0.02)	0.00(0.02)	0.00(0.02)

449   [1]. H_{ij}^{M} = maternal heterosis between lines i and j. *P < 0.05 (significant difference at $\alpha = 0.05$).

450

Table 14. [1]Maternal heterosis (standard error) for individual fatty acid composition (mg/ 100 g muscle) of the *longissimus lumborum* muscle.

Trait	$^{1}H_{AH}^{M}$	H_{AL}^{M}	H_{AV}^{M}	H_{HV}^{M}	H_{LH}^{M}	H_{LV}^{M}
C14:0	-2.7(1.6)	-1.0(1.8)	0.1(1.6)	-0.3(1.3)	0.5(1.3)	-0.2(1.3)
C15:0	-0.37(0.3)	-0.03(0.3)	0.14(0.3)	0.04(0.3)	0.08(0.3)	0.01(0.3)
C16:0	-21(13)	5(15)	8(13)	1(11)	3(11)	3(11)
C16:1	-4(3)	0(3)	2(3)	1(2)	1(2)	1(2)
C17:0	-0.43(0.35)	0.08(0.40)	0.16(0.35)	-0.11(0.29)	-0.03(0.29)	-0.07(0.29)
C18:0	-4.1(2.8)	-0.9(3.3)	1.4(2.8)	0.2(2.3)	0.8(2.3)	-0.1(2.3)
C18:1 n-7	-0.96(0.7)	-0.17(0.8)	0.39(0.7)	0.05(0.6)	0.29(0.6)	0.10(0.6)
C18:1 n-9	-25(16)	0(18)	9(16)	2(13)	3(13)	-1(13)
C18:2 n-6	-11(11)	7(13)	6(11)	-2(9)	0(9)	1(9)

C18:3 n-3	-1.4(1.3)	1.0(1.5)	1.1(1.3)	-0.2(1.1)	0.1(1.1)	0.2(1.1)
C20:2 n-6	-0.10(0.10)	0.10(0.12)	0.03(0.10)	-0.03(0.09)	0(0.09)	0.10(0.09)
C20:3 n-6	0.02(0.10)	0.03(0.12)	0.06(0.10)	-0.16(0.9)	-0.12(0.09)	-0.07(0.09)
C20:4 n-6	-0.8(0.73)	-0.80(0.84)	-1.23(0.73)	0.81(0.60)	0.21(0.60)	-0.08(0.60)
C20:5 n-3	0.16(0.33)	-0.23(0.39)	0.07(0.33)	-0.30(0.28)	-0.08(0.28)	0.13(0.28)
C22:4 n-6	0.04(0.12)	-0.08(0.14)	0.03(0.12)	-0.05(0.10)	-0.08(0.10)	-0.11(0.10)
C22:5 n-3	-0.39(0.25)	-0.34(0.28)	-0.19(0.25)	0.40(0.21)	0.03(0.21)	0.29(0.21)
C22:6 n-3	-1.1(0.9)	-1.9(1.1)	-1.7(0.9)	0.3(0.7)	-0.1(0.7)	0.0(0.7)

452   [1]. H_{ij}^{M} = maternal heterosis between lines i and j. *P < 0.05 (significant difference at α = 0.05).