



**Relationship between inbreeding and milk production traits
in two Italian dairy sheep breeds**

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4 1 INBREEDING DEPRESSION FOR MILK TRAITS IN DAIRY SHEEP5
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8 3 **Relationship between inbreeding and milk production traits in two Italian dairy sheep**
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40 17 **ABSTRACT**41
42
43 18 The effects of inbreeding in livestock species breeds have been well documented and
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45 19 they have a negative impact on profitability. The objective of this study was to evaluate the
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47 20 levels of inbreeding in Sarda (SAR, n = 785) and Valle del Belice (VdB, n = 473) dairy sheep
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49 21 breeds and their impact on the milk production traits. Two inbreeding coefficients (F) were
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51 22 estimated: using pedigree (F_{PED}), or runs of homozygosity (ROH) (F_{ROH}) at different minimum
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53 23 ROH length. Ewes were genotyped with 38,779 single nucleotide polymorphisms mapped on
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55 24 the last available release. A mixed-linear model was used to evaluate the impact of inbreeding
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57 25 coefficients on production traits within each breed. VdB showed larger inbreeding coefficients
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4 26 compared to SAR, with both breeds showing lower estimates as the minimum ROH length
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6 27 increased. Significant inbreeding depression was found only for milk yield, with a loss of
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8 28 around 7 g/d (for SAR) and 9 g/d (VdB) for a 1% increase of F_{ROH} . The present study confirms
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10 29 how the use of genomic information can be used to manage intra-breed diversity and to
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12 30 calculate the effects of inbreeding on phenotypic traits.
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17 32 **1 | INTRODUCTION**

19 33 A main cause of inbreeding occurrence in livestock populations is the increase of
20 34 average relationship among animals due to implementation of breeding programs. A negative
21 35 consequence is represented by the inbreeding depression, i.e., a general reduction of animal
22 36 fitness and performances, together with an increased frequency of genetic defects. Inbreeding
23 37 depression can be estimated using the individual inbreeding coefficient (F), defined as the
24 38 probability that both alleles at any locus within an individual are identical by descent. Values
25 39 of F have been traditionally computed from the pedigree information (F_{PED}) (Lynch and Walsh,
26 40 1998). However, pedigrees can contain several errors (Weller et al., 2004; Legarra et al., 2014)
27 41 or they cannot even be recorded (Mészáros et al., 2015). Pedigree error rate of approximately
28 42 10% was reported in Mexican Holstein population (García-Ruiz et al., 2019). This problem is
29 43 exacerbated in some situations as, for example, the semi-extensive sheep farming systems,
30 44 where relationship recording is hampered by the limited use of artificial insemination (AI) and
31 45 the simultaneous presence of more rams in the same flock (Hayes & Goddard, 2008). Larger
32 46 unknown fatherhood rates were reported for Latxa (around 50%) and Manech/Basco-Béarnaise
33 47 (around 20%) sheep populations (Legarra et al., 2014).
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54 48 The availability of high throughput single nucleotide polymorphism (SNP) platforms
55 49 for many livestock species has opened new perspectives for an accurate estimation of
56 50 relationship and inbreeding also in difficult conditions. Among different metrics that can be
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4 51 derived from genomic information, Runs of Homozygosity (ROH), i.e., contiguous stretches of
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6 52 homozygous genotypes that occur in an individual due to parental transmission of identical
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8 53 haplotypes (Gibson et al., 2006), are becoming a widely adopted genomic tool to study the
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10 54 genetic structure of populations (Mastrangelo et al., 2018; Macciotta et al., 2021). They have
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12 55 been used to detect selection signatures, deleterious mutations (e.g., Sumreddee et al., 2019), to
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14 56 develop association studies with production traits (Cesarani et al., 2021), and to study the
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16 57 temporal framework of inbreeding events (Gibson et al., 2006; Bosse et al., 2021). In particular,
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18 58 the ROH-based inbreeding coefficient (F_{ROH}) is considered a powerful method of detecting
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20 59 inbreeding effects among several alternative estimates of inbreeding (e.g., Keller et al., 2011;
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22 60 Bjelland et al., 2013). Inbreeding depression at genome wide (Martikainen et al., 2017) or
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24 61 chromosomal (Martikainen et al., 2018) levels was estimated using F_{ROH} coefficients in Finnish
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26 62 Ayrshire cattle.

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32 63 Previous studies already investigated the inbreeding effects on production traits in sheep
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34 64 breeds (Barczak et al., 2009; Dorostkar et al., 2012; Kiya et al., 2019). Most of these analyses
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36 65 in sheep were carried out using pedigree-based inbreeding coefficients and growth traits
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38 66 (Gholizadeh and Ghafouri-Kesbi, 2016). More recently, genomic and pedigree inbreeding
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40 67 depression was estimated for semen traits in the Basco-Béarnaise dairy sheep breed (Antonios
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42 68 et al., 2021), whereas inbreeding depression from homozygous regions was studied for litter
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44 69 size in six different sheep breeds (Tao et al., 2021a).

47 70 In this work, the level of inbreeding and the inbreeding depression on milk production
48
49 71 traits in two Italian dairy sheep breeds is estimated using pedigree and genomic information.

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54 73 **2 | MATERIALS AND METHODS**

56 74 Animal Care and Use Committee approval was not needed as data were obtained from
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58 75 preexisting databases.

2.1 | Sampling, genotyping, and quality control

A sample of 785 and 473 ewes of Sarda (SAR) and Valle del Belice (VdB) dairy sheep breeds, respectively, was used for this study. SAR is the largest Italian sheep breed with about 3 million animals (Casu et al., 2022); VdB is the main breed reared for milk production in Sicily, the biggest Italian Island, with about 154,000 heads (www.vetinfo.it). Animals were genotyped with the Infinium Ovine SNP50 v1 BeadChip (Illumina Inc., San Diego, California). Markers were mapped on the 4.0 version of the *Ovis aries* assembly. Quality control was performed within each breed with the following parameters: call rate greater than 0.975, minor allele frequency greater than 0.01, *P*-value for the deviation from the Hardy-Weinberg equilibrium greater than 0.01. Moreover, call rate for each ewe was greater than 0.95. After quality control, 38,779 common SNPs were retained for the analyses.

2.2 | Phenotypic data

For all genotyped ewes, daily milk production traits (i.e., kg of milk per day, MY; fat percentage, FP; and protein percentage, PP) were available (Table 1). Average values for SAR were 1.75 ± 0.44 (MY), 5.96 ± 1.41 (FP), and 5.44 ± 0.71 (PP). VdB showed lower MY (1.39 ± 0.54), but larger fat (6.95 ± 1.05) and protein (5.73 ± 0.66) percentages. Records from primiparous ewes were 21 and 37% for SAR and VdB, respectively. As far as the lactation stage was concerned, VdB had more available data at the beginning of lactation (76% of records in the first class of days in milk), whereas SAR data was more concentrated at the middle of lactation (55% of the observations in the third class of days in milk).

2.3 | Inbreeding estimation

Two different inbreeding coefficients were estimated: i) pedigree inbreeding (F_{PED}), calculated using the official pedigrees of the two breeds through inbupgf90 (Mistzal et al.,

2014); ii) ROH-based inbreeding (F_{ROH}), computed as the ratio between the sum of consecutive ROH length per animal and the total genome length. Consecutive ROH were detected using the R package detectRUNS (Biscarini et al., 2018), for each breed separately, with the following criteria: minimum 15 homozygotes SNPs spanned in at least 1 Mb; no heterozygote or missing markers allowed. According to different minimum ROH length size, five different F_{ROH} coefficients were estimated: i) F_{ROH1} , using ROH > 1 Mb; ii) F_{ROH2} , using ROH > 2 Mb; iii) F_{ROH4} , using ROH > 4 Mb; iv) F_{ROH8} , using ROH > 8 Mb; v) F_{ROH16} , using ROH > 16 Mb.

2.4 | Inbreeding depression estimation

The extent of inbreeding depression was estimated separately by breed through the following mixed-linear model:

$$y = \text{herd} + \text{parity} + \text{month} + \text{DIM} + \text{sampling} + \text{inbreeding} + \text{animal} + e \quad (1)$$

where:

y was the considered milk trait (i.e., kg of milk per day, MY; fat percentage, FP; and protein percentage, PP); herd was the random effect of the herd (45 levels and 4 levels for SAR and VdB, respectively); parity was the fixed effect of parity (2 levels: primiparous and pluriparous); month was the fixed effect of lambing month (6 and 9 levels for SAR and VdB, respectively); DIM was the fixed effect of days in milk (4 levels: 1 = DIM ≤ 150; 2 = DIM > 150 and DIM ≤ 200; 3 = DIM > 200 and DIM ≤ 250; 4 = DIM > 250); sampling was the random effect of the sampling month; inbreeding was the considered inbreeding coefficients (i.e., F_{PED} and the five F_{ROH}); animal was the random additive genetic effect; e was the random residual effect. The extent of inbreeding depression at chromosome level was also investigated by fitting the chromosome-wide ROH-based coefficients. The animal effect was modeled using the genomic relationship matrix (GRM) built according to VanRaden (2008).

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4 124 Phenotypes for SAR animals were sampled within only year (2014), whereas for VdB the
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6 125 phenotypes were retrieved from 2005 to 2012. For this reason, the mixed model for VdB also
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8 126 included the year as fixed effect. The mixed-linear models were performed using the SAS
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10 127 PROC MIXED (SAS Inc. 2012).

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15 129 **3 | RESULTS AND DISCUSSION**

17 130 **3.1 | Inbreeding estimation**

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20 131 For SAR, the average F_{ROHI} was $8.5\pm 4.3\%$, with a maximum value of 34.87%, whereas
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22 132 the average F_{PED} value was $5.3\pm 6.4\%$, considering only the animals with inbreeding, or
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24 133 $1.8\pm 4.5\%$, considering all animals in the analysis (Table 1). For VdB, the average F_{ROHI} and
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26 134 F_{PED} values were $10.87\pm 6.38\%$ (max 36.96%) and 15.3 ± 8.1 ($8.1\pm 9.6\%$ considering all
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28 135 animals), respectively. As expected, in both breeds, average F_{ROH} values decreased as the
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30 136 minimum ROH length increased, with VdB showing constantly higher values than SAR. This
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32 137 decreasing trend is justified by the lower number of ROH detected as the minimum length
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34 138 increases. F_{ROHI} values estimated in the present study for SAR are in agreement with other
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36 139 reports in Sarda dairy sheep (Cesarani et al., 2022), but they are higher than those estimated for
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38 140 Sarda dairy rams (4.1%; Cesarani et al., 2019). The difference with the coefficients estimated
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40 141 in males can be identified in the use of different SNP sets and the consideration of ROH mapped
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42 142 on chromosome OAR 27 in the present study. A slightly lower F_{ROHI} value was estimated in
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44 143 VdB ($8.4\pm 6.1\%$ vs $10.9\pm 6.4\%$ of the present study) by Mastrangelo et al. (2017), who computed
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46 144 ROH using a different software and different parameters (e.g., minimum number of 40 SNPs).
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48 145 Mastrangelo et al. (2018) reported ROH-based inbreeding estimates for both breeds analyzed
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50 146 in this study: while F_{ROHI} estimate for VdB ($9.9\pm 7.7\%$) was similar to the one computed here,
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52 147 value for SAR ($4.1\pm 3.5\%$) was half of the one estimated in the present work. Beside a different
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54 148 number of SNPs and animals considered in their study, also in Mastrangelo et al. (2018), the
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4 149 sexual OAR27 was excluded and different settings were used to define a ROH. Lower
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6 150 inbreeding coefficients were estimated in other sheep breeds such Lacaune ($F_{\text{ROH}} = 0.04$, and
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8 151 $F_{\text{PED}} = 0.03$; Rodríguez-Ramilo et al., 2019) and Latxa Cara Rubia ($F_{\text{ROH}} = 0.03$, and $F_{\text{PED}} =$
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10 152 0.02 ; Granado-Tajada et al., 2020). However, consistent with our results, Nosrati et al. (2021)
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13 153 found F_{ROH} values ranging from 0.9% to 22% in Southwest European sheep breeds.
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15 154 Table 2 shows the correlations among the different inbreeding coefficients within each
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17 155 breed. All correlations were highly significant. In SAR, F_{PED} showed larger correlation with
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19 156 F_{ROH} as the minimum ROH length increased. This pattern was already reported in sheep (e.g.,
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21 157 Rodríguez-Ramilo et al., 2019) and cattle (e.g., Hidalgo et al., 2021). It is interesting to notice
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23 158 the negative correlation between F_{PED} and the five F_{ROH} coefficients found for VdB. According
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25 159 to the theory and to the reports available in literature, this result was quite unexpected; however,
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27 160 this negative correlation confirmed the poor quality of the available pedigree for the VdB breed
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29 161 and the higher reliability of the genomic-based inbreeding (Biscarini et al., 2020). As expected,
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31 162 the five F_{ROH} coefficients were largely and positively correlated each other. Similar correlation
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33 163 estimates among F_{PED} , and F_{ROH} found for SAR were reported for French (Rodríguez-Ramilo
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35 164 et al., 2019) and Laxta (Granado-Tajada et al., 2020) sheep breeds. Inbreeding coefficients are
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37 165 related to selection intensity and population structure and the accuracy of their estimates depend
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39 166 on reliability and completeness of data. However, the latter have a stronger impact on F_{PED}
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41 167 which strongly depends on depth and completeness of pedigree. The high dependency of F_{PED}
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43 168 on quality of data is confirmed by the average F_{PED} value highlighted in this study: the very
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45 169 high standard deviation is due to coefficients equal to zero for some animals that have
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47 170 incomplete or short pedigree. In particular, underestimated pedigree-based inbreeding
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49 171 coefficients can be caused by pedigrees with large number of missing ancestors (Barczak et al.,
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51 172 2009). On the contrary, to estimate inbreeding coefficients using genomic information (e.g.,
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53 173 ROH) there is no need to have known relatives of animals and therefore they can be estimated
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4 174 also in populations in which pedigree is not accurate or not even recorded. Moreover, several
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6 175 studies showed that inbreeding based on ROH provides a better measure of individual
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8 176 inbreeding than using pedigree information (Ferenčaković et al., 2013; Forutan et al., 2018).
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10 177 Thus, F_{ROH} has been largely adopted as inbreeding coefficients to study depression phenomena
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13 178 in cattle (e.g., Doekes et al., 2019; Hidalgo et al., 2021; Pilon et al., 2021) and sheep (Antonios
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15 179 et al., 2021; Tao et al., 2021a).

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20 181 **3.2 | Inbreeding depression estimation**

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22 182 Different studies on cattle showed that genomic estimates of inbreeding can be used
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24 183 instead of pedigree estimates to calculate the effects of inbreeding on milk production traits
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26 184 (Bjelland et al 2013; Pryce et al., 2014). However, investigations in sheep using genomic data
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29 185 have been mainly focused on fertility and growth traits, instead of on milk production traits.

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31 186 The estimates of inbreeding depression from the mixed model analysis always exhibited
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33 187 a negative sign even if coefficients for FP and PP were not statistically significant (Table 3).
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35 188 Values are expressed as the change in the phenotype for a 1% increase in inbreeding
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38 189 coefficients.

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40 190 Both F_{PED} and all F_{ROH} were significantly associated to MY in SAR breed, whereas only
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42 191 the F_{ROH} coefficients were significantly associated to MY in VdB breed (F_{PED} was not
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44 192 significant for MY in VdB). At chromosome level (Supplementary Table 1), nine autosomes
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46 193 showed signals of inbreeding depression. Significant coefficients were estimated in SAR on
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48 194 OARs 3, 21, and 26 for MY and OARs 6 and 26 for PP, respectively. The significant signals
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50 195 for VdB were found on OARs 1, 2, 11, and 25 (MY) and on OAR18 (FP). Raadsma et al. (2009)
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52 196 carried out a meta-analysis on quantitative trait loci (QTL) affecting milk traits in sheep. These
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54 197 authors reported regions significantly affecting milk production in four chromosomes
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56 198 highlighted in the present study. In particular, these authors found two regions on OAR2, six
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4 199 regions on OAR3, one region on OAR6, and two regions on OAR25 associated with fat, protein,
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6 200 or milk production. Chromosome 6, significant for PP in SAR, is well-known to present
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8 201 important quantitative trait loci (QTL) affecting milk production traits in sheep and cattle (e.g.,
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10 202 Diez-Tascón et al., 2001; Kucerova et al., 2005; Arnyasi et al., 2009). Moreover, Usai et al.
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12 203 (2019) found on OAR6 three significant regions in a genome-wide analysis carried out in Sarda
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14 204 dairy sheep. Two of these regions were identified by only one SNP each, whereas the third one
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16 205 included 802 SNPs. The latter was a long region (36.2–105.2 Mb) significant for both fat and
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18 206 protein contents; within this interval, the authors found the strongest signal for protein content.
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20 207 In this same position, a QTL for protein content was reported also for Churra sheep ().
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22 208 Interestingly, the inbreeding coefficients estimated in OAR26 showed a negative effect for both
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24 209 MY and PP in SAR breed. In this chromosome, a QTL involved in the udder attachment, which
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26 210 could be associated with milk production traits, has been found in Spanish Churra dairy sheep
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28 211 (Gutiérrez-Gil et al., 2008).

212 The negative effect of inbreeding depression showed a reduction in MY ranging from 6
213 to 10 g/d (for SAR) and from 9 to 11 g/d (for VdB) according to the considered coefficients.
214 This would correspond to a decrease of 1.3-2.1 kg and of 1.9-2.3 kg in 210-day lactation in
215 SAR and VdB, respectively. Due to the lack of estimates of genomic inbreeding depression on
216 milk production traits in sheep, our results were compared to reports in cattle. Bjelland et al.
217 (2013) reported a decrease in total milk yield to 205 d postpartum of 20 kg per 1% increase in
218 F_{ROH} in Holstein cattle. Moreover, Doekes et al. (2019) found that an increase of 1% in F_{ROH}
219 in Dutch Holstein-Friesian dairy cattle resulted in 36.3 kg decrease in 305-day milk yield. These
220 authors reported an average milk production of 8,091 kg and, thus, the milk loss associated with
221 inbreeding depression represent less than 0.5% of the total yield. In our case, the milk loss is
222 on percentage slightly higher: a loss of about 2 kg represents the 0.8% of the average milk yield
223 (250 kg) of Italian dairy sheep.

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4 224 Since ROH length is an indicator of the age of inbreeding (short ROH are associated
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6 225 with old events, whereas long ROH with recent events), the five F_{ROH} coefficients indicate the
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8 226 effect on old and recent inbreeding. For the three traits in both breeds, the coefficient estimated
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10 227 for F_{ROH16} were the largest, indicating a more negative effect of recent inbreeding compared to
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12 228 the old one. The more unfavorable effect of recent inbreeding is in agreement with a recent
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14 229 study in Basco-Béarnaise dairy sheep breed on motility traits (Antonios et al., 2021). These
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16 230 authors reported coefficients of -0.905 and -1.534 for ROH_{Total} (using all ROH) and $F_{ROHRecent}$
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18 231 ($ROH > 17$ Mb), respectively. Tao et al. (2021b) reported larger negative effects of F_{ROH}
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20 232 computed using only longer ROH (i.e., associated with recent inbreeding) for body weight in
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22 233 Qira black sheep: -0.60 (0.18) and -0.84 (0.40) kg for 1% increase in F_{ROH} estimated using
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24 234 ROH between 5 and 20 Mb and > 20 Mb, respectively. Recently, the effects of F_{ROH} on litter
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26 235 size were analyzed in six sheep breeds: Wadi, Hu, Icelandic, Finnsheep, Romanov, and Texel
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28 236 (Tao et al., 2021a). These authors found negative estimates (and significantly different from
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30 237 zero) for F_{ROH} computed using only regions between 4 and 8 Mb, or higher than 8 Mb, in Hu
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32 238 sheep breed. On the contrary, Doekes et al. (2019) stated that no clear differences between old
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34 239 and recent inbreeding were found on inbreeding depression for yield, fertility, and udder traits
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36 240 in Dutch Holstein–Friesian dairy cattle. Moreover, a negative effect of both total (i.e., based on
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38 241 ROH with a minimum length of 4 Mb) and recent (i.e., based on ROH with a minimum length
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40 242 of 17 Mb) F_{ROH} was reported on semen motility by Antonios et al. (2021). Several authors
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42 243 reported that this result can be explained considering the “purging effect”. Inbreeding arising
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44 244 from a distant common ancestor should have less effect on fitness compared with inbreeding
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46 245 from a recent common relative because natural selection over long periods of time should act
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48 246 to purge deleterious alleles from the population (Holt et al., 2005). However, it should be
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50 247 pointed out that very short ROH are likely to be false positive.
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4 248 The small number of signals of inbreeding depression can be associated to the general
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6 249 limited magnitude of the selection pressure in sheep compared to cattle. The population
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8 250 structures of both breeds are not organized in large half-sib families, as the case of the dairy
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10 251 cattle populations, and genetic connections among flocks are rather poor because of the limited
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12 252 exchange of rams and use of AI. Moreover, the lack of significance for coefficients of the mixed
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14 253 model can be likely attributed to a lack of statistical power due to the small sample size. Also,
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16 254 a poor quality of the data, especially for the pedigree in VdB as confirmed also by the negative
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18 255 correlation between F_{PED} and F_{ROH} values, could have had an effect. In fact, animals are mainly
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20 256 raised in semi-extensive farms, and the pedigree registration is often not accurate because the
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22 257 matings are not under control of the farmers. However, most of the paper analyzing the
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24 258 inbreeding depression in cattle and sheep, reported significant coefficients for few analyzed
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26 259 traits or breeds. For example, Antonios et al. (2021) studied the effect of 8 different inbreeding
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28 260 coefficients on 3 different traits but found significance just for 5 out of 24 coefficients tested.
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30 261 Also, Tao et al. (2021a) found significant inbreeding depression for just one of the six analyzed
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32 262 sheep breeds, whereas only 11 out of 28 were significant in Tao et al. (2021b). Finally, Hidalgo
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34 263 et al. (2021) analyzed the inbreeding depression in Romosinuano cattle breed, and they found
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36 264 negative coefficients for both pedigree-based and ROH-based inbreeding; however, only for
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38 265 two coefficients, the F_{PED} computed for ungenotyped animals, were significant, whereas the
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40 266 other six inbreeding coefficients computed for genotyped animals were not significantly
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42 267 different from zero.

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269 **4 | CONCLUSIONS**

270 In this study, we have reported the estimates of inbreeding depression on milk
271 production traits in Sarda and Valle del Belice dairy sheep using pedigree and genomic
272 information. Although the magnitude of the inbreeding depression measured by the F_{ROH} is

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4 273 rather small, the effect is not negligible with current inbreeding level (about 1.5-2.3 kg of milk
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6 274 loss over the whole lactation of 210 d for a 1% increase in the inbreeding coefficient). The
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8 275 present study confirmed how the use of genomic information instead of pedigree estimates can
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10 276 be also used to monitor inbreeding, to manage intra-breed diversity and to calculate the effects
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13 277 of inbreeding on phenotypic traits.
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448 **Table 1.** Basic statistics of the analyzed dataset and inbreeding coefficients (F) estimated in
 449 the two sheep breeds using pedigree (F_{PED}) and genomic data (F_{ROH}).

	Sarda	Valle del Belice
Data, n		
Primiparous	168	177
Pluriparous	617	296
<hr/>		
DIM class 1	73	360
DIM class 2	214	68
DIM class 3	435	35
DIM class 4	63	10
<hr/>		
Traits		
Milk, kg/d	1.75±0.44	1.39±0.54
Fat, %	5.96±1.41	6.95±1.05
Protein, %	5.44±0.71	5.73±0.66
<hr/>		
Inbreeding¹, %		
F_{PED}	5.3±6.44 (265)	15.3±8.1 (250)
F_{ROH1}	8.63±4.24 (785)	10.87±6.38 (473)
F_{ROH2}	7.21±4.21 (784)	9.52±6.38 (473)
F_{ROH4}	5.66±4.02 (782)	7.88±6.23 (472)
F_{ROH8}	3.64±3.51 (757)	5.86±5.76 (454)
F_{ROH16}	2.41±2.84 (496)	4.63±4.71 (315)

450 ¹ Mean±SD refer to values of animals with inbreeding different from 0 reported in parenthesis.

452 **Table 2.** Correlations (above diagonal) and their significance (below diagonal) among pedigree
 453 (F_{PED}) and genomic (F_{ROH}) inbreeding coefficients.

	F_{PED}	F_{ROH1}	F_{ROH2}	F_{ROH4}	F_{ROH8}	F_{ROH16}
<i>Sarda</i>						
F_{PED}		0.44	0.45	0.426	0.436	0.58
F_{ROH1}	***		1.00	0.99	0.96	0.86
F_{ROH2}	***	***		0.99	0.96	0.87
F_{ROH4}	***	***	***		0.98	0.90
F_{ROH8}	***	***	***	***		0.94
F_{ROH16}	***	***	***	***	***	
<i>Valle del Belice</i>						
F_{PED}		-0.08	-0.08	-0.09	-0.09	-0.08
F_{ROH1}	**		1.00	0.99	0.96	0.91
F_{ROH2}	**	***		0.99	0.97	0.92
F_{ROH4}	**	***	***		0.99	0.94
F_{ROH8}	**	***	***	***		0.97
F_{ROH16}	*	***	***	***	***	

454 *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$;

456 **Table 3.** Inbreeding depression and standard errors for milk production traits using pedigree
 457 (F_{PED}) and genomic data (F_{ROH}).

	Milk (kg/d)	Fat (%)	Protein (%)
<i>Sarda</i>			
F_{PED}	-0.006(0.002)*	-0.007(0.009) ^{NS}	-0.006(0.005) ^{NS}
F_{ROH1}	-0.007(0.003)*	-0.005(0.011) ^{NS}	-0.007(0.006) ^{NS}
F_{ROH2}	-0.007(0.003)*	-0.005(0.011) ^{NS}	-0.008(0.006) ^{NS}
F_{ROH4}	-0.007(0.003)*	-0.005(0.011) ^{NS}	-0.007(0.006) ^{NS}
F_{ROH8}	-0.008(0.003)*	-0.005(0.013) ^{NS}	-0.008(0.007) ^{NS}
F_{ROH16}	-0.010(0.004)*	-0.014(0.017) ^{NS}	-0.013(0.009) ^{NS}
<i>Valle del Belice</i>			
F_{PED}	-0.377(0.236) ^{NS}	-0.036(0.462) ^{NS}	-0.138(0.282) ^{NS}
F_{ROH1}	-0.010(0.004)**	-0.006(0.007) ^{NS}	-0.002(0.004) ^{NS}
F_{ROH2}	-0.009(0.004)*	-0.006(0.007) ^{NS}	-0.003(0.004) ^{NS}
F_{ROH4}	-0.009(0.004)*	-0.005(0.007) ^{NS}	-0.003(0.004) ^{NS}
F_{ROH8}	-0.009(0.004)*	-0.008(0.008) ^{NS}	-0.002(0.005) ^{NS}
F_{ROH16}	-0.011(0.005)*	-0.015(0.009) ^{NS}	-0.006(0.006) ^{NS}

458 *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p > 0.05$

460 **Supplementary Table 1.** Inbreeding depression estimates for milk production traits at
 461 chromosomal level.

Breed	Trait ¹	Chromosome	Estimate
Sarda	MY	3	-0.004(0.001)*
	MY	21	-0.003(0.001)*
	MY	26	-0.002(0.0001)*
	PP	6	-0.005(0.002)*
	PP	26	-0.005(0.002)*
Valle del Belice	MY	1	-0.005(0.002)*
	MY	2	-0.006(0.002)*
	MY	11	-0.003(0.002)*
	MY	25	-0.008(0.003)*
	FP	18	-0.008(0.003)*

462 ¹ MY = milk yield (kg/d); FP = fat percentage; PP = protein percentage. * = P < 0.05

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