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Homozygosity genomic patterns depression in Murciano-granadina goats

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Abstract

Patterns of homozygosity can be influenced by several factors, such as demography, recombination, and selection. Using the goat SNP50 Bead Chip, we genotyped 3171 goats belonging to 117 populations with a worldwide distribution. Our objectives were to characterize the number and length of runs of homozygosity (ROH) and to detect ROH hotspots in order to gain new insights into the consequences of neutral and selection processes on the genome-wide homozygosity patterns of goats. The proportion of the goat genome covered by ROH is, in general, less than 15% with an inverse relationship between ROH length and frequency i.e. short ROH (0.20) FROH values. For populations from Asia, the average number of ROH is smaller and their coverage is lower in goats from the Near East than in goats from Central Asia, which is consistent with the role of the Fertile Crescent as the primary center of goat domestication. We also observed that local breeds with small population sizes tend to have a larger fraction of the genome covered by ROH compared to breeds with tens or hundreds of thousands of individuals. Five regions on three goat chromosomes i.e. 11, 12 and 18, contain ROH hotspots that overlap with signatures of selection. Patterns of homozygosity (average number of ROH of 77 and genome coverage of 248 Mb; FROH<0.15) are similar in goats from different geographic areas. The increased homozygosity in local breeds is the consequence of their small population size and geographic isolation as well as founder effects and recent inbreeding. The existence of three ROH hotspot that co-localize with signatures of selection has also played an important role in increasing the homozygosity of specific regions in the goat breeds analysed in this work display low levels of homozygosity, which is favorable for their genetic management and viability.

Keywords: Homozygosity, genomic, patterns, depression, murciano, granadina, goats

1. Introduction

In Italy, there are more than 1 million goats of which 77.5% are females (ISTAT 2020) ^[1]. However, less than 56 thousand spread in 633 herds were officially registered in 2020 in the Italian Breeders Association (AIA 2021) ^[2]. Despite being Saanen (SA) and Camosciata delle Alpi or Alpine (AL) the main goat breeds reared for milk production in Italy, Murciano-Granadina (MG) was introduced in the Veneto region in 2016 due its milk quality and less pronounced reproductive seasonality which allows less fluctuations in milk production across the year (Delgado *et al.* 2017) ^[3]. Moreover, MG presents a high rusticity and adaptability letting to be raised under harsh conditions - such as the ones in the Mediterranean area - while maintaining milk quality and production (Leon *et al.* 2012; Delgado *et al.* 2017) ^[4, 32, 3]. Nowadays, the Veneto region account for more than 50% of MG goats and herds in Italy (AIA 2021) ^[2]. MG breed is a Spanish native breed originated in 1975 from crossing goats of Murciana and Granadina breeds (MAPA 2021) ^[5], which had been introduced in semi-intensive farming systems in Europe, Africa and South America due to its high adaptability. According to Guan *et al.* (2021) ^[7], genetic selection in the MG population has focused on milk yield for a long time. Currently, the national association 'Asociación Nacional de Caprino de Raza Murciano-Granadina' (CAPRIGRAN 2022) ^[6] is in charge of its official routine evaluation, and a comprehensive overview of traits under selection, including the casein genotype, is publicly available (<https://caprigran.com/en/breeding-program/>). Morphologically, MG is characterised by black or brown coats with or without presence of horns and animals are smaller (50 kg of live bodyweight) than cosmopolitan dairy breeds such as SA and AL (MAPA 2021) ^[5]. Moreover, MG is considered a permanent polyestric breed due to its less pronounced seasonal reproductive behaviour and its reproductive management is based on the 'male effect' without applying artificial photoperiod or hormones (Delgado *et al.* 2017) ^[3]. It should be noted that these management practices need to be applied in SA and AL goats when a farmer want to keep its milk production all the year.

Although MG is less productive, milk quality characteristics are more favorable than SA and AL for cheese manufacturing (Vacca *et al.* 2018; Guan *et al.* 2021) [36, 7]. Therefore, the aim of this study was to evaluate the performance in terms of milk yield and composition of MG compared to SA and AL breeds in the Veneto region using large-scale milk data collected in commercial farms during a complete year belonging to purebred SA, AL or MG goats between 5 and 300 d in milk (DIM) and from parity 1 11, and goats with less than 3 observations within lactation were discarded. For milk yield (kg/d) and fat, protein, casein and lactose content (%), values that deviated more than 3 SD from the mean were treated as missing data. The final dataset included 11,682 test-day records from 1947 goats located in 7 single- and 7 multi-breed herds. The frequency for each breed was: 10 herds, 705 goats and 4,145 observations (AL); 8 herds, 830 goats and 5,382 observations (SA); 4 herds, 412 goats and 2,155 observations (MG). Single-breed herds were 4, 1 and 2 for AL, SA and MG, respectively. For multibreed herds, three breed combinations were available in the dataset: SA \times AL (5 herds), SA \times MG (1 herd) and SA \times AL \times MG (1 herd). The average number of lactations and DIM were 3.10 ± 2.00 and 150.12 ± 73.18 for AL, 2.64 ± 1.64 and 141.00 ± 70.60 for SA, and 2.30 ± 1.41 and 150.70 ± 67.97 for MG.

2. Literature Review

Runs of homozygosity (ROH) can be defined as genomic regions that display a series of consecutive homozygous genotypes (Broman and Weber, 2019) [8, 25]. Their length and frequency depend on a complex array of factors including demography, recombination, and selection (Szpiech *et al.*, 2013) [9]. There is convincing evidence that demographic history has had a key influence on the genomic patterns of homozygosity in several domestic animal species (Peripolli *et al.*, 2017) [10]. While long ROH reflect recent inbreeding, which can be caused by population decline, unbalanced paternal contributions and selection, short and abundant ROH are often due to ancestral family relatedness (Kirin *et al.*, 2010) [11]. Local recombination rate is negatively correlated with ROH frequency because recombination events decrease the probability that an individual possesses two copies of the same long haplotype (Pemberton *et al.*, 2012) [12]. In pigs, the largest ROH are more frequent in regions of low recombination and ROH distribution is negatively correlated with GC content (Bosse *et al.*, 2012) [13]. Regions of low recombination were also detected across the sheep genome (Fariello *et al.*, 2021) [14]. Selection is another important evolutionary force that can increase homozygosity. Positive selection to improve productive/reproductive traits and maintain breed standards can also decrease variability in targeted regions of the genome, and therefore ROH might result from footprints of selection (signatures of selection) (Curik *et al.*, 2021; Zavarez *et al.*, 2015) [15, 16]. The recent availability of a caprine high-throughput genotyping chip (Tosser-Klopp *et al.*, 2021) [17] and a reference goat genome (Bickhart *et al.*, 2017; Dong *et al.*, 2016) [18, 19]. Tosser-Klopp has made it possible to characterize the genomic patterns of homozygosity of several populations from Egypt (Kim *et al.*, 2016) [20], Spain and Africa (Manunza *et al.*, 2016) [21], Switzerland (Burren *et al.*, 2016) [22] and Italy (Talent *et al.*, 2017) [23]. Moreover, combining information provided by the genomic distribution of ROH and selection statistics (e.g.

FST, iHS and hapFLK) has facilitated the identification of several genomic regions under positive selection in goats (Kim *et al.*, 2017; Burren *et al.*, 2016; Brito *et al.*, 2017) [20, 22, 24]. However, a comprehensive picture of the genome-wide patterns of homozygosity in goats sampled at a worldwide scale is still lacking. By comparing a wide range of caprine populations that differ in geographic origin, inbreeding and admixture levels and that undergo different management and selection pressures, we investigated the impact of such factors on the abundance and distribution of ROH in the goat genome sample size. After these flattering steps, the final dataset included 3171 animals belonging to 105 breeds and 12 crossbred populations (see Additional file 1: Table S1) and 46,654 SNPs. To investigate the factors that influence the patterns of homozygosity in the goat genome, we performed comparisons based on (1) population characteristics, (2) geographical origin and (3) sampling locations of transboundary breeds.

3. Methodology

Information on individual goat milk samples was retrieved from the official routine milk testing of the Veneto Regional Breeders Association (Veneto, Italy). In goats milk sampling is performed every 4 weeks in Italy and in the present study the period from January to December 2020 was considered. In the Veneto region, goats feeding is mainly based on forage or hay plus concentrates. The MG herds included in the study kidded all-round year. Moreover, some SA and AL herds applied reproductive practices to also allow out-of-season kidding. However, as dealing with largescale milk data collected from the official routine milk testing, there was no access to more detailed information on the specific practices that farmers applied. Milk chemical composition (fat, protein, casein and lactose content) was assessed through midinfrared spectroscopy using goat-specific models implemented in Milko Scan FT6000 (FOSS Analytical A/ S, Hillerød, Denmark). Fat-corrected milk at 3.5% (FCM 3.5%) was estimated according to Pulina *et al.* (1991) [31] as: $FCM\ 3.5\% = \frac{1}{4} \text{milk yield} (0.634 - 0.1046 \text{ fat } \%)$. Moreover, fat-to-protein ratio (F/P) was calculated. Somatic cell count (SCC, cells/mL) was determined using a Fossomatic 7 DC (FOSS Analytical A/S) and transformed into SCS through the formula of Wiggans and Shook (1987) [27]: $SCS = \frac{1}{4} \log_2 (SCC/100)$. The original dataset (n = 14,561) was edited to retain herds which included at least 75 lactating goats from SA, AL and/or MG dairy breed. Records not belonging to purebred SA, AL or MG goats between 5 and 300 d in milk (DIM) and from parity 1 11, and goats with less than 3 observations within lactation were discarded. For milk yield (kg/d) and fat, protein, casein and lactose content (%), values that deviated more than 3 SD from the mean were treated as missing data. The final dataset included 11,682 test-day records from 1947 goats located in 7 single- and 7 multi-breed herds. The frequency for each breed was: 10 herds, 705 goats and 4,145 observations (AL); 8 herds, 830 goats and 5,382 observations (SA); 4 herds, 412 goats and 2,155 observations (MG). Single-breed herds were 4, 1 and 2 for AL, SA and MG, respectively. For multibreed herds, three breed combinations were available in the dataset: SA \times AL (5 herds), SA \times MG (1 herd) and SA \times AL \times MG (1 herd). The average number of lactations and DIM were 3.10 ± 2.00 and 150.12 ± 73.18 for AL, 2.64 ± 1.64 and 141.00 ± 70.60 for SA, and 2.30 ± 1.41 and 150.70 ± 67.97 for MG.

Statistical analysis Data editing and statistical analyses were carried out in R software version 4.1.2 (R Core Team 2022) [29]. Pearson’s correlations were calculated using the package ‘Hmisc’ version 4.7 (Frank and Harrell 2022) [28] and were considered weak if equal or below 0.30, moderate if between 0.31 and 0.70 and strong if equal or above 0.71. Before the analysis of variance, the normality distribution of the data was verified based on the visual inspection of datapoints, skewness and kurtosis through the ‘moments’ package version 0.14.1 (Komsta and Novomestky 2022) [30]. The homoscedasticity of the data was verified by the Barlett test of homogeneity of variance using the ‘Stats’ package version 0.1.0. Daily milk yield, composition traits, and SCS were analysed through the following mixed model: $y_{ijklmno} = \mu + \beta_i + \beta_j + \beta_k + \beta_l + \beta_{ij} + \beta_{ik} + \beta_{il} + \beta_{jk} + \beta_{jl} + \beta_{kl} + \beta_{m} + \beta_{n} + \beta_{o} + \epsilon_{ijklmno}$ where $y_{ijklmno}$ is the dependent variable; μ is the overall intercept of the model; β_i is the fixed effect of the i th breed ($i = 1/4$ SA, AL and MG); β_j is the fixed effect of the j th stage of lactation ($j = 1/10$; the first being a class from 5 to 30 DIM, followed by 8 classes of 30 DIM each, and the last being a class from 271 to 300 DIM); β_k is the fixed effect of the k th parity ($k = 1/5$ with the last including parity from 5 to 11); β_l is the fixed effect of the l th kidding season ($l = 1/4$; Winter, Spring, Summer, Autumn); β_{ij} is the fixed interaction effect between breed and stage of lactation; β_{ik} is the fixed interaction effect between breed and parity; β_{il} is the fixed interaction effect between breed and kidding season; β_{jk} is the fixed interaction effect between stage of lactation and parity; β_{kl} is the fixed interaction effect

between parity and the kidding season; G_m is the random effect of the m th animal (1,947 goats) $N(0, r^2 G)$, where $r^2 G$ is the goat variance; H_n is the random effect of the n th herd-test-date (104 levels) $N(0, r^2 H)$ where $r^2 H$ is the herd-test-date variance; $e_{ijklmno}$ is the random residual $N(0, r^2 e)$, where $r^2 e$ is the residual variance. The random effects were assumed to be independent. The analysis was conducted using the ‘lme4’ package version 1.1-29 (Bates *et al.* 2015) [26] and multiple comparisons of least-squares mean were performed for the main effect of breed, parity class, stage of location, kidding season and their interaction using the Bonferroni adjustment. Significance was set at $p < 0.05$ unless otherwise stranded and MG breed and to casein content in MG. Milk yield was inversely correlated with fat, protein, casein, F/P ratio and SCS, and positive correlated with lactose ($p < 0.01$). A stronger correlation was observed in MG than in SA and AL between milk yield, and fat, F/P ratio and SCS, whereas a weaker correlation was observed with protein or casein. However, FCM 3.5% was also weakly correlated with fat content in MG. Protein and casein content was moderately correlated with fat content, being that correlation stronger in MG than in SA breed (Table 1). Fat was weakly positive correlated to lactose and SCS ($p < 0.01$). Protein and casein were weakly positively correlated with SCS ($p < 0.001$), being stronger in SA and AL than in MG breed. The F/P was weakly correlated with lactose and SCS. Lactose was moderately negative correlated ($p < 0.001$) with SCS, being the correlation slight weaker in AL.

4. Results

Table 1: shows the trait, breed, milk yield, FCM, fat, protein, casein, fat to protein and its lactose

Murciano-Granadina breed (MG).								
Trait ^b	Breed	Milk yield, kg/d	FCM 3.5%, kg/d	Fat, %	Protein, %	Casein, %	Fat-to-protein	Lactose, %
FCM 3.5%, kg/d	SA	0.97						
	AL	0.97						
	MG	0.96						
Fat, %	SA	-0.26	-0.04					
	AL	-0.17	0.05					
	MG	-0.41	-0.19					
Protein, %	SA	-0.37	-0.29	0.39				
	AL	-0.25	-0.15	0.51				
	MG	-0.14	-0.06	0.54				
Casein, %	SA	-0.36	-0.27	0.42	0.99			
	AL	-0.24	-0.13	0.54	1.00			
	MG	-0.13	-0.04	0.54	1.00			
Fat-to-protein	SA	-0.13	0.08	0.91	ns	0.02		
	AL	-0.04	0.16	0.84	-0.02	0.02		
	MG	-0.40	-0.20	0.83	ns	ns		
Lactose, %	SA	0.10	0.13	0.13	0.06	0.12	0.10	
	AL	0.08	0.10	0.08	0.10	0.15	0.03	
	MG	0.09	0.10	0.09	ns	0.08	0.09	
SCS	SA	-0.23	-0.22	0.06	0.23	0.20	-0.02	-0.41
	AL	-0.21	-0.17	0.17	0.22	0.21	0.07	-0.33
	MG	-0.32	-0.28	0.24	0.15	0.13	0.18	-0.39

^ans: not significant

Table 2: Number of records (n) and least squares means (LSM) with standard error (SE) of milk yield and quality traits.

Trait ^d	Saanen		Alpine		Murciano-Granadina	
	n	LSM ± SE	n	LSM ± SE	n	LSM ± SE
Milk yield, kg/d	5360	2.89 ± 0.04 ^a	4127	2.46 ± 0.05 ^b	2144	1.96 ± 0.04 ^c
FCM 3.5%, kg/d	4902	2.74 ± 0.04 ^a	3536	2.53 ± 0.05 ^b	1965	2.08 ± 0.04 ^c
Fat, %	5331	3.03 ± 0.03 ^c	4103	3.77 ± 0.04 ^b	2135	4.32 ± 0.03 ^a
Protein, %	5325	3.33 ± 0.02 ^b	4102	3.56 ± 0.02 ^a	2120	3.56 ± 0.02 ^a
Casein, %	4592	2.50 ± 0.01 ^b	3321	2.67 ± 0.02 ^a	1754	2.70 ± 0.01 ^a
Fat-to-protein	5281	0.91 ± 0.01 ^c	4068	1.00 ± 0.01 ^b	2108	1.20 ± 0.01 ^a
Lactose, %	5340	4.40 ± 0.01 ^b	4098	4.41 ± 0.01 ^b	2136	4.74 ± 0.01 ^a
SCS	5281	6.28 ± 0.07 ^a	4145	6.02 ± 0.08 ^b	2155	5.64 ± 0.07 ^c

^{a,b,c}Values with different superscripts within a row are significantly different ($p \leq 0.05$).
^dFCM 3.5%: fat-corrected milk at 3.5%; SCS: somatic cell score.

4.1 Breed-specific correlations

Phenotypic correlations were always significant ($p < 0.05$) with only few exceptions (Table 1). For instance, F/P ratio was not correlated to protein content in SA (0.05), with the lowest and greatest productivity in MG (milk yield, 1.96 ± 0.04 kg/d; FCM 3.5%, 2.08 ± 0.04 kg/d) and SA (milk yield, 2.89 ± 0.04 kg/d; FCM 3.5%, 2.74 ± 0.04 kg/d), respectively. On the other hand, fat content and F/P showed the opposite pattern ($p < 0.0001$). However, protein and casein content of MG was similar to AL breed ($p < 0.001$) and greater than SA breed. The greatest lactose content ($4.74 \pm 0.01\%$) and the lowest SCS (5.64 ± 0.07) were observed in MG ($p < 0.001$); whereas SA presented the greatest SCS (6.28 ± 0.07 ; $p < 0.001$).

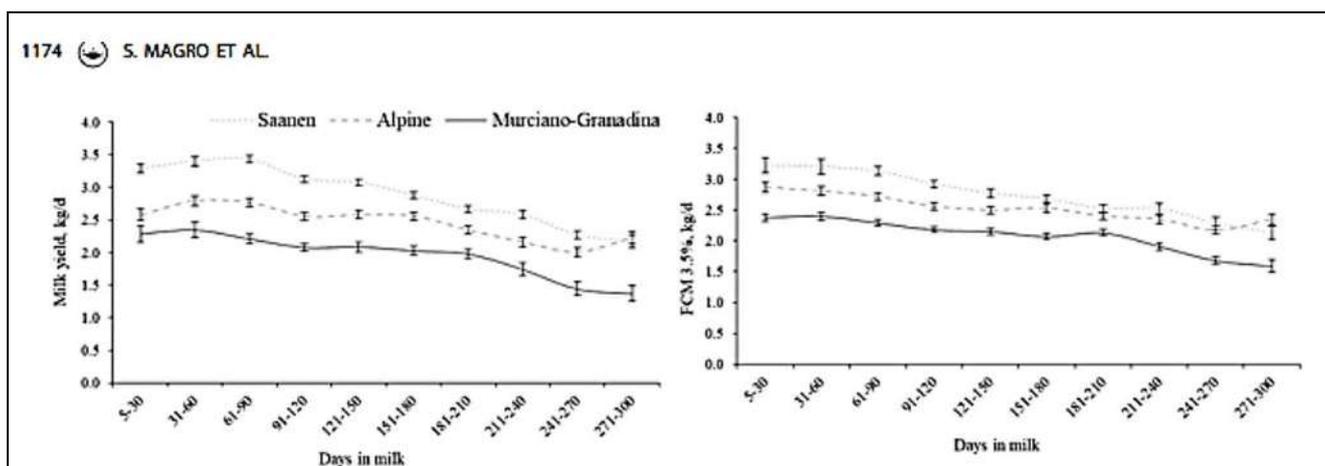
4.2 Effect of stage of lactation within breed

Variations of milk production, gross composition and SCS are depicted in Figure 1. Milk yield peaked at 31-60 DIM in MG (2.35 ± 0.12 kg/d) and AL (2.80 ± 0.07 kg/d) goats, whereas SA goats peaked in the following DIM class (4.43 ± 0.06 kg/d). However, when considering FCM 3.5%, all breeds peaked at 5-30 DIM. After the peak, milk yield gradually decreased until the end of lactation. Overall, SA breed showed greater productivity across lactation compared to MG ($p < 0.05$), whereas AL showed intermediate performance. Fat content was stable until 151-180 DIM in MG, then it steadily increased until reaching $4.91 \pm 0.09\%$ at the end of lactation. On the other hand, fat content reaches the lowest point at 121-150 DIM in SA ($2.60 \pm 0.04\%$) and AL ($3.28 \pm 0.05\%$) breeds. Protein and casein content showed a similar pattern throughout the lactation. Despite the fact that SA and AL breeds behaved similarly, MG goats slightly differ showing a greater persistency in early- and mid-lactation compared to other breeds. The lactation curve of F/P ratio was similar across breeds, with better and less favorable ratio for MG (always > 1.00) and

SA (always to the other breeds). The greatest values were observed at the beginning of the lactation (5-30 DIM), followed by a steadily decrease towards the end of lactation (271-300 DIM). The SCS generally increased across lactation in all breeds, with small differences in early lactation (Figure 1)

4.3 Effect of parity within breed

Variations in milk production, gross composition and SCS are depicted in Figure 2. In MG, primiparous yielded (Milk production, 2.52 ± 0.07 kg/d; FCM 3.5%, 2.60 ± 0.07 kg/d; $p < 0.001$) more milk compared to the older goats, i.e. those in the last parity class (Milk production, 1.54 ± 0.10 kg/d; FCM 3.5%, 1.70 ± 0.09 kg/d; $p < 0.001$). On the contrary, SA and AL goats milk production and FCM 3.5% steadily increased until reaching the greatest yield in goats at their fourth lactation. In particular, milk production and FCM 3.5% were 3.13 ± 0.07 and 2.95 ± 0.07 kg/d, respectively, in SA and 2.76 ± 0.07 and 2.86 ± 0.07 kg/d, respectively, in AL. Although SA yielded more milk than the other breeds ($p < 0.05$), productivity of the first and second parity was similar to MG. Milk fat content of MG and AL increased with parity, reaching the greatest content in the last parity class, i.e. from fifth lactation onwards (4.72 ± 0.08 and $3.97 \pm 0.05\%$ for MG and AL). Also, the SA breed presented the greatest content at the fifth parity onwards ($3.25 \pm 0.06\%$), however, such estimate did not significantly differ from that referred to first parity goats ($3.10 \pm 0.07\%$). Protein and casein content were greater on the first and the last parity for all three breeds. However, the variability between parities was larger in MG goats. Moreover, SA usually showed the lowest fat, protein and casein content. While lactose content decreased linearly with parity in SA breed, moving from $4.50 \pm 0.02\%$ (first parity) to $4.33 \pm 0.01\%$ in the last parity class (p



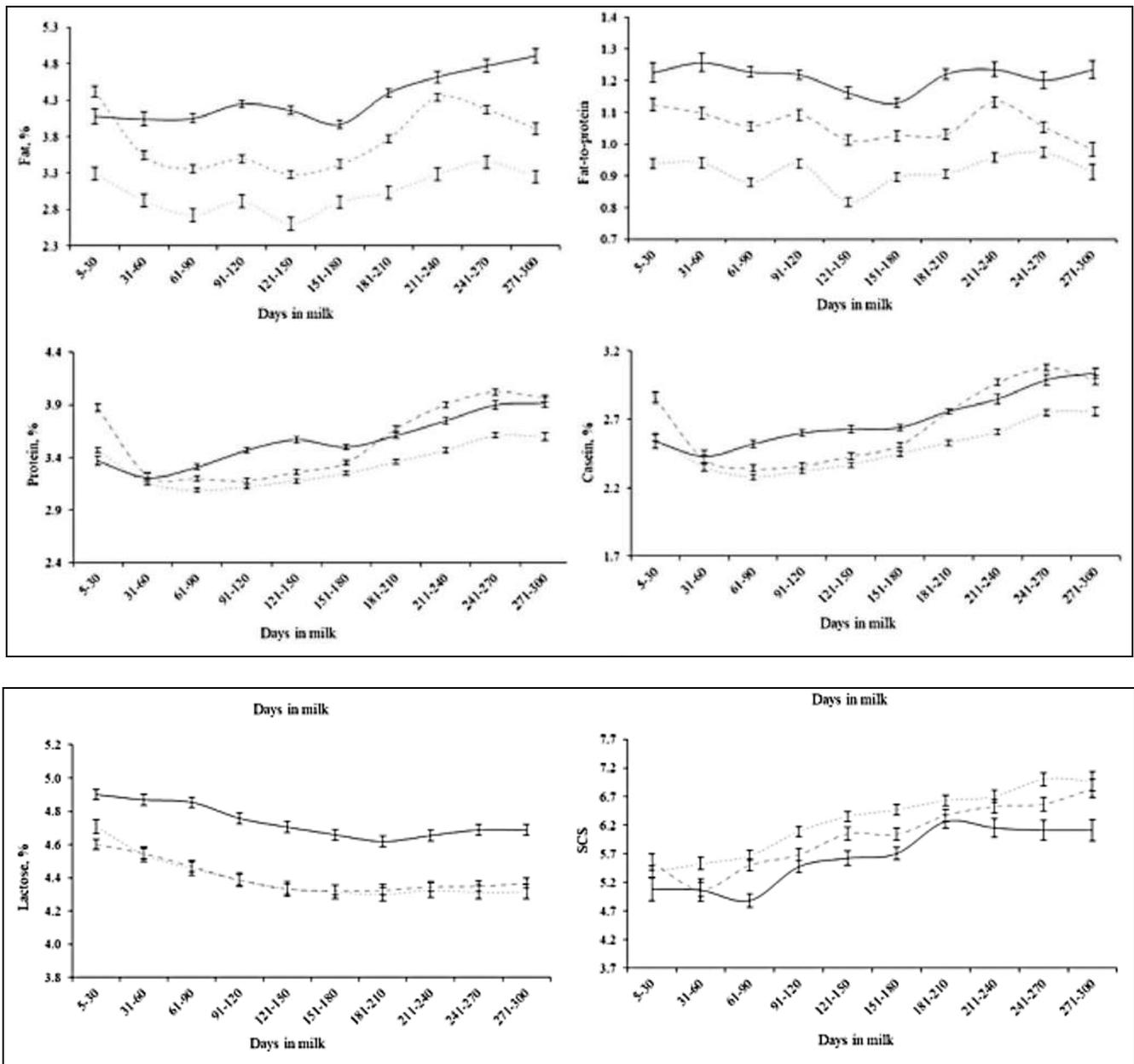
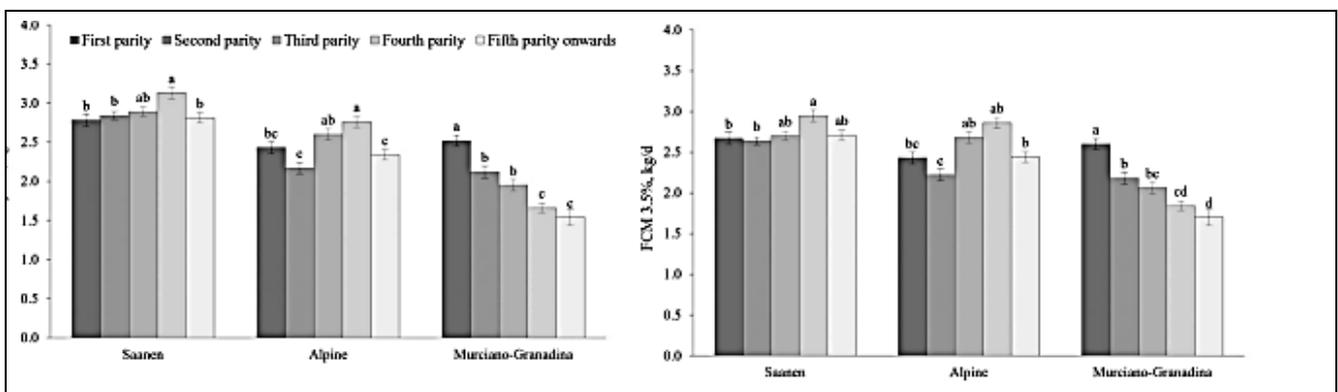


Fig 1: Variations of milk production, gross composition and SCS are depicted



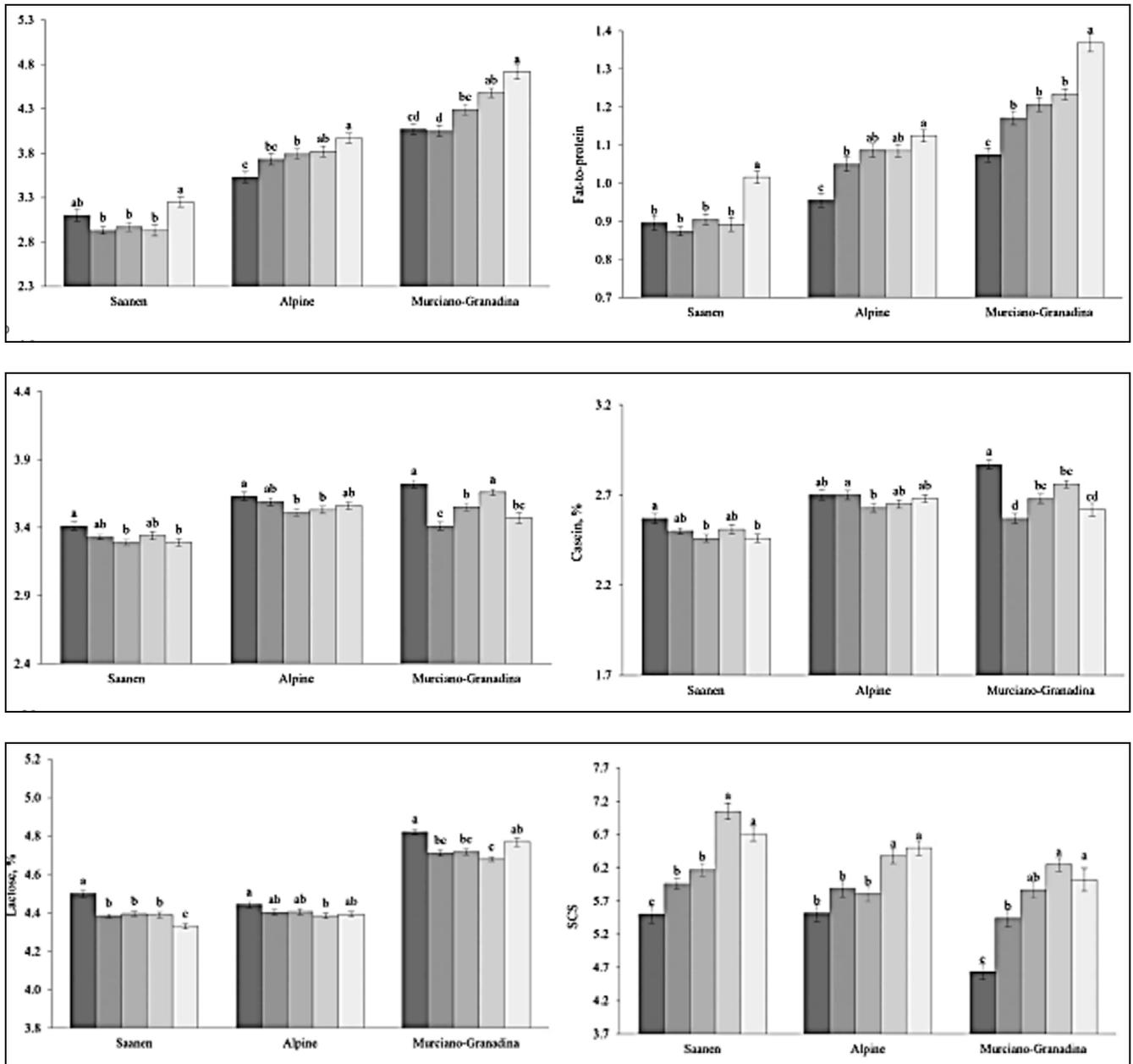
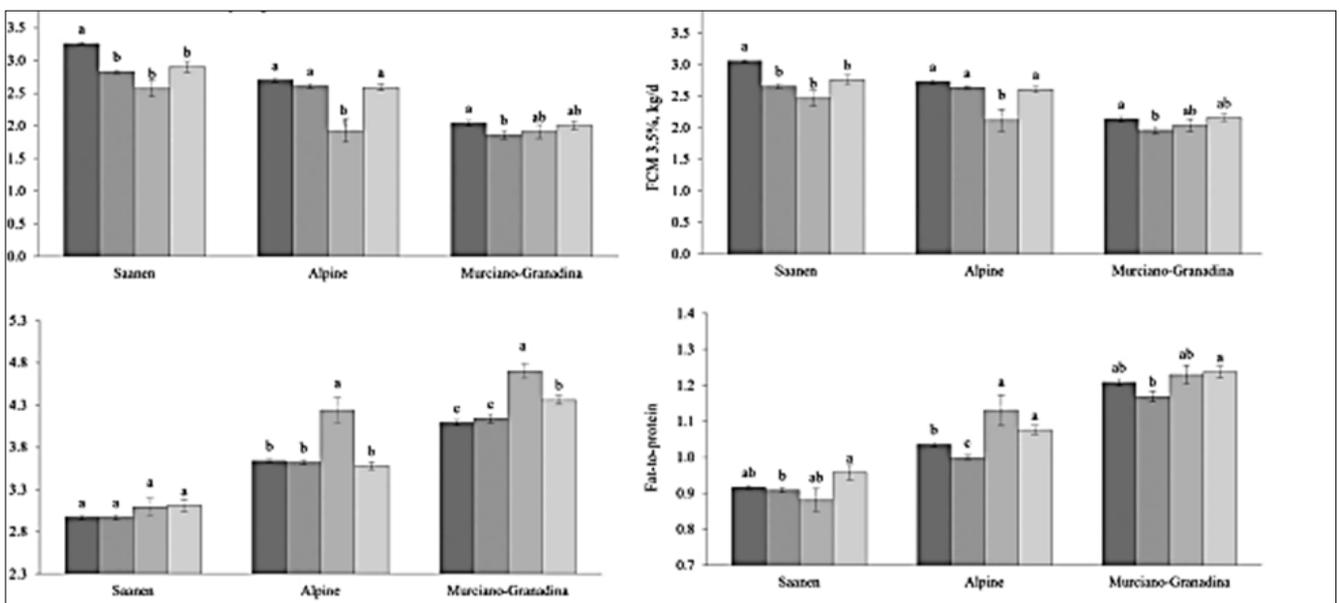


Fig 2: Least-squares means of milk yield, fat-corrected milk at 3.5% (FCM 3.5%), gross composition and somatic cell score (SCS) across parities. The standard error is indicated with a bar. Values with different superscripts within each breed are significantly different ($p < 0.05$).



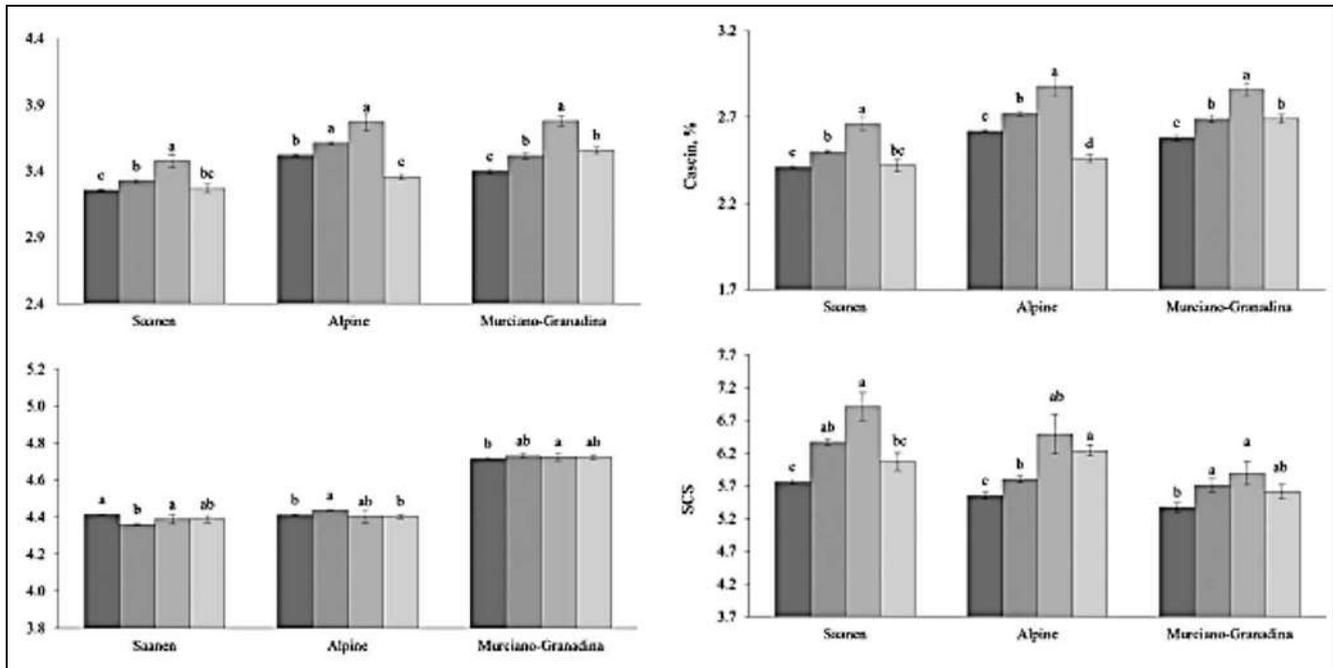


Fig 3: Least-squares means of milk yield, fat-corrected milk at 3.5% (FCM 3.5%), gross composition and somatic cell score (SCS) across kidding seasons. The standard error is indicated with a bar. Values with different superscripts within each breed are significantly different ($p < 0.05$)

5. Conclusions

This study demonstrates that the newly introduced MG was able to adapt very well to the dairy goat management practices and conditions in northern Italy, showing a superior milk quality compared to SA and AL commonly present in this area. Findings suggested that MG, whose reproductive behavior is less sensitive to season compared to SA and AL, performs efficiently under farming system of Veneto region and can be a genetic resource of interest for the current Italian context. Therefore, the introduction of MG may guarantee a more stable milk and cheese production across the year due to their less pronounced seasonality, which may allow farmers to ensure constant milk supplies throughout the year.

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