Genomic selection of milk fatty acid composition in Sarda dairy sheep: Effect of different phenotypes and relationship matrices on heritability and breeding value accuracy

Genomic selection of milk fatty acid composition in Sarda dairy sheep: effect of different phenotypes and relationship matrices on heritability and breeding values accuracy. *by Cesarani et al.* Nowadays consumers are mostly interested in dairy products with improved quality. Sheep breeders may achieve this objective thanks to recent availability of genomic tools. This paper investigates the combined use of genomic selection and mid infrared milk spectra to selective purpose for improving milk fatty acid profile.

Genomic selection of milk fatty acid composition in Sarda dairy sheep: effect of different phenotypes and relationship matrices on heritability and breeding values accuracy

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ABSTRACT

Fatty acid (FA) composition is one of the most important aspects of milk nutritional quality. However, the inclusion of this trait as breeding goal for dairy species is hampered by the logistics and high costs of phenotype recording. Fourier transform Infrared Spectroscopy (FTIR) is a valid and cheap alternative to laboratory gas chromatography (GC) for predicting milk FA composition. Moreover, as for other novel phenotypes, the efficiency of selection for these traits can be enhanced by using genomic data. Objective of this research was to compare traditional versus genomic selection approaches for estimating genetic parameters and breeding values of milk fatty acid composition in dairy sheep using either GC measured or FTIR predicted FA as phenotypes. Milk FA profiles were available for a total of 923 Sarda breed ewes. The youngest 100 had their own phenotype masked to mimic selection candidates. Pedigree relationship information and genotypes were available for 923 and 769 ewes, respectively. Three statistical approaches were used: the classical pedigree based BLUP; the GBLUP that considers the genomic relationship matrix **G**; the single step GBLUP (ssGBLUP) where pedigree and genomic relationship matrices are blended into a single **H** matrix. Heritability estimates using pedigree were lower than ssGBLUP, and very similar between GC and FTIR regarding the statistical approach used. For some FA, mostly associated with animal diet (i.e. C18:2ω6, C18:3ω3), random effect of combination of flock and test date (FTD) explained a relevant quota of total variance, reducing accordingly h^2 estimates. Genomic approaches (GBLUP and ssGBLUP) outperformed the traditional pedigree method both for GC and FTIR FA. Prediction accuracies in older cohort were larger than young cohort. Genomic prediction accuracy (obtained using either **G** or **H** relationship matrix) in young cohort of animals, where their own phenotype were masked, were similar for GC and FTIR. Multiple trait analysis slightly affected GEBV accuracies. These results

suggest that FTIR predicted milk FA composition could represent a valid option for the inclusion of this trait in breeding programs.

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

INTRODUCTION

Dairy sheep breeding programs have been historically aimed at improving total milk yield per lactation (Carta et al., 2009). Although sheep milk is almost totally destined to cheese making (Pulina et al., 2018), selection for milk composition is carried out only in few breeds (Macciotta et al., 2005; Astruc et al., 2008). This is mostly because of the high recording costs compared to the income per ewe (Carta et al., 2009; Rupp et al., 2016). On the other hand, the increasing consumer interest on dairy product nutritional quality pushes toward the inclusion of fine milk composition traits among breeding goals of dairy species. An example is represented by the conjugated linoleic acid (CLA), known for its relationships with human health (Banni et al., 2003; Bhattacharya et al., 2006; Mele et al., 2011). Ruminant dairy products are among the most important sources of CLA in human diets (Nudda et al., 2014). Although animal feeding is considered the most important factor affecting milk fatty acid (FA) composition (Cabiddu et al., 2005; Sanchez et al., 2010), genetic variation for these traits has been reported in cattle (Stoop et al., 2008; Pegolo et al., 2016) and sheep (Sanchez et al. 2010; Correddu et al. 2018) suggesting the possibility for a genetic improvement.

The inclusion of milk FA composition as breeding goal for dairy sheep programs is constrained by logistics and costs of phenotype recording. The standard method for measuring milk FA composition is the gas chromatography (GC) analysis, that is expensive and time consuming. A population-scale recording of milk FA appears therefore rather unfeasible for species where also the routine phenotyping of milk components is economically unbearable. A valid alternative to GC is represented by Fourier transform Infrared (FTIR) spectroscopy.

This technique, implemented in milk lab equipment currently used for routine milk composition analysis, produces a spectrum of approximately one thousand variables that could be used for large scale prediction of novel phenotypes, including FA (e.g. Cecchinato et al., 2009; De Marchi et al 2011; McParland et al., 2011; Dehareng et al., 2012; Fleming et al., 2016). Good prediction accuracies of milk FA based on FTIR spectrum have been reported for dairy cattle (Arnould and Soyeurt, 2009; De Marchi et al., 2011). Similar results, even though with a certain degree of variability and in a limited number of studies, have been reported for dairy sheep (Ferrand-Calmels et al., 2014; Caredda et al. 2016; Correddu et al., 2018). Fatty acid predicted by FTIR exhibited genetic variation both in dairy cattle (e.g. Soyeurt et al., 2006; Bastin et al., 2013; Narayana et al., 2017) and sheep (Sanchez et al., 2010; Boichard et al., 2014). Moreover, genetic correlations ranging from 60% to 99% between FTIR predicted and GC measured milk FA have been reported both in cattle (Bonfatti et al., 2017) and sheep (Correddu et al., 2018).

Dairy sheep breeding programs are based on the classical quantitative genetic approach, with a pyramidal organization of the population, large scale registration of phenotypes and pedigree, and genetic evaluations of AI rams based on progeny testing (Carta et al., 2009; Baloche et al., 2014). The availability of high throughput SNP panel for sheep has opened the perspective of genomic selection (GS) also for this species. Researches have been carried out on dairy (Duchemin et al., 2012; Baloche et al., 2014), meat, and wool sheep (Daetwyler et al., 2012). An improvement of genomic breeding value (GEBV) accuracies over the traditional pedigree index has generally been observed, even though to a lesser extent compared to dairy cattle (Legarra et al., 2014).

Genomic studies on milk FA in cattle have focused mostly on the study of their genetic determinism (Stoop et al., 2009; Bouwman et al. 2011; Buitenhuis et al., 2014). In dairy sheep, the molecular basis of FA have been investigated by candidate gene (Crisà et al,

2010; Moioli et al., 2012), and QTL detection (Carta et al., 2008) approaches. Genomic selection studies for FA compositions are limited to beef cattle (Uemoto et al., 2011; Chen et al., 2015; Zhu et al. 2017) and meat sheep (Rovadoscki et al., 2018). One of the main advantange of GS over traditional selection is that, once a reference population with both phenotypic and genotypic records has been settled, breeding values of animals without their own phenotypes can be predicted with a reasonable accuracy (Meuwissen et al., 2001; Hayes et al., 2009). Therefore, GS seems to be an appealing option for novel traits that are difficult to measure routinely as milk FA composition (Boichard and Brochard, 2012; Daetwyler et al., 2012).

Aim of the present work is to explore the feasibility of breeding for milk FA composition in a dairy sheep breed by combining the use of FTIR predicted phenotypes and the genomic selection technology. At this purpose breeding values prediction were carried out running a pedigree based and two genomic models, using either FTIR predicted and GC measured FA as phenotypes. Moreover, the effect of the different phenotypes used and of the estimation methods on heritability was tested.

MATERIALS AND METHODS

Data

A sample of 923 Sarda breed dairy ewes farmed in 47 flocks located in the island of Sardinia (Italy) were considered. Milk samples, one per animal, were collected from February to June 2015 (**Table 1**). In this study 13 individuals FA (C4:0, C6:0, C8:0, C10:0, C12:0, C14:0, C16:0, C18:0, C18:1t11, C18:1c9, C18:2ω6, C18:3ω3, CLAc9t11), 5 groups of FA and a ratio between groups of FA were analyzed. Groups of FA were calculated as follow (Appendix, **Table A1**): SFA, sum of individual saturated fatty acids; MUFA, sum of individual monounsaturated fatty acids; PUFA, sum of individual polyunsaturated fatty acids;

TFA-VA, sum of individual trans FA with the exclusion of C18:1t11 (vaccenic acid); Denovo, sum of individual FA that are de novo synthesized in the mammary gland; PUFA n-6:PUFA n-3, ratio between the sum of individual PUFA n6 and the sum of all individual PUFA n3. Milk FA (g FA/100 g total FA) composition was both measured by gas chromatography (FA_GC) and predicted by partial least square regression (PLS) using the FTIR spectra (FA_FTIR) generated by milk analysis performed with Milkoscan FT6000 instrument (Foss, Hillerød, Denmark). PLS was carried out by extracting 18 latent factors. Prediction accuracies were tested by using a calibration data set of 700 ewes and a validation data set of 223 ewes, respectively. One-hundred replicates randomly assigning animals to the two data sets were performed. Details for GC analysis are reported in the work of Correddu et al., (2018).

Genotypes obtained with the Infinium Ovine SNP50 v1 BeadChip (Illumina Inc., San Diego, California) were available for 769 ewes out of 923. Quality control of SNP genotypes was carried out with PLINK software (Purcell et al., 2007). All genotyped ewes had a call rate greater than 0.95. A SNP was discharged if: the call rate was lower than 0.975 (867 markers removed), the minor allele frequency (MAF) was lower than 0.01 (1,309 markers removed), it deviated significantly from the Hardy Weinberg Equilibrium ($P < 0.01$, 1,264 markers removed), or it did not map to the OAR_v3.1 assembly (6,182 markers removed). After quality control, all genotyped ewes and 44,619 SNPs across 27 chromosomes were retained for the analysis. A pedigree with 633,317 animals was also available.

Variance component estimation

Variance components for FA_GC and FA_FTIR traits were estimated by restricted maximum likelihood (REML) using three mixed linear models that differed in the relationship matrix used.

The following mixed linear model was implemented:

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

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 $\mathbf{N}(0, \mathbf{I}\sigma^2_e)$ 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:

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

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

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

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

Breeding Value Predictions

Breeding values were predicted using model [1] with the traditional (ABLUP) and the two GS (GBLUP and ssGBLUP) approaches, respectively. From the 769 animals with genotypes and own phenotypes, records of the 100 youngest ewes (born after November 2012) were masked in order to mimic the condition of candidate animals.

Accuracy of breeding values animals were estimated as:

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

where SEP is the standard error of prediction, derived from the diagonal element of the LHS inverse of the mixed model equations. In order to ensure a fair comparison among accuracies obtained in the three different methods, the same variance components (the ones estimated with ABLUP) were used in the three approaches for breeding values predictions and computation of accuracy.

Moreover, in order to reduce GEBV bias in the ssGBLUP, a weighing factor omega (ω) equal to 0.95 was applied in construction of the inverse of the **H** matrix (Tsuruta et al., 2013):

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

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

Being FA genetically correlated traits (Carta et al. 2008; Sanchez et al., 2010), GEBV accuracy may be modified if a multiple trait approach is used. However, considering the large number of FA analyzed in the present study, the effect of genetic correlations among FA on GEBV accuracy was investigated by a series of bivariate analyses using the ssGBLUP approach. Thus for each single FA, two accuracies were available: one obtained with the

univariate approach and another obtained as the mean accuracy of the 17 bivariate analyses involving that specific FA.

RESULTS

Basic statistics (**Table 3**) of the milk FA_GC and FA_FTIR, and coefficients of determination of the regression between FA_GC and FA_FTIR ($R^2_{GC\text{-}FTIR}$) essentially confirm previous reports on dairy sheep (Ferrand-Calmels et al., 2014; Caredda et al., 2016; Correddu et al., 2018).

Genetic Parameters of Milk Fatty Acid profile

Heritability estimates showed relevant variations across different FA, phenotyping methods (GC vs FTIR), and models (**Table 4**). Overall, low to moderate values were obtained, apart from C4:0 and C16:0. Largest heritabilities were observed for the C4:0 FA_FTIR in the GBLUP (0.56), and for the C16:0 FA_GC in the ABLUP (0.46) (**Table 4**), respectively. A similar pattern was detected for intra-flock heritabilities (**Table 5**), that exhibited larger values compared to h^2, especially for FA characterized by a larger flock-test date variance (**Table 6**) (e.g. C18:0, C18:1t11, C18:1c9, C18:2ω6, C18:3ω3, CLAc9,t11 and ω6:ω3). Lowest estimates (nearly zero) were obtained for SFA and MUFA in the ABLUP, and for C18:2ω6 in all the three prediction models for FA_FTIR.

The considered phenotype, FA_GC or FA_FTIR, affected the h^2 results, even though no defined patterns were observed. For example, FA_GC estimates were markedly larger than FA_FTIR for C16:0 in all models (**Table 4**). On the contrary, FA_GC estimates were smaller for C4:0, especially for the two genomic models. It should be also noticed that the h^2 estimated with ABLUP were close to zero for SFA and MUFA using FA_FTIR phenotypes. In order to highlight recurrent pattern in the additive genetic component, σ^2_a for FA_GC was regressed onto σ^2_a for FA_FTIR (**Figure 1**) for the three models used. Additive genetic

variances estimated using FA_GC and FA_FTIR were from moderately to strongly correlated depending on (co)variance matrix used.

The h^2 and h^2_{IF} estimated with ABLUP were generally lower than those obtained with the two genomic approaches, both for FA_GC and FA_FTIR (**Tables 4** and **5**). Exceptions were the C16:0 and C18:0, that showed an opposite behavior. In particular, largest differences were found for C4:0 and C16:0 as individual FA, and for SFA and MUFA as groups, respectively. GBLUP and ssGBLUP estimates were very similar (**Table 4,** and **5**). Differences among h^2 estimates were mainly due to changes in the additive genetic components as shown in Appendix (**Table A2**). In particular, for most of the FA analyzed no differences in σ^2_a were observed with genomic methods. In our study, largest values of R^2 of the regression between σ^2_a FA_GC and σ^2_a FA_FTIR were observed using genomic models (0.84 and 0.91) in comparison to the traditional pedigree models (0.45, **Figure 1**). Finally, σ^2_a estimates of C16:0, C18:0, C18:1c9, SFA and MUFA were always higher for FA_GC than FA_FTIR.

The FTD contribution to total phenotypic variance was moderate to large. It was on average >0.5 across all different prediction models and phenotypes (**Table 6**), ranging from 0.17 to 0.88. The variance components for FTD were nearly the same in the three different models, while differences (up to 15%) were highlighted between FA_GC and FA_FTIR (e.g. C4:0, C14:0, C18:1t11, C18:2ω6, C18:3ω3, CLA, PUFA, ω3: ω6 and TFAnoVA).

Accuracy of EBV and GEBV predictions

Accuracies of breeding values were low to moderate, ranging from 0.05 to 0.84, and from 0.02 to 0.45 in the oldest and youngest cohort, respectively (**Table 7**). The palmitic acid (C16:0) showed the largest accuracy for FA_GC across the different prediction models, both for oldest (0.84) and youngest animals (0.45). The largest GEBV accuracy for FA_FTIR was

observed for the butyric acid (C4:0). The linoleic acid (C18:2ω6) showed the lowest accuracy in most of the scenarios considered. Accuracies of FA groups reflected their composition, with saturated FA showing the lowest and PUFA and TFAnoVA the highest accuracies, respectively.

The cohort of animals with own phenotypes exhibited larger prediction accuracies compared to young animals without phenotype (overall average difference +0.24) in all scenarios (**Table 7**). The largest difference (+0.30) was observed for the stearic acid (C18:0), whereas the smallest for the saturated FA group (+0.09).

Differences were also observed between the phenotype (FA_GC vs FA_FTIR) for all the three models and for the two cohorts of animals (**Table 7**), even though without a defined pattern. The major difference between FA_GC and FA_FTIR were observed in the older cohort (from -0.23 up to 0.48 for C6:0 and C16:0, respectively). Accuracies differed mainly in the ABLUP approach for both young and older cohorts. The difference between FA_GC and FA_FTIR tended to reduce in genomic methods applied to young animals (**Table 7**). Regardless of the statistical model used, the largest difference between FA_GC and FA_FTIR was observed for the C16:0 (on average difference of 0.45 ad 0.18 for old and young animals, respectively). Relevant differences (at least >15%) between FA_CG and FA_FTIR were observed also for C18:0, C18:2ω6, SFA and MUFA both in older and younger animals.

As far as the three models are concerned, genomic prediction accuracies were constantly higher than in ABLUP (**Table 7**). In particular, differences between ABLUP and genomic methods were larger in young animals. In this cohort, positive changes up to +0.12 (+0.17) and +0.10 (+0.21) were observed in the comparison GBLUP-ABLUP (ssGBLUP-ABLUP) for FA_GC and FA_FTIR, respectively. Among the two genomic approaches, the ssGBLUP accuracies were always larger than GBLUP ones both in young and old animal cohorts.

Bivariate GEBV accuracies for the young animals were generally of the same magnitude of those obtained using the univariate approach (**Table 8**). Differences were exhibited by some FA_FTIR: in particular the GEBV accuracy for linoleic, SFA and MUFA showed an increase (>0.03) moving from univariate to multivariate approach.

DISCUSSION

Fatty acid composition is a key feature in defining sheep milk nutritional quality. Its genetic improvement is an appealing option for enhancing market value of dairy sheep products. However, breeding for milk FA composition in sheep is hampered by difficulties in phenotyping and in implementing appropriate selection strategies. Use of equations for predicting FA from milk FTIR spectra is widely recognized as a cost-effective solution for obtaining FA profiles in milk of different ruminant species (Ferrand-Calmels et al. 2014). At the same time, early experiences of genomic selection on meat, wool (Daetwyler et al., 2012) and dairy sheep (e.g Duchemin et al., 2012; Legarra et al. 2014; Baloche et al. 2014) have reported an increase of breeding value accuracy and selection response compared to the traditional pedigree-based method.

Results of the present study, although referred to a sample of limited size, showed an effect of both investigated phenotypes (i.e. FA_GC or FA_FTIR) and of the information used to structure the genetic covariance among animals (pedigree, genomic, or both) on genetic parameter estimates and breeding value prediction accuracies.

Genetic Parameters of Milk Fatty Acid profile

Heritability estimates based on pedigree models were consistent with a previous work carried out on a similar data set (Correddu et al., 2018), whereas genomic based h^2 resulted higher and lower than pedigree based for saturated (<C14) and unsaturated FA, respectively. 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

and causative mutations that makes **G** unable for capturing all the genetic variance of the trait in comparison with **A**. Such a limitation of **G** is likely to be more pronounced in sheep populations that, in comparison to cattle, are characterized by a lower LD at relatively short distance (Kijas et al., 2014). However, the reliability of pedigrees in sheep is often questionable due to the uncorrected parentage assignment or the high number of unknown parents. Thus, the use of genomic relationship matrices could allow to estimate more accurately relationship among animals because the realized fraction of allele shared between individual is directly computed (Hayes and Goddard, 2008; Legarra et al., 2014), with subsequent large heritability estimates.

Accuracy of EBV and GEBV predictions

In our study breeding value accuracies for FA milk profile were low to moderate. Considering the sample size, the genetic architecture of milk FA composition, and the number of records per ewe our results are in accordance to genomic selection theory (Goddard and Hayes, 2009). Animals with their own phenotypes exhibited larger accuracies compared to young animals. However, the addition of genotype information to the breeding value prediction resulted in an improvement of accuracy, also in latter group. Other studies in sheep underlined the higher accuracy of genomic methods compared to the pedigree-based approach for milk and meat production traits (Daetwyler et al., 2012; Legarra et al., 2014; Baloche et al., 2014). Moreover, GS studies carried out in beef cattle on muscle FA composition reported for some of FA investigated also in this study a similar pattern of GEBV accuracy (Chang et al., 2015; Chiaia et al., 2017; Zhu et al., 2017).

The similar magnitude of GEBV accuracy for FA_FTIR and FA_GC is an interesting for a possible implementation breeding program for milk FA composition in dairy sheep, due to the considerable reduction of phenotyping cost. The predictive ability of FTIR spectra ($R^2_{GC\text{-}FTIR}$, 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.

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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

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

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 ($R^2_{CG-FTIR}$).

		FA_GC		FA_FTIR		
Fatty Acid	Trait	Mean	SD	Mean	SD	$R^2_{CG-FTIR}$
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.

	Ablup		Gblup		ssGblup	
Trait	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.

	Ablup		Gblup		ssGblup	
Trait	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

	Ablup		Gblup		ssGblup	
Trait	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.

[2]Cohort of sheep born after November 2012 with SNP genotypes available and own milk FA records masked to mimic a candidate set of younger sheep.
[3]Sum of the individual saturated fatty acids.
[4]Sum of the individual monounsaturated fatty acids.
[5]Sum of the individual polyunsaturated fatty acids; odd- and branched-chain fatty acids.
[6]Ratio between the sum of individual PUFA ω6 fatty acids and the sum of individual PUFA ω3 fatty acids.
[7]Trans Fatty Acid (TFA) without Vaccenic acid (VA).
[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.

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).

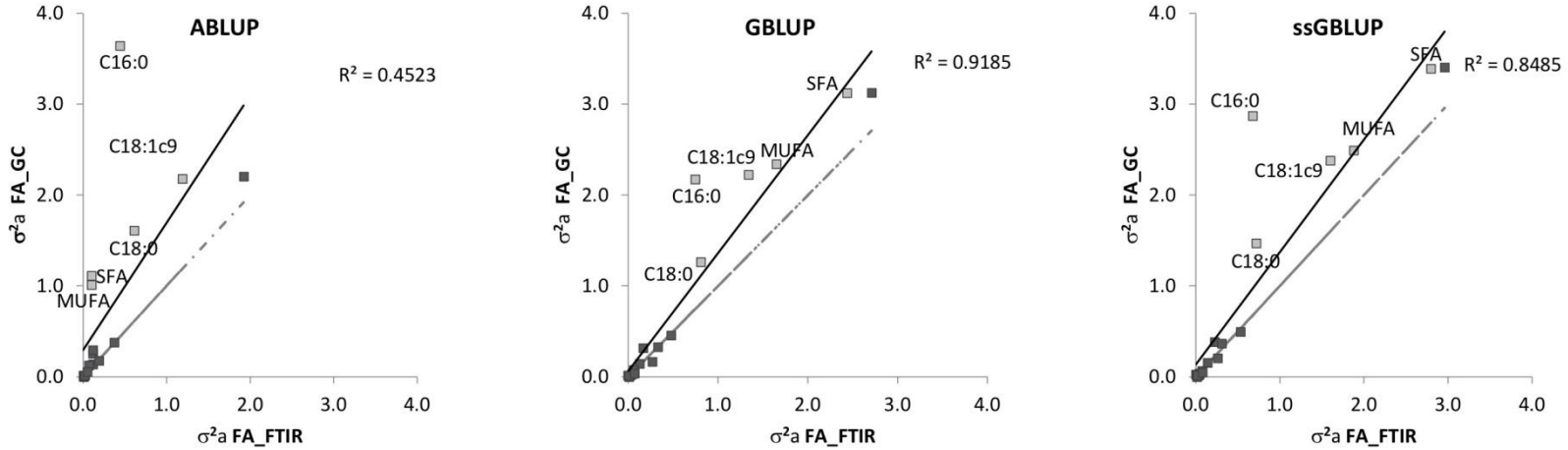
	FA_GC			FA_FTIR		
Trait	Mean	s.d.	Diff.[1]	Mean	s.d.	Diff.[1]
C4_0	0.35	0.01	0.00	0.35	0.01	-0.02
C6_0	0.28	0.02	0.01	0.32	0.02	-0.02
C8_0	0.33	0.02	0.00	0.33	0.01	-0.01
C10_0	0.34	0.01	-0.01	0.34	0.01	-0.01
C12_0	0.34	0.01	0.00	0.34	0.01	-0.01
C14_0	0.32	0.02	0.00	0.29	0.02	0.01
C16_0	0.43	0.01	-0.02	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 CAPTION

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.



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501 **APPENDIX**

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 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

[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.

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