1 **Genomic selection of milk fatty acid composition in Sarda dairy sheep: effect of different**

2 **phenotypes and relationship matrices on heritability and breeding values accuracy.** *by*

3 *Cesarani et al.* Nowadays consumers are mostly interested in dairy products with improved

4 quality. Sheep breeders may achieve this objective thanks to recent availability of genomic

5 tools. This paper investigates the combined use of genomic selection and mid infrared milk

6 spectra to selective purpose for improving milk fatty acid profile.

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8 GENOMIC SELECTION FOR SHEEP MILK FATTY ACIDS

9

10 **Genomic selection of milk fatty acid composition in Sarda dairy sheep: effect of different**

11 **phenotypes and relationship matrices on heritability and breeding values accuracy**

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18 **ABSTRACT**

19   Fatty acid (FA) composition is one of the most important aspects of milk nutritional

20 quality. However, the inclusion of this trait as breeding goal for dairy species is hampered by

21 the logistics and high costs of phenotype recording. Fourier transform Infrared Spectroscopy

22 (FTIR) is a valid and cheap alternative to laboratory gas chromatography (GC) for predicting

23 milk FA composition. Moreover, as for other novel phenotypes, the efficiency of selection for

24 these traits can be enhanced by using genomic data. Objective of this research was to compare

25 traditional versus genomic selection approaches for estimating genetic parameters and

26 breeding values of milk fatty acid composition in dairy sheep using either GC measured or

27 FTIR predicted FA as phenotypes. Milk FA profiles were available for a total of 923 Sarda

28 breed ewes. The youngest 100 had their own phenotype masked to mimic selection

29 candidates. Pedigree relationship information and genotypes were available for 923 and 769

30 ewes, respectively. Three statistical approaches were used: the classical pedigree based

31 BLUP; the GBLUP that considers the genomic relationship matrix **G**; the single step GBLUP

32 (ssGBLUP) where pedigree and genomic relationship matrices are blended into a single **H**

33 matrix. Heritability estimates using pedigree were lower than ssGBLUP, and very similar

34 between GC and FTIR regarding the statistical approach used. For some FA, mostly

35 associated with animal diet (i.e. C18:2ω6, C18:3ω3), random effect of combination of flock

36 and test date (FTD) explained a relevant quota of total variance, reducing accordingly h^2

37 estimates. Genomic approaches (GBLUP and ssGBLUP) outperformed the traditional

38 pedigree method both for GC and FTIR FA. Prediction accuracies in older cohort were larger

39 than young cohort. Genomic prediction accuracy (obtained using either **G** or **H** relationship

40 matrix) in young cohort of animals, where their own phenotype were masked, were similar for

41 GC and FTIR. Multiple trait analysis slightly affected GEBV accuracies. These results

42   suggest that FTIR predicted milk FA composition could represent a valid option for the

43   inclusion of this trait in breeding programs.

44   **Keywords**: Mid infrared spectra, REML, FTIR, genomic selection

45

46   **INTRODUCTION**

47   Dairy sheep breeding programs have been historically aimed at improving total milk

48   yield per lactation (Carta et al., 2009). Although sheep milk is almost totally destined to

49   cheese making (Pulina et al., 2018), selection for milk composition is carried out only in few

50   breeds (Macciotta et al., 2005; Astruc et al., 2008). This is mostly because of the high

51   recording costs compared to the income per ewe (Carta et al., 2009; Rupp et al., 2016). On the

52   other hand, the increasing consumer interest on dairy product nutritional quality pushes

53   toward the inclusion of fine milk composition traits among breeding goals of dairy species.

54   An example is represented by the conjugated linoleic acid (CLA), known for its relationships

55   with human health (Banni et al., 2003; Bhattacharya et al., 2006; Mele et al., 2011). Ruminant

56   dairy products are among the most important sources of CLA in human diets (Nudda et al.,

57   2014). Although animal feeding is considered the most important factor affecting milk fatty

58   acid (FA) composition (Cabiddu et al., 2005; Sanchez et al., 2010), genetic variation for these

59   traits has been reported in cattle (Stoop et al., 2008; Pegolo et al., 2016) and sheep (Sanchez et

60   al. 2010; Correddu et al. 2018) suggesting the possibility for a genetic improvement.

61   The inclusion of milk FA composition as breeding goal for dairy sheep programs is

62   constrained by logistics and costs of phenotype recording. The standard method for measuring

63   milk FA composition is the gas chromatography (GC) analysis, that is expensive and time

64   consuming. A population-scale recording of milk FA appears therefore rather unfeasible for

65   species where also the routine phenotyping of milk components is economically unbearable.

66   A valid alternative to GC is represented by Fourier transform Infrared (FTIR) spectroscopy.

67 This technique, implemented in milk lab equipment currently used for routine milk

68 composition analysis, produces a spectrum of approximately one thousand variables that

69 could be used for large scale prediction of novel phenotypes, including FA (e.g. Cecchinato et

70 al., 2009; De Marchi et al 2011; McParland et al., 2011; Dehareng et al., 2012; Fleming et al.,

71 2016). Good prediction accuracies of milk FA based on FTIR spectrum have been reported

72 for dairy cattle (Arnould and Soyeurt, 2009; De Marchi et al., 2011). Similar results, even

73 though with a certain degree of variability and in a limited number of studies, have been

74 reported for dairy sheep (Ferrand-Calmels et al., 2014; Caredda et al. 2016; Correddu et al.,

75 2018). Fatty acid predicted by FTIR exhibited genetic variation both in dairy cattle (e.g.

76 Soyeurt et al., 2006; Bastin et al., 2013; Narayana et al., 2017) and sheep (Sanchez et al.,

77 2010; Boichard et al., 2014). Moreover, genetic correlations ranging from 60% to 99%

78 between FTIR predicted and GC measured milk FA have been reported both in cattle

79 (Bonfatti et al., 2017) and sheep (Correddu et al., 2018).

80 Dairy sheep breeding programs are based on the classical quantitative genetic

81 approach, with a pyramidal organization of the population, large scale registration of

82 phenotypes and pedigree, and genetic evaluations of AI rams based on progeny testing (Carta

83 et al., 2009; Baloche et al., 2014). The availability of high throughput SNP panel for sheep

84 has opened the perspective of genomic selection (GS) also for this species. Researches have

85 been carried out on dairy (Duchemin et al., 2012; Baloche et al., 2014), meat, and wool sheep

86 (Daetwyler et al., 2012). An improvement of genomic breeding value (GEBV) accuracies

87 over the traditional pedigree index has generally been observed, even though to a lesser extent

88 compared to dairy cattle (Legarra et al., 2014).

89 Genomic studies on milk FA in cattle have focused mostly on the study of their

90 genetic determinism (Stoop et al., 2009; Bouwman et al. 2011; Buitenhuis et al., 2014). In

91 dairy sheep, the molecular basis of FA have been investigated by candidate gene (Crisà et al,

92   2010; Moioli et al., 2012), and QTL detection (Carta et al., 2008) approaches. Genomic

93   selection studies for FA compositions are limited to beef cattle (Uemoto et al., 2011; Chen et

94   al., 2015; Zhu et al. 2017) and meat sheep (Rovadoscki et al., 2018). One of the main

95   advantange of GS over traditional selection is that, once a reference population with both

96   phenotypic and genotypic records has been settled, breeding values of animals without their

97   own phenotypes can be predicted with a reasonable accuracy (Meuwissen et al., 2001; Hayes

98   et al., 2009). Therefore, GS seems to be an appealing option for novel traits that are difficult

99   to measure routinely as milk FA composition (Boichard and Brochard, 2012; Daetwyler et al.,

100   2012).

101   Aim of the present work is to explore the feasibility of breeding for milk FA

102   composition in a dairy sheep breed by combining the use of FTIR predicted phenotypes and

103   the genomic selection technology. At this purpose breeding values prediction were carried out

104   running a pedigree based and two genomic models, using either FTIR predicted and GC

105   measured FA as phenotypes. Moreover, the effect of the different phenotypes used and of the

106   estimation methods on heritability was tested.

107

108   **MATERIALS AND METHODS**

109   *Data*

110   A sample of 923 Sarda breed dairy ewes farmed in 47 flocks located in the island of

111   Sardinia (Italy) were considered. Milk samples, one per animal, were collected from February

112   to June 2015 (**Table 1**). In this study 13 individuals FA (C4:0, C6:0, C8:0, C10:0, C12:0,

113   C14:0, C16:0, C18:0, C18:1t11, C18:1c9, C18:2ω6, C18:3ω3, CLAc9t11), 5 groups of FA

114   and a ratio between groups of FA were analyzed. Groups of FA were calculated as follow

115   (Appendix, **Table A1**): SFA, sum of individual saturated fatty acids; MUFA, sum of

116   individual monounsaturated fatty acids; PUFA, sum of individual polyunsaturated fatty acids;

117   TFA-VA, sum of individual trans FA with the exclusion of C18:1t11 (vaccenic acid);

118   Denovo, sum of individual FA that are de novo synthesized in the mammary gland; PUFA n-

119   6:PUFA n-3, ratio between the sum of individual PUFA n6 and the sum of all individual

120   PUFA n3. Milk FA (g FA/100 g total FA) composition was both measured by gas

121   chromatography (FA_GC) and predicted by partial least square regression (PLS) using the

122   FTIR spectra (FA_FTIR) generated by milk analysis performed with Milkoscan FT6000

123   instrument (Foss, Hillerød, Denmark). PLS was carried out by extracting 18 latent factors.

124   Prediction accuracies were tested by using a calibration data set of 700 ewes and a validation

125   data set of 223 ewes, respectively. One-hundred replicates randomly assigning animals to the

126   two data sets were performed. Details for GC analysis are reported in the work of Correddu et

127   al., (2018).

128   Genotypes obtained with the Infinium Ovine SNP50 v1 BeadChip (Illumina Inc., San

129   Diego, California) were available for 769 ewes out of 923. Quality control of SNP genotypes

130   was carried out with PLINK software (Purcell et al., 2007). All genotyped ewes had a call rate

131   greater than 0.95. A SNP was discharged if: the call rate was lower than 0.975 (867 markers

132   removed), the minor allele frequency (MAF) was lower than 0.01 (1,309 markers removed), it

133   deviated significantly from the Hardy Weinberg Equilibrium ($P < 0.01$, 1,264 markers

134   removed), or it did not map to the OAR_v3.1 assembly (6,182 markers removed). After

135   quality control, all genotyped ewes and 44,619 SNPs across 27 chromosomes were retained

136   for the analysis. A pedigree with 633,317 animals was also available.

137   ***Variance component estimation***

138   Variance components for FA_GC and FA_FTIR traits were estimated by restricted

139   maximum likelihood (REML) using three mixed linear models that differed in the relationship

140   matrix used.

141   The following mixed linear model was implemented:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Qf} + \mathbf{Za} + \mathbf{e} \qquad [1]$$

where **y** is the vector of investigated FA; **X** is the incidence matrix linking records to fixed effects and **b** the related vector; **Q** is the incidence matrix for random flock test-date combination (**FTD**) effect and **f** the related vector (71 classes) distributed as $N(0, \mathbf{I}\sigma^2_{FTD})$ where **I** is an identity matrix and σ^2_{FTD} is the associated variance component; **Z** is the incidence matrix for random genetic effects, relating records to animals and **a** is the vector of breeding values (**a** distributed according to the relationship matrix used); **e** is the vector of random residuals distributed as $N(0, \mathbf{I}\sigma^2_e)$ where σ^2_e is the residual variance. The fixed effects (**Table 1**) considered in the model were: parity (8 classes), days in milk (5 classes), lambing month (4 classes), altitude of farm (3 classes).

The additive genetic effect was modelled using three genetic (co)variance structures. In the first model (**ABLUP**), the pedigree relationship matrix (**A**) was used and the animal effect was distributed as $N(0, \mathbf{A}\sigma^2_a)$ where σ^2_a is the additive genetic variance. The other two genomic models used the genomic relationship matrix (**G**) (**GBLUP**) or a blend of genomic and pedigree relationship matrices (**H**) in a single-step framework (**ssGBLUP**) with **a** distributed as $N(0, \mathbf{G}\sigma^2_a)$ and $N(0, \mathbf{H}\sigma^2_a)$, respectively. From whole pedigree, three generations were traced back from the phenotyped animals; the composition and number of animals of the different relationship matrices are reported in **Table 2**. **G** and **H** matrices were computed according to VanRaden (2008) and Aguilar et al. (2010), respectively. AIREML algorithm implemented in blupf90 family software was used for estimating variance components (Mistzal et al., 2015). Heritability (h^2) and intra-flock heritability (h^2_{IF}) were computed respectively as:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_{FTD}^2 + \sigma_e^2)$$

$$h^2_{IF} = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2);$$

166 moreover, variance explained by FTD (r^2_{FTD}) was computed as:

167 $$r^2_{FTD} = \sigma^2_{FTD}/(\sigma^2_a + \sigma^2_{FTD} + \sigma^2_e)$$

168 ***Breeding Value Predictions***

169   Breeding values were predicted using model [1] with the traditional (ABLUP) and the

170 two GS (GBLUP and ssGBLUP) approaches, respectively. From the 769 animals with

171 genotypes and own phenotypes, records of the 100 youngest ewes (born after November

172 2012) were masked in order to mimic the condition of candidate animals.

173   Accuracy of breeding values animals were estimated as:

174 $$accuracy = \sqrt{1 - SEP^2/\sigma^2_a}$$

175 where SEP is the standard error of prediction, derived from the diagonal element of the LHS

176 inverse of the mixed model equations. In order to ensure a fair comparison among accuracies

177 obtained in the three different methods, the same variance components (the ones estimated

178 with ABLUP) were used in the three approaches for breeding values predictions and

179 computation of accuracy.

180   Moreover, in order to reduce GEBV bias in the ssGBLUP, a weighing factor omega

181 (ω) equal to 0.95 was applied in construction of the inverse of the **H** matrix (Tsuruta et al.,

182 2013):

183 $$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \omega\,\mathbf{A}^{-1}_{22} \end{bmatrix}$$

184 where $\mathbf{A}_{22}$ is the pedigree-based relationship matrix for genotyped animals

185 Being FA genetically correlated traits (Carta et al. 2008; Sanchez et al., 2010), GEBV

186 accuracy may be modified if a multiple trait approach is used. However, considering the large

187 number of FA analyzed in the present study, the effect of genetic correlations among FA on

188 GEBV accuracy was investigated by a series of bivariate analyses using the ssGBLUP

189 approach. Thus for each single FA, two accuracies were available: one obtained with the

190 univariate approach and another obtained as the mean accuracy of the 17 bivariate analyses

191 involving that specific FA.

192

193   **RESULTS**

194   Basic statistics (**Table 3**) of the milk FA_GC and FA_FTIR, and coefficients of

195 determination of the regression between FA_GC and FA_FTIR ($R^2_{GC\text{-}FTIR}$) essentially confirm

196 previous reports on dairy sheep (Ferrand-Calmels et al., 2014; Caredda et al., 2016; Correddu

197 et al., 2018).

Genetic Parameters of Milk Fatty Acid profile

199   Heritability estimates showed relevant variations across different FA, phenotyping

200 methods (GC vs FTIR), and models (**Table 4**). Overall, low to moderate values were

201 obtained, apart from C4:0 and C16:0. Largest heritabilities were observed for the C4:0

202 FA_FTIR in the GBLUP (0.56), and for the C16:0 FA_GC in the ABLUP (0.46) (**Table 4**),

203 respectively. A similar pattern was detected for intra-flock heritabilities (**Table 5**), that

204 exhibited larger values compared to h^2, especially for FA characterized by a larger flock-test

205 date variance (**Table 6**) (e.g. C18:0, C18:1t11, C18:1c9, C18:2ω6, C18:3ω3, CLAc9,t11 and

206 ω6:ω3). Lowest estimates (nearly zero) were obtained for SFA and MUFA in the ABLUP,

207 and for C18:2ω6 in all the three prediction models for FA_FTIR.

208   The considered phenotype, FA_GC or FA_FTIR, affected the h^2 results, even though

209 no defined patterns were observed. For example, FA_GC estimates were markedly larger than

210 FA_FTIR for C16:0 in all models (**Table 4**). On the contrary, FA_GC estimates were smaller

211 for C4:0, especially for the two genomic models. It should be also noticed that the h^2

212 estimated with ABLUP were close to zero for SFA and MUFA using FA_FTIR phenotypes.

213 In order to highlight recurrent pattern in the additive genetic component, σ^2_a for FA_GC was

214 regressed onto σ^2_a for FA_FTIR (**Figure 1**) for the three models used. Additive genetic

215 variances estimated using FA_GC and FA_FTIR were from moderately to strongly correlated

216 depending on (co)variance matrix used.

217 The h^2 and h^2_{IF} estimated with ABLUP were generally lower than those obtained with

218 the two genomic approaches, both for FA_GC and FA_FTIR (**Tables 4** and **5**). Exceptions

219 were the C16:0 and C18:0, that showed an opposite behavior. In particular, largest differences

220 were found for C4:0 and C16:0 as individual FA, and for SFA and MUFA as groups,

221 respectively. GBLUP and ssGBLUP estimates were very similar (**Table 4,** and **5**).

222 Differences among h^2 estimates were mainly due to changes in the additive genetic

223 components as shown in Appendix (**Table A2**). In particular, for most of the FA analyzed no

224 differences in σ^2_a were observed with genomic methods. In our study, largest values of R^2 of

225 the regression between σ^2_a FA_GC and σ^2_a FA_FTIR were observed using genomic models

226 (0.84 and 0.91) in comparison to the traditional pedigree models (0.45, **Figure 1**). Finally, σ^2_a

227 estimates of C16:0, C18:0, C18:1c9, SFA and MUFA were always higher for FA_GC than

228 FA_FTIR.

229 The FTD contribution to total phenotypic variance was moderate to large. It was on

230 average >0.5 across all different prediction models and phenotypes (**Table 6**), ranging from

231 0.17 to 0.88. The variance components for FTD were nearly the same in the three different

232 models, while differences (up to 15%) were highlighted between FA_GC and FA_FTIR (e.g.

233 C4:0, C14:0, C18:1t11, C18:2ω6, C18:3ω3, CLA, PUFA, ω3: ω6 and TFAnoVA).

234 ***Accuracy of EBV and GEBV predictions***

235 Accuracies of breeding values were low to moderate, ranging from 0.05 to 0.84, and

236 from 0.02 to 0.45 in the oldest and youngest cohort, respectively (**Table 7**). The palmitic acid

237 (C16:0) showed the largest accuracy for FA_GC across the different prediction models, both

238 for oldest (0.84) and youngest animals (0.45). The largest GEBV accuracy for FA_FTIR was

239   observed for the butyric acid (C4:0). The linoleic acid (C18:2ω6) showed the lowest accuracy

240   in most of the scenarios considered. Accuracies of FA groups reflected their composition,

241   with saturated FA showing the lowest and PUFA and TFAnoVA the highest accuracies,

242   respectively.

243   The cohort of animals with own phenotypes exhibited larger prediction accuracies

244   compared to young animals without phenotype (overall average difference +0.24) in all

245   scenarios (**Table 7**). The largest difference (+0.30) was observed for the stearic acid (C18:0),

246   whereas the smallest for the saturated FA group (+0.09).

247   Differences were also observed between the phenotype (FA_GC vs FA_FTIR) for all

248   the three models and for the two cohorts of animals (**Table 7**), even though without a defined

249   pattern. The major difference between FA_GC and FA_FTIR were observed in the older

250   cohort (from -0.23 up to 0.48 for C6:0 and C16:0, respectively). Accuracies differed mainly in

251   the ABLUP approach for both young and older cohorts. The difference between FA_GC and

252   FA_FTIR tended to reduce in genomic methods applied to young animals (**Table 7**).

253   Regardless of the statistical model used, the largest difference between FA_GC and FA_FTIR

254   was observed for the C16:0 (on average difference of 0.45 ad 0.18 for old and young animals,

255   respectively). Relevant differences (at least >15%) between FA_CG and FA_FTIR were

256   observed also for C18:0, C18:2ω6, SFA and MUFA both in older and younger animals.

257   As far as the three models are concerned, genomic prediction accuracies were

258   constantly higher than in ABLUP (**Table 7**). In particular, differences between ABLUP and

259   genomic methods were larger in young animals. In this cohort, positive changes up to +0.12

260   (+0.17) and +0.10 (+0.21) were observed in the comparison GBLUP-ABLUP (ssGBLUP-

261   ABLUP) for FA_GC and FA_FTIR, respectively. Among the two genomic approaches, the

262   ssGBLUP accuracies were always larger than GBLUP ones both in young and old animal

263   cohorts.

264   Bivariate GEBV accuracies for the young animals were generally of the same

265   magnitude of those obtained using the univariate approach (**Table 8**). Differences were

266   exhibited by some FA_FTIR: in particular the GEBV accuracy for linoleic, SFA and MUFA

267   showed an increase (>0.03) moving from univariate to multivariate approach.

268

269   **DISCUSSION**

270   Fatty acid composition is a key feature in defining sheep milk nutritional quality. Its

271   genetic improvement is an appealing option for enhancing market value of dairy sheep

272   products. However, breeding for milk FA composition in sheep is hampered by difficulties in

273   phenotyping and in implementing appropriate selection strategies. Use of equations for

274   predicting FA from milk FTIR spectra is widely recognized as a cost-effective solution for

275   obtaining FA profiles in milk of different ruminant species (Ferrand-Calmels et al. 2014). At

276   the same time, early experiences of genomic selection on meat, wool (Daetwyler et al., 2012)

277   and dairy sheep (e.g Duchemin et al., 2012; Legarra et al. 2014; Baloche et al. 2014) have

278   reported an increase of breeding value accuracy and selection response compared to the

279   traditional pedigree-based method.

280   Results of the present study, although referred to a sample of limited size, showed an

281   effect of both investigated phenotypes (i.e. FA_GC or FA_FTIR) and of the information used

282   to structure the genetic covariance among animals (pedigree, genomic, or both) on genetic

283   parameter estimates and breeding value prediction accuracies.

284   *Genetic Parameters of Milk Fatty Acid profile*

285   Heritability estimates based on pedigree models were consistent with a previous work

286   carried out on a similar data set (Correddu et al., 2018), whereas genomic based h^2 resulted

287   higher and lower than pedigree based for saturated (<C14) and unsaturated FA, respectively.

288   A large variation among different FA was observed, regardless the considered approach or the

289   phenotype used, in agreement with previous studies (Sanchez et al., 2010; Boichard et al.,

290   2014). Differences among FA are mainly related to their metabolic pathway. Some FA are

291   synthetized *de novo* in the mammary gland, others are mostly related to the animal diet, and

292   others came from of body reserve mobilization. Thus, larger heritability is expected for FA

293   whose milk concentration is under enzymatic control (i.e. de novo FA) compared to FA that

294   are related to the animal diet (Arnould and Soyeurt, 2009). The higher value of heritability

295   observed for Denovo FA compared to those coming from diet or body fat reserve (e.g.: C18

296   FA) seemed to confirm the stronger genetic regulation for the former group of FA (e.g. Bastin

297   et al., 2011; Narayana et al., 2017). Morever, lowest h^2 values were highlighted for C18:2ω6

298   and C18:3ω3 (**Table 4** and **5**), regardless the model used. It is well known that these two FA

299   are strongly dependent on their concentration in animals' diet (e.g. Fleming et al., 2016;

300   Pegolo et al. 2017).

301   Differences between h^2 estimated using FA_GC and FA_FTIR were in most of cases

302   low to moderate. FA_FTIR produced larger h^2 estimates for short chain FA (Figures 1),

303   whereas an opposite trend can be observed for medium and long-chain FA. A similar pattern

304   was also observed in cattle using GC (Stoop et al., 2008; Duchemin et al., 2013). The largest

305   differences were found for FA (e.g.C16:0 and C4:0) that exhibited lowest FTIR prediction

306   accuracies. In dairy cattle, larger heritabilities for FA_GC compared to FA_FTIR have been

307   reported (Rutten et al., 2010; Bonfatti et al., 2017). In particular, Bonfatti et al (2017) pointed

308   out that the differences were due to a reduction of the σ^2_a in FA_FTIR (-0.52%) compared to

309   FA_GC. In the present work, the use of FA_FTIR phenotypes resulted in most of cases (short

310   chain FAs) in smaller estimates for all the three variance components (**Table A2**).

311   Apart from the values obtained for palmitic and stearic acids, pedigree based h^2 were

312   in most of cases lower than those obtained using genomic information. In particular, most of

313   FA showed an increase of σ^2_a and a reduction of σ^2_e (especially for FA_FTIR) when moving

314 from traditional pedigree to genomic methods, respectively (**Table A2**). Veerkamp et al.

315 (2011) working on a dairy cattle sample of comparable size, found larger heritabilities for

316 milk yield, dry matter intake and body weight, when **A** instead of **G** was used. This result, due

317 to a reduction of σ^2_a when genomic information was used, was explained with the different

318 structure of the two relationship matrices, especially as far as the base population is

319 considered.

320   The higher heritability observed in the present work for genomic models can be

321 ascribed to a series of reasons. The first are the considered traits. Milk FA content is

322 characterized by a relevant sensitivity to environmental conditions. This peculiarity is

323 enhanced in the typical farming system of the Sarda sheep, where natural pastures represent

324 the main feeding source (Carta et al., 2009; Nudda et al. 2014). Moreover, it should be

325 remembered that only one record per animal was available. This condition, that undoubtedly

326 reduces the reliability of the measure, is rather frequent in studies on FA genetic parameter

327 estimation using FA_GC also in cattle (e.g. Stoop et al., 2008; Mele et al., 2009; Pegolo et al.,

328 2016). On the other hand, the recording of a single measure per animal is more representative

329 of the practical situation of a breeding scheme where innovative phenotypes are considered

330 among the selection goals. A second reason is represented by the structure of the considered

331 dairy sheep population, quite different from usual dairy cattle populations of genomic studies.

332 It consisted of only females, sired by 445 rams (2.07 ± 1.7 with a maximum of 15 daughter per

333 ram). Such a structure can be considered representative of the Sarda breed, in which natural

334 mating is the main reproductive technique (Carta et al., 2009). A third reason can be found in

335 the genetic structure of dairy sheep populations. Contrarily to what observed in the present

336 study, larger heritabilities were found when **A** was fitted in comparison with **G** on dairy cattle

337 (Veerkamp et al., 2010; Haile-Mariam et al., 2013; Loberg et al., 2015). The authors

338 explained these results with the imperfect linkage disequilibrium (LD) existing between SNP

339   and causative mutations that makes **G** unable for capturing all the genetic variance of the trait

340   in comparison with **A**. Such a limitation of **G** is likely to be more pronounced in sheep

341   populations that, in comparison to cattle, are characterized by a lower LD at relatively short

342   distance (Kijas et al., 2014). However, the reliability of pedigrees in sheep is often

343   questionable due to the uncorrected parentage assignment or the high number of unknown

344   parents. Thus, the use of genomic relationship matrices could allow to estimate more

345   accurately relationship among animals because the realized fraction of allele shared between

346   individual is directly computed (Hayes and Goddard, 2008; Legarra et al., 2014), with

347   subsequent large heritability estimates.

348   *Accuracy of EBV and GEBV predictions*

349   In our study breeding value accuracies for FA milk profile were low to moderate.

350   Considering the sample size, the genetic architecture of milk FA composition, and the number

351   of records per ewe our results are in accordance to genomic selection theory (Goddard and

352   Hayes, 2009). Animals with their own phenotypes exhibited larger accuracies compared to

353   young animals. However, the addition of genotype information to the breeding value

354   prediction resulted in an improvement of accuracy, also in latter group. Other studies in sheep

355   underlined the higher accuracy of genomic methods compared to the pedigree-based approach

356   for milk and meat production traits (Daetwyler et al., 2012; Legarra et al., 2014; Baloche et

357   al., 2014). Moreover, GS studies carried out in beef cattle on muscle FA composition reported

358   for some of FA investigated also in this study a similar pattern of GEBV accuracy (Chang et

359   al., 2015; Chiaia et al., 2017; Zhu et al., 2017).

360   The similar magnitude of GEBV accuracy for FA_FTIR and FA_GC is an interesting

361   for a possible implementation breeding program for milk FA composition in dairy sheep, due

362   to the considerable reduction of phenotyping cost. The predictive ability of FTIR spectra

363   ($R^2_{GC\text{-}FTIR}$, see **Table 3**) might have affected the accuracy of genomic predictions: a moderate

correlations between $R^2_{GC\text{-}FTIR}$ and (G)EBV accuracy were observed (0.46 and 0.45 in ssGBLUP for old and young cohort, respectively).

Regarding the prediction model, the slightly higher accuracies found using ssGBLUP could be ascribable to the blended (co)variance structure that can takes benefits from the inclusion of all relatives of non-genotyped and genotypes ewes with recorded traits (Aguilar et al., 2010; Legarra et al., 2014). Finally, when the selection intensity is not so high (as in Sarda sheep), the use of genomic selection with genotyped females may help to improve milk composition traits even of un-phenotyped animals (young cohort) as already suggested in a simulation study by Gorjanc et al. (2015).

However, the complex genetic correlation pattern that exist among the different FA should be carefully taken into account (Carta et al. 2008; Sanchez et al. 2010) when implementing a coherent selection goal aimed at improving the milk FA composition. Actually, the use of a bivariate approach resulted in negligible differences of GEBV accuracies compared to the univariate models (in many cases of 0.01), and only in few cases a slight improvement (0.03-0.07) was observed. Apart from a sampling effect, other possible explanations can be found in the relevant literature. Previous studies using either simulated (Calus and Veerkamp, 2011; Guo et al., 2014) or real type traits (Tsuruta et al. 2011) data reported from zero to low advantages for multiple trait GEBV accuracy over single trait evaluations. According to these authors, superiority of multiple over single trait accuracies depends on the amount of unphenotyped animals (i.e., missing data), and on the heritability and genetic relationship among considered traits. In the present work, the number of unphenotyped animals was equal for both traits considered in the bivariate analysis, i.e., the scenario that according to previous simulation studies (Calus and Veerkamp, 2011; Guo et al., 2014) did not result in any improvement of accuracy. Moreover, accuracy gains here observed

(Table 8) were for traits with low heritability. This result is also in agreement to what previously reported (Jia and Jannink, 2012; Guo et al., 2014).

CONCLUSIONS

The Fourier Transform Infrared spectrography is commonly used in dairy industry for milk composition recordings, as well as genomic selection is an effective tool to rank the best candidates for breeding purpose. The results presented in the current investigation, confirmed that in dairy sheep FTIR predicted FA are heritable traits, exhibiting from low to moderate heritabilities. These figures are comparable to those estimated from more expensive and time consuming GC measured phenotypes. Moreover, breeding value accuracies obtained with genomic selection methods were always higher than those estimated with traditional pedigree based approach, and ssGBLUP outperformed the GBLUP method. The use of a bivariate model result in a slight improvement of GEBV accuracy for only few traits. Results of the present study, although referred to a sample of limited size, suggest that the combination of FTIR predictions and genomic selection technology could represent an interesting option for the genetic improvement of milk FA composition in dairy sheep.

413   **Table 1.** Flock statistics and distribution of records for fixed effects considered in the analysis

Observations	n	%
Flocks	47	
Ewes/flock	19.6±7.2	
Parity		
1	186	20
2	123	13
3	151	16
4	164	18
5	116	13
6	95	10
7	68	7
>7	20	2
Lambing Month		
Jan	142	15
Feb-Mar	130	14
Oct-Nov	377	41
Dec	274	30
Altitude		
Mountain (>500 m)	135	15
Hill (200-500 m)	480	52
Plain (<200 m)	308	33
Total	923	100

414

415 **Table 2.** Type of relationship matrices used and number of animals for the three (co)variance

416 structures

	Matrix		
Animals	**A**	**G**	**H**
With genotypes and own phenotypes	769	769	769
Without genotypes and with own phenotypes	154	-	154
Other relatives without phenotype	3,924	-	3,924
Total number of animals	4,847	769	4,847

417

418   **Table 3.** Descriptive statistics of fatty acids measured using gas chromatography (FA_GC) or

419   predicted using Fourier Transformed Infrared spectrum (FA_FTIR) and coefficients of

420   determination ($R^2_{CG\text{-}FTIR}$).

Fatty Acid	Trait	FA_GC		FA_FTIR		
		Mean	SD	Mean	SD	$R^2_{CG\text{-}FTIR}$
Butyric acid	C4:0	2.68	0.37	2.67	0.34	0.79
Caproic acid	C6:0	1.76	0.36	1.76	0.34	0.87
Caprylic acid	C8:0	1.61	0.45	1.60	0.43	0.89
Capric acid	C10:0	5.55	1.73	5.53	1.67	0.91
Lauric acid	C12:0	3.50	0.99	3.49	0.94	0.87
Myristic acid	C14:0	10.85	1.52	10.83	1.39	0.79
Palmitic acid	C16:0	25.97	2.95	25.97	2.58	0.69
Stearic acid	C18:0	10.24	2.49	10.25	2.20	0.72
Vaccenic acid (VA)	C18:1t11	2.06	1.04	2.05	0.92	0.75
Oleic acid	C18:1c9	17.14	3.58	17.20	3.34	0.85
Linoleic acid	C18:2ω6	2.09	0.50	2.09	0.40	0.51
α-Linolenic acid	C18:3ω3	0.89	0.50	0.89	0.43	0.68
Conjugated linoleic acid	CLAc9,t11	1.03	0.47	1.03	0.41	0.72
Saturated fatty acids	SFA	67.72	3.88	67.67	3.60	0.82
Monounsaturated fatty acids	MUFA	25.83	3.58	25.88	3.29	0.81
Polyunsaturated fatty acids	PUFA	6.44	1.45	6.44	1.32	0.79
PUFA n-6:PUFA *n*-3	ω6:ω3	2.47	1.15	2.48	1.01	0.70
Trans Fatty Acid (TFA) – VA	TFAnoVA	4.56	1.52	4.55	1.35	0.77
de novo synthesized FA[1]	Denovo[1]	23.56	4.62	23.74	4.30	0.90

421   [1] Denovo = C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are de novo synthesized
422   in the mammary gland.
423

Table 4. Heritability (h^2) for milk fatty acid composition measured by gas chromatography (FA_GC) or predicted by Fourier Transform Infrared Spectra (FA_FTIR) using pedigree relationship matrix (ABLUP), genomic relationship matrix (GBLUP), blended genomic-pedigree matrix (ssGBLUP), respectively. SE of heritability were reported in brackets.

Trait	Ablup		Gblup		ssGblup	
	FA_GC	FA_FTIR	FA_GC	FA_FTIR	FA_GC	FA_FTIR
C4:0	0.22 (.10)	0.27 (.11)	0.36 (.09)	0.56 (.10)	0.34 (.09)	0.49 (.10)
C6:0	0.04 (.06)	0.12 (.07)	0.16 (.06)	0.23 (.06)	0.17 (.06)	0.25 (.06)
C8:0	0.10 (.06)	0.12 (.06)	0.16 (.06)	0.20 (.06)	0.17 (.06)	0.22 (.06)
C10:0	0.13 (.06)	0.14 (.06)	0.16 (.07)	0.18 (.06)	0.17 (.06)	0.19 (.06)
C12:0	0.15 (.07)	0.15 (.07)	0.16 (.07)	0.16 (.06)	0.17 (.06)	0.17 (.06)
C14:0	0.12 (.09)	0.07 (.08)	0.15 (.08)	0.10 (.07)	0.19 (.08)	0.12 (.07)
C16:0	0.46 (.11)	0.07 (.07)	0.26 (.08)	0.12 (.07)	0.35 (.09)	0.11 (.07)
C18:0	0.29 (.10)	0.14 (.08)	0.23 (.08)	0.19 (.07)	0.26 (.08)	0.16 (.07)
C18:1t11	0.14 (.06)	0.09 (.05)	0.09 (.05)	0.08 (.00)	0.07 (.05)	0.09 (.04)
C18:1c9	0.17 (.07)	0.10 (.06)	0.17 (.06)	0.12 (.07)	0.18 (.06)	0.14 (.05)
C18:2ω6	0.07 (.06)	0.00 (.00)	0.08 (.06)	0.00 (.00)	0.12 (.06)	0.00 (.00)
C18:3ω3	0.03 (.02)	0.03 (.04)	0.01 (.01)	0.07 (.04)	0.02 (.02)	0.08 (.04)
CLAc9,t11	0.12 (.06)	0.13 (.06)	0.10 (.06)	0.09 (.05)	0.08 (.06)	0.10 (.05)
SFA[1]	0.07 (.09)	0.01 (.08)	0.20 (.08)	0.18 (.08)	0.22 (.08)	0.20 (.08)
MUFA[2]	0.08 (.07)	0.01 (.07)	0.18 (.07)	0.15 (.07)	0.19 (.07)	0.17 (.07)
PUFA[3]	0.09 (.05)	0.11 (.07)	0.08 (.05)	0.15 (.06)	0.10 (.05)	0.14 (.06)
ω6:ω3[4]	0.05 (.02)	0.05 (.03)	0.04 (.02)	0.08 (.03)	0.04 (.02)	0.08 (.03)
TFAnoVA[5]	0.14 (.07)	0.06 (.06)	0.15 (.06)	0.18 (.06)	0.16 (.06)	0.17 (.06)
Denovo[6]	0.11 (.07)	0.11 (.07)	0.15 (.06)	0.15 (.06)	0.16 (.06)	0.16 (.06)

[1]Sum of the individual saturated fatty acids.
[2]Sum of the individual monounsaturated fatty acids.
[3]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.
[4]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
[5]Trans Fatty Acid (TFA) without Vaccenic acid (VA).
[6]Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland.

Table 5. Intra-Flock heritability (h^2_{IF}) for milk fatty acid composition measured by gas chromatography (FA_GC) or predicted by Fourier Transform Infrared Spectra (FA_FTIR) using pedigree relationship matrix (ABLUP), genomic relationship matrix (GBLUP), blended genomic-pedigree matrix (ssGBLUP), respectively. SE of h^2_{IF} were reported in brackets.

Trait	Ablup		Gblup		ssGblup	
	FA_GC	FA_FTIR	FA_GC	FA_FTIR	FA_GC	FA_FTIR
C4:0	0.28 (.12)	0.34 (.13)	0.45 (.11)	0.68 (.11)	0.42 (.11)	0.59 (.11)
C6:0	0.09 (.14)	0.29 (.15)	0.38 (.13)	0.55 (.12)	0.40 (.12)	0.58 (.11)
C8:0	0.25 (.15)	0.30 (.15)	0.41 (.13)	0.52 (.12)	0.43 (.12)	0.55 (.12)
C10:0	0.31 (.14)	0.34 (.15)	0.38 (.13)	0.45 (.12)	0.41 (.12)	0.48 (.12)
C12:0	0.29 (.14)	0.32 (.14)	0.33 (.12)	0.35 (.12)	0.33 (.12)	0.36 (.12)
C14:0	0.19 (.14)	0.11 (.13)	0.23 (.13)	0.16 (.12)	0.28 (.12)	0.20 (.12)
C16:0	0.76 (.15)	0.13 (.13)	0.47 (.13)	0.23 (.12)	0.59 (.12)	0.20 (.12)
C18:0	0.50 (.15)	0.24 (.14)	0.40 (.14)	0.33 (.13)	0.44 (.13)	0.29 (.12)
C18:1t11	0.38 (.14)	0.31 (.15)	0.24 (.12)	0.27 (.14)	0.19 (.12)	0.30 (.13)
C18:1c9	0.44 (.16)	0.30 (.15)	0.45 (.13)	0.34 (.12)	0.47 (.12)	0.39 (.12)
C18:2ω6	0.17 (.14)	0.00 (.00)	0.18 (.14)	0.00 (.00)	0.28 (.13)	0.00 (.00)
C18:3ω3	0.22 (.13)	0.10 (.13)	0.06 (.09)	0.23 (.13)	0.13 (.10)	0.27 (.13)
CLAc9,t11	0.28 (.14)	0.35 (.15)	0.24 (.13)	0.24 (.14)	0.19 (.13)	0.27 (.13)
SFA[1]	0.12 (.14)	0.01 (.13)	0.33 (.13)	0.29 (.13)	0.35 (.12)	0.33 (.12)
MUFA[2]	0.16 (.15)	0.01 (.13)	0.36 (.13)	0.29 (.12)	0.38 (.10)	0.33 (.12)
PUFA[3]	0.26 (.15)	0.26 (.15)	0.25 (.13)	0.38 (.14)	0.30 (.13)	0.35 (.14)
ω6:ω3[4]	0.42 (.16)	0.23 (.14)	0.30 (.13)	0.37 (.13)	0.30 (.12)	0.36 (.13)
TFAnoVA[5]	0.30 (.16)	0.16 (.15)	0.33 (.13)	0.44 (.14)	0.35 (.13)	0.40 (.14)
Denovo[6]	0.23 (.14)	0.23 (.14)	0.32 (.13)	0.32 (.13)	0.35 (.12)	0.35 (.12)

[1]Sum of the individual saturated fatty acids.
[2]Sum of the individual monounsaturated fatty acids.
[3]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.
[4]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
[5]Trans Fatty Acid (TFA) without Vaccenic acid (VA).
[6]Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland.

Table 6. Proportion of phenotypic variance[1] explained by FTD (r^2_{FTD}) estimated in the three approaches

Trait	Ablup		Gblup		ssGblup	
	FA_GC	FA_FTIR	FA_GC	FA_FTIR	FA_GC	FA_FTIR
C4:0	0.22	0.20	0.22	0.18	0.20	0.17
C6:0	0.59	0.58	0.59	0.59	0.58	0.58
C8:0	0.61	0.62	0.62	0.62	0.61	0.61
C10:0	0.59	0.60	0.60	0.61	0.59	0.60
C12:0	0.50	0.55	0.51	0.55	0.50	0.55
C14:0	0.35	0.41	0.36	0.41	0.35	0.41
C16:0	0.40	0.47	0.44	0.48	0.41	0.47
C18:0	0.42	0.43	0.43	0.44	0.42	0.43
C18:1t11	0.63	0.71	0.64	0.71	0.64	0.71
C18:1c9	0.63	0.67	0.62	0.66	0.62	0.66
C18:2ω6	0.59	0.47	0.58	0.47	0.58	0.47
C18:3ω3	0.86	0.72	0.86	0.71	0.86	0.71
CLAc9,t11	0.58	0.64	0.59	0.64	0.58	0.64
SFA[2]	0.40	0.40	0.40	0.39	0.39	0.39
MUFA[3]	0.52	0.50	0.51	0.49	0.51	0.49
PUFA[4]	0.68	0.60	0.68	0.60	0.67	0.59
ω6:ω3[5]	0.88	0.79	0.88	0.79	0.88	0.78
TFAnoVA[6]	0.56	0.61	0.56	0.60	0.55	0.60
Denovo[7]	0.54	0.54	0.55	0.55	0.54	0.54
Mean±sd	0.55±0.16	0.55±0.14	0.56±0.16	0.55±0.14	0.55±0.16	0.55±0.14

[1]SE between 0.02 and 0.06 for FA_GC and ranging from 0.04 to 0.04 for FA_FTIR.
[2]Sum of the individual saturated fatty acids.
[3]Sum of the individual monounsaturated fatty acids.
[4]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids;
[5]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
[6]Trans Fatty Acid (TFA) without Vaccenic acid (VA).
[7]Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland

462   **Table 7**. EBV and GEBV accuracy of prediction for milk fatty acids obtained with gas chromatography (FA_GC) or predicted by Fourier

463   Transform Infrared spectra (FA_FTIR) using the three relationship matrices: pedigree (**A,** Ablup), genomic (**G**, Gblup) or pedigree and SNP

464   blended using a single-step genomic approach (**H**, ssGblup).

	Oldest animals[1]						Youngest aninals[2]					
	FA_GC			FA_FTIR			FA_GC			FA_FTIR		
Trait	Ablup	Gblup	ssGblup	Ablup	Gblup	ssGblup	Ablup	Gblup	ssGblup	Ablup	Gblup	ssGblup
C4:0	0.52	0.54	0.56	0.57	0.59	0.60	0.19	0.28	0.35	0.21	0.31	0.37
C6:0	0.29	0.32	0.36	0.52	0.54	0.55	0.10	0.18	0.27	0.18	0.28	0.34
C8:0	0.48	0.50	0.52	0.53	0.55	0.56	0.17	0.26	0.33	0.18	0.28	0.34
C10:0	0.54	0.56	0.57	0.56	0.58	0.59	0.19	0.29	0.35	0.20	0.30	0.35
C12:0	0.52	0.54	0.56	0.55	0.56	0.58	0.18	0.28	0.34	0.19	0.29	0.35
C14:0	0.43	0.45	0.48	0.32	0.35	0.39	0.15	0.24	0.32	0.11	0.20	0.28
C16:0	0.83	0.84	0.83	0.35	0.38	0.41	0.29	0.41	0.45	0.12	0.21	0.29
C18:0	0.68	0.69	0.70	0.48	0.50	0.52	0.24	0.35	0.40	0.17	0.26	0.33
C18:1t11	0.59	0.60	0.61	0.54	0.56	0.57	0.20	0.31	0.36	0.19	0.29	0.34
C18:1c9	0.63	0.65	0.65	0.53	0.55	0.56	0.22	0.32	0.38	0.18	0.28	0.34
C18:2ω6	0.39	0.42	0.45	0.05	0.09	0.21	0.14	0.23	0.30	0.02	0.10	0.23
C18:3ω3	0.45	0.47	0.50	0.30	0.33	0.37	0.16	0.25	0.32	0.10	0.19	0.28
CLAc9,t11	0.51	0.53	0.55	0.57	0.58	0.60	0.18	0.28	0.34	0.20	0.30	0.35
SFA[3]	0.33	0.36	0.40	0.09	0.12	0.23	0.12	0.20	0.29	0.03	0.11	0.23
MUFA[4]	0.38	0.41	0.44	0.11	0.14	0.24	0.13	0.22	0.30	0.04	0.11	0.24
PUFA[5]	0.49	0.52	0.53	0.49	0.51	0.53	0.17	0.27	0.33	0.17	0.27	0.33
ω6:ω3[6]	0.61	0.63	0.64	0.46	0.48	0.50	0.21	0.32	0.37	0.16	0.25	0.32
TFAnoVA[7]	0.53	0.55	0.56	0.38	0.41	0.44	0.18	0.28	0.34	0.13	0.22	0.30
Denovo[8]	0.46	0.48	0.50	0.49	0.51	0.53	0.16	0.25	0.32	0.17	0.27	0.33
Mean	0.51	0.53	0.55	0.42	0.44	0.47	0.18	0.27	0.34	0.14	0.24	0.31
SD	0.13	0.12	0.11	0.17	0.16	0.13	0.04	0.05	0.04	0.06	0.06	0.04

465   [1]Cohort of sheep born before December 2012 with SNP genotypes and own milk FA records available.

24

466   [2]Cohort of sheep born after November 2012 with SNP genotypes available and own milk FA records masked to mimic a candidate set of
467   younger sheep.
468   [3]Sum of the individual saturated fatty acids.
469   [4]Sum of the individual monounsaturated fatty acids.
470   [5]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.
471   [6]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
472   [7]Trans Fatty Acid (TFA) without Vaccenic acid (VA).
473   [8]Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland.
474

Table 8. Average accuracies and s.d. of GEBV predicted in young animal (n=100) by ssGBLUP using a series of bi-traits analysis both for gas chromatography measured (FA_GC) and Fourier transform IR predicted fatty acids (FA_FTIR).

Trait	FA_GC			FA_FTIR		
	Mean	s.d.	Diff.[1]	Mean	s.d.	Diff.[1]
C4_0	0.35	0.01	0.00	0.35	0.01	-0.02
C6_0	0.28	0.02	0.01	0.32	0.02	-0.02
C8_0	0.33	0.02	0.00	0.33	0.01	-0.01
C10_0	0.34	0.01	-0.01	0.34	0.01	-0.01
C12_0	0.34	0.01	0.00	0.34	0.01	-0.01
C14_0	0.32	0.02	0.00	0.29	0.02	0.01
C16_0	0.43	0.01	-0.02	0.31	0.02	0.02
C18_0	0.38	0.01	-0.02	0.33	0.01	0.00
C18_1c9	0.36	0.01	-0.01	0.36	0.01	0.02
C18_1t11	0.38	0.01	0.00	0.35	0.02	0.01
C18_2n6	0.31	0.01	0.01	0.27	0.02	0.04
C18_3n3	0.32	0.01	0.00	0.31	0.02	0.03
CLAc9t11	0.34	0.01	0.00	0.34	0.01	-0.01
SFA[2]	0.31	0.02	0.02	0.30	0.03	0.07
MUFA[3]	0.32	0.01	0.02	0.31	0.02	0.07
PUFA[4]	0.32	0.01	-0.01	0.33	0.02	0.00
n6_n3[5]	0.37	0.01	0.00	0.33	0.01	0.01
TFA_no_VA[6]	0.34	0.01	0.00	0.32	0.02	0.02
De novo[7]	0.32	0.01	0.00	0.33	0.01	0.00

[1] for each FA diff = (average accuracy of 17 bi-traits models – single trait accuracy)
[2] Sum of the individual saturated fatty acids.
[3] Sum of the individual monounsaturated fatty acids.
[4] Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.
[5] Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
[6] Trans Fatty Acid (TFA) without Vaccenic acid (VA).
[7] Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland.

Figure 1. Regressions of additive genetic variance estimated using fatty acids measured through gas chromatography (FA_FC) and fatty acids predicted by Fourier Transform Infrared Spectra (FA_FTIR) within each investigated method: pedigree relationship matrix (ABLUP), genomic relationship matrix (GBLUP), blended genomic-pedigree matrix (ssGBLUP). Dashed line represent the equivalent line (y=x).

498   Cesarani. Figure 1.
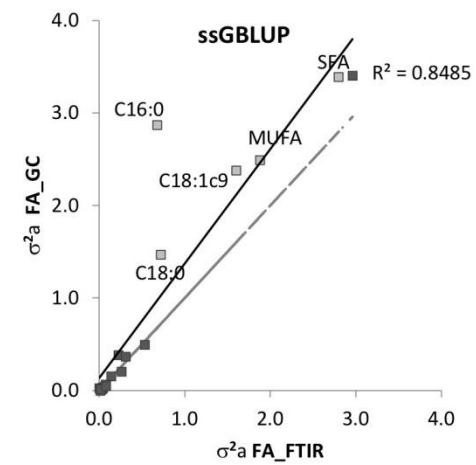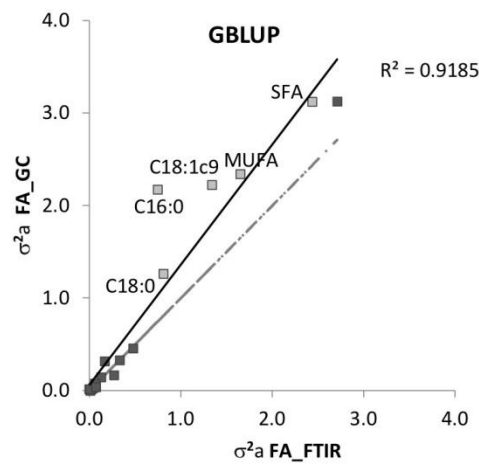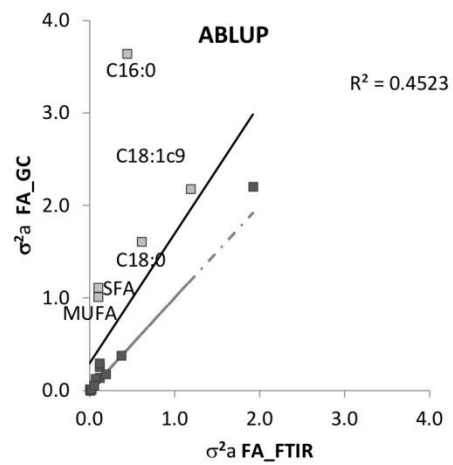
501 <div align="center">**APPENDIX**</div>

502

503 **Table A1**. Single FA used to define groups of FA analyzed.

504

Group of FA	Single fatty acid
SFA: sum of individual saturated fatty acids	C4:0, C6:0, C0, C8:0, C9:0, C10:0, C11:0, C12:0, isoC13:0, anteisoC13:0, isoC14:0, C14:0, isoC15:0, anteisoC15:0, C15:0, isoC16:0, C16:0, isoC17:0, anteisoC17:0, C17:0, isoC18:0, C18:0, C19:0, C20:0, C22:0, C23:0, C24:0, C25:0, C26:0
MUFA: sum of individual monounsaturated fatty acids	C10:1, C14:1c9, C15:1, C16:1t4, C16:1t5, C16:1t6+t7, C16:1t9, C16:1t10, C16:1t11+t12, C16:1c7, C16:1c9, C16:1c10, C16:1c11, C17:1c6+c7, C17:1c8, C17:1c9, C18:1t4, C18:1t5, C18:1t6+t8, C18:1t9, C18:1t10, C18:1t11, C18:1t12, C18:1t13+t14, C18:1c9, C18:1t15+c10, C18:1c11, C18:1c12, C18:1c13, C18:1t16+c14, C18:1c15, C18:1c16, C20:1c5, C20:1c9, C20:1c11, C20:1c15, C22:1ω9, C24:1c15
PUFA: sum of individual polyunsaturated fatty acids	C18:2t10t14, C18:2t11t15, C18:2t9t12, C18:2c9t13, C18:2t8c13, C18:2c9t12, C18:2t9c12, C18:2t11c15, C18:2ω6, C18:2t12c15, C18:2c12c15, CLAc9t11, CLAt9c11, CLAt10c12, CLAt11c13, CLAt12t14, CLAt11t13, CLAt9t11, C20:2ω9, C20:2ω6, C22:2ω6, C18:3ω6, C18:3ω3, C20:3ω9, C20:3ω6, C20:3, C20:3ω3, C22:3ω6, C18:4ω3, C20:4ω6, C20:4ω3, C22:4ω6, C20:5ω3, C22:5ω3, C22:6ω3
TFA-VA	sum of individual trans FA excluding C18:1t11 (Vaccenic acid)
PUFA n-6:PUFA n-3	ratio between the sum of individual PUFA ω6 and the sum of all individual PUFA ω3
Denovo de novo synthesized in the mammary gland.	C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0

Table A2. Variance components estimation (animal, flock test date and residual) for measured and predicted fatty acids across the three

506 methods

| | ABLUP | | | | | | GBLUP | | | | | | ssGBLUP | | | | | |
| | FA_GC | | | FA_FTIR | | | FA_GC | | | FA_FTIR | | | FA_GC | | | FA_FTIR | | |
	σ_a^2	σ_f^2	σ_e^2	σ_a^2	σ_f^2	σ_e^2	σ_a^2	σ_f^2	σ_e^2	σ_a^2	σ_f^2	σ_e^2	σ_a^2	σ_f^2	σ_e^2	σ_a^2	σ_f^2	σ_e^2
C4:0	0.02	0.02	0.06	0.02	0.02	0.05	0.04	0.02	0.04	0.05	0.02	0.02	0.04	0.02	0.05	0.04	0.02	0.03
C6:0	0.00	0.07	0.05	0.01	0.06	0.03	0.02	0.07	0.03	0.02	0.06	0.02	0.02	0.07	0.03	0.03	0.06	0.02
C8:0	0.02	0.12	0.06	0.02	0.11	0.05	0.03	0.12	0.04	0.04	0.11	0.03	0.03	0.12	0.04	0.04	0.11	0.03
C10:0	0.38	1.70	0.81	0.37	1.62	0.70	0.46	1.75	0.73	0.48	1.65	0.59	0.50	1.74	0.71	0.53	1.65	0.57
C12:0	0.14	0.46	0.33	0.12	0.45	0.25	0.15	0.48	0.31	0.13	0.46	0.24	0.16	0.47	0.31	0.14	0.46	0.24
C14:0	0.26	0.73	1.07	0.12	0.73	0.93	0.32	0.74	1.02	0.17	0.74	0.88	0.39	0.72	0.97	0.22	0.73	0.84
C16:0	3.64	3.19	1.10	0.44	2.90	2.79	2.17	3.68	2.44	0.75	2.96	2.50	2.87	3.42	1.98	0.68	2.93	2.61
C18:0	1.61	2.28	1.56	0.61	1.82	1.83	1.26	2.41	1.89	0.81	1.90	1.64	1.47	2.32	1.79	0.72	1.86	1.77
C18:1t11	0.13	0.59	0.21	0.07	0.56	0.16	0.08	0.60	0.26	0.06	0.58	0.17	0.07	0.60	0.28	0.07	0.57	0.16
C18:1c9	2.18	8.22	2.73	1.19	7.80	2.72	2.22	8.10	2.69	1.34	7.72	2.58	2.38	8.22	2.67	1.60	7.81	2.42
C18:2ω6	0.02	0.13	0.08	0.00	0.07	0.08	0.02	0.13	0.07	0.00	0.07	0.08	0.03	0.13	0.07	0.00	0.07	0.08
C18:3ω3	0.01	0.21	0.03	0.01	0.13	0.05	0.00	0.21	0.03	0.01	0.13	0.04	0.00	0.21	0.03	0.01	0.13	0.04
CLAc9t11	0.02	0.12	0.06	0.02	0.10	0.04	0.02	0.12	0.06	0.01	0.11	0.04	0.02	0.12	0.07	0.02	0.10	0.04
SFA[1]	1.11	6.17	8.00	0.10	5.31	7.97	3.12	6.16	6.14	2.44	5.36	5.77	3.39	6.12	6.08	2.80	5.40	5.59
MUFA[2]	1.01	6.68	5.26	0.10	5.46	5.39	2.34	6.63	4.03	1.65	5.46	3.93	2.49	6.65	4.03	1.88	5.52	3.82
PUFA[3]	0.18	1.41	0.49	0.19	1.06	0.52	0.17	1.44	0.50	0.27	1.08	0.44	0.21	1.42	0.47	0.26	1.07	0.47
ω6:ω3[4]	0.06	1.11	0.09	0.05	0.72	0.15	0.04	1.12	0.10	0.07	0.73	0.12	0.05	1.11	0.10	0.08	0.72	0.13
TFAnoVA[5]	0.30	1.25	0.69	0.12	1.13	0.60	0.33	1.26	0.67	0.33	1.12	0.41	0.37	1.24	0.66	0.31	1.12	0.45
Denovo[6]	2.21	11.18	7.29	1.92	9.68	6.31	3.13	11.47	6.43	2.71	9.94	5.57	3.41	11.38	6.34	2.96	9.86	5.50

507 [1]Sum of the individual saturated fatty acids

508 [2]Sum of the individual monounsaturated fatty acids.

509 [3]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.

510 [4]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.

511 [5]Trans Fatty Acid (TFA) without Vaccenic acid (VA).

512 [6]Sum of C6:0, C8:0, C10:0, C11:0, C12:0, iso-C13:0, C14:0 that are *de novo* synthesized in the mammary gland.

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