Genetic parameters of weeping teats in Italian Saanen and Alpine dairy goats and their relationship with milk production and somatic cell score

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ABSTRACT

This paper reports a quantitative genetics analysis of weeping teats (WT), an abnormality of the mammary gland in goats. Weeping teats are characterized by milk oozing out of the teat or by the presence of multiple cysts near its base. This abnormality has been routinely recorded in Italian Alpine and Saanen goats since 2000 using a score of 0 or 1 (0 = defect not present, 1 = defect present). No information is available on the genetic background of WT or its relationship with production or other udder-related traits. Data obtained by the Italian National Sheep and Goat Breeders Association (Rome, Italy) were used to estimate both heritability of WT and its genetic correlation with milk yield, somatic cell score, and udder traits. The final data set used in the analysis included 2,178 Saanen and 2,309 Alpine primiparous goats kidding from 2009 to 2014. The pedigree data included 7,333 Saanen and 7,421 Alpines, respectively. A threshold–linear multivariate animal model was used to estimate variance and covariance components. A genealogical data analysis was also implemented, including genealogical data completeness, inbreeding, and identification of possible most recent common ancestors. On average, around 4 and 13% of primiparous Saanen and Alpine females kidding from 2009 to 2014 showed mammary gland abnormality, respectively. Weeping teats heritability was 0.27 and 0.26 for Saanen and Alpine, respectively. Genetic correlations between milk production or somatic cell score ranged from −0.16 in Saanen to 0.43 in Alpine, but the standard error of the estimates was very large. Positive genetic correlations were observed among WT and teat characteristics in both Saanen and Alpine. The average inbreeding of abnormality carriers was 2.4 and 5.1 for Saanen and Alpine, respectively. The genealogical data analysis identified 4 common ancestors of affected does in Saanen and 2 in Alpine. These results indicate that WT have a possible genetic background. A genome-wide association study might help in understanding the polygenic or monogenic determination of this abnormality.

Key words: weeping teat, goat, heritability, genetic correlation, ancestor

INTRODUCTION

The small ruminant dairy industry has been experiencing a significant demographic increase over recent years in both developing and developed countries. Different needs and traditions have driven such a growth, considering goat milk as an alternative dairy product for human consumption (Yangilar, 2013; Lérias et al., 2014). Moreover, European countries such as France, Spain, Greece, and Italy have a long-standing cheese-making tradition (FAO, 2019) that boosts and supports breeding of dairy goats (Faccia et al., 2015).

As of the end of 2018, 54.984 goats from 26 different breeds were officially milk recorded in Italy (AIA, 2019; Sandrucci et al., 2019). Routine genetic evaluation for milk yields and type traits has been in place for both Saanen and Alpine since 2000, although a national progeny testing program has yet to be established. Linear type trait appraisal in small ruminants is now a routine procedure in many countries, supplying data for genetic evaluation, breeding programs, and farm management (Manfredi et al., 2001; Wiggans and Hubbard, 2001; Carta et al., 2009; McLaren et al., 2016). In Italy, type evaluation for goats started in 2000 and consists of both the classical scoring on a linear scale and the recording of possible defects with potential functional impact, such as supernumerary teats (Smith and Sherman, 2009). A recent study from Martin et al. (2018) confirmed their large heritability, hence their genetic origin. An additional and less known udder defect is the "weeping teat" (**WT**; Plummer and Plummer, 2012), which can be observed in Figures 1 and 2. The abnormality is characterized by milk-secreting tissue in

Figure 1. Alpine goat with weeping teats. Courtesy of S. Milanesi, Lombardy Breeders Association, Lombardy, Italy.

the wall of the teat. Three situations may arise: (1) if the milk passes through local pores into the teat cistern, there will be no visual evidence of the presence of this tissue; (2) if milk filters through skin pores, it is released and detectable on the outer surface of the udder or the teat; and (3) when the glandular tissue does not communicate with either the outer layer of skin or the teat cistern, a cyst may form in the wall of the teat and interfere with milking (Yeruham et al., 2005).

In humans, the presence of ectopic or accessory mammary tissue, defined as residual breast tissue persisting from embryologic development, has been detected in up
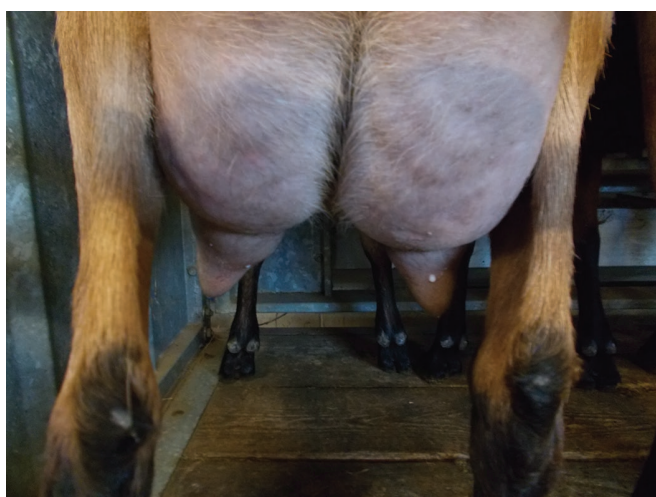

Figure 2. Rear udder view of an alpine goat affected by weeping teats. Courtesy of S. Milanesi, Lombardy Breeders Association, Lombardy, Italy.

to 6% of the population (DeFilippis and Arleo, 2014). It is prevalent in Asian populations (Bakker et al., 2005) and lowest in Caucasians, possibly highlighting a genetic component. It has been agreed that ectopic breast tissue is a general definition that includes both supernumerary breasts as well as "aberrant" breast tissue, described as "an island of breast tissue usually located in proximity to the normal breast" (Marshall et al., 1994). Different from supernumerary breasts, aberrant breast tissue lacks organized secretory systems (DeFilippis and Arleo, 2014).

In goats, WT has been found to be especially prevalent in breeds selected for high milk production (Plummer and Plummer, 2012; Biffani et al., 2018). The observed incidence in commercial breeds in Italy is 3.6 and 7.5% for primiparous Saanen and Alpine, respectively. A phenotypic correlation was observed in a preliminary study by Biffani et al. (2018), where normal Saanen goats showed between 0.10 and 0.16 kg/d more milk than WT does. However, evidence of the presence of this abnormality and its phenotypic and genetic parameters in livestock remains undocumented and anecdotic. An additional issue is the economic impact of WT on farm profitability, which is difficult to objectively quantify. Indeed, economic loss as a consequence of WT is due not only to possible milk yield reduction but also to the exclusion of a proportion of females from the mating pool; the latter reduces the intensity of selection, thereby limiting the achievable genetic progress. However, the defect is routinely recorded, and culling of affected animals is generally recommended.

To date, to the authors' best knowledge, no scientific evidence has demonstrated that WT has a genetic background. Furthermore, the possible genetic relationships of WT with milk production, SCS, or udder traits has never been investigated. The aims of the current study were to elucidate the genetic component of WT in Saanen and Alpine primiparous goats reared in Italy and to investigate its relationship with milk yield and udder-related traits.

MATERIALS AND METHODS

Ethics Statement

Animal welfare and use committee approval was not needed for this study because data sets were obtained from pre-existing databases based on routine animal recording procedures.

Data

Data for the present study were obtained by the Italian National Sheep and Goat Breeders Association

Table 1. Total number of primiparous goats in Saanen and Alpine breeds kidding from 2009 to 2014 and proportion of females showing the presence of weeping teats (WT) defect

Item	Year of kidding						Average
	2009	2010	2011	2012	2013	2014	
Saanen							
Total goats (no.)	503	501	500	404	218	52	
Positive for WT[1] (%)	1.8	0.6	2	9.2	5.5	0	3.8
Alpine							
Total goats (no.)	481	468	418	476	446	20	
Positive for WT (%)	3.1	3.8	8.4	21.8	29.6	0	13.3

[1]Does showing the presence of WT defect.

(Rome, Italy) and consisted of production and linear appraisal records from 2000 to 2015. The data came from 5,150 Saanen and 5,021 Alpine first-parity goats from 131 different herds. Production data comprised 43,284 and 31,566 test-day milk yield (**MY**) and SCC records for Saanen and Alpine goats, respectively. The linear appraisal records included the presence (1) or absence (0) of WT and the following 9 type traits: fore udder, udder profile, udder floor position, rear udder, rear udder attachment, teat length (**TL**), teat form, teat angle, and teat orientation. The definition of the traits is as used in Manfredi et al. (2001). Test-day records were merged with the linear records by retaining only the production record closest to the date of linear appraisal. Data editing consisted of retaining only herds with at least 2 does with reported presence of WT defect and deleting test days recorded after 210 DIM. Furthermore, only goats that had their first kidding between 10 and 30 mo of age and from year 2008 were retained. The variable SCC was log-transformed into SCS using the formula $SCS = \log_2(SCC/100,000) + 3$ (Ali and Shook, 1980). Before the analysis, MY, SCS, and linear type traits were scaled to a mean equal to 100 and standard deviation of 10. A pedigree file was prepared for each breed, excluding goats with unknown sire. Contemporary groups were defined by combining herd, year, and season of kidding. Finally, 2,178 Saanen

with a pedigree containing 7,333 individuals and 2,309 Alpine with a pedigree containing 7,421 individuals were used in the analysis. The total number of Saanen and Alpine recorded goats per year of kidding and the frequencies of the WT phenotypes are presented in Table 1. Average WT frequency was 3.8 and 13.3% in Saanen and Alpine, respectively. In both breeds an increasing trend can be observed, with a remarkable increase in year 2012 and 2013 for the Alpine breed. No WT cases were observed in goats kidding in 2014. The average daily milk production (kg), SCS, and DIM for Saanen and Alpine breeds by year of kidding are shown in Table 2. The average daily milk production was 2.50 and 2.32 kg for Saanen and Alpine, respectively. The highest daily production was observed in 2013 for the Saanen (2.63 kg/d) and in 2014 for the Alpine (2.43 kg/d). The average SCS was 5.51 and 4.63 for Saanen and Alpine, respectively. The peak in daily SCS was observed in 2009 (5.73) and 2012 (4.92) for Saanen and Alpine, respectively. The average DIM at which the appraisal visit occurred was 127 for Saanen and 119 for Alpine.

Genetic Parameter Estimation

Variance and covariance components for all traits were estimated fitting a threshold–linear multivariate

Table 2. Average daily milk production, SCS, and DIM for Saanen and Alpine breeds by year of kidding

Item	Year of kidding						Average
	2009	2010	2011	2012	2013	2014	
Milk (kg)							
Saanen	2.60 ± 0.82	2.51 ± 0.95	2.51 ± 0.82	2.59 ± 0.94	2.63 ± 0.94	2.15 ± 0.63	2.50
Alpine	2.38 ± 0.95	2.19 ± 0.93	2.33 ± 0.9	2.19 ± 1.03	2.38 ± 0.91	2.43 ± 0.72	2.32
SCS							
Saanen	5.73 ± 1.58	5.44 ± 1.79	5.35 ± 1.77	5.67 ± 1.53	5.18 ± 1.51	5.69 ± 1.49	5.51
Alpine	4.74 ± 1.86	4.9 ± 1.94	4.9 ± 2	4.92 ± 1.85	4.58 ± 1.91	3.72 ± 1.72	4.63
DIM							
Saanen	130.6 ± 37	118.8 ± 43	112.1 ± 37	139.3 ± 29	120.2 ± 44	142.2 ± 29	127
Alpine	112.7 ± 35	131.5 ± 43	107.0 ± 42	127.0 ± 38	114.7 ± 35	121.4 ± 54	119

animal model. The trait WT was considered binary using a probit link function, whereas MY, SCS, and type traits were considered Gaussian.

The model used for both breeds was

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wc} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of t observed production, linear type traits, or WT unobserved liabilities; $\mathbf{b}$ is a vector of systematic effects, including number of kids (2 levels), year-month of kidding (47 levels), age-season of kidding (31 levels), and linear covariates for DIM and log(DIM); $\mathbf{a}$ is a vector of random additive direct genetic effects; $\mathbf{c}$ is a vector of random herd-year-season of kidding (**HYS**) effects; $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are incidence matrices for $\mathbf{b}$, $\mathbf{a}$, and $\mathbf{c}$, respectively; and $\mathbf{e}$ is a vector of random residuals. Assumptions of the model are

$$E(a) = E(c) = E(e) = 0,$$
$$E(y) = (\mathbf{I_t} \otimes X)b,$$

where E is the expectation of a random variable, with variances and covariances

$$Var \begin{vmatrix} a \\ c \\ e \end{vmatrix} = \begin{vmatrix} \mathbf{A} \otimes \mathbf{G} & 0 & 0 \\ 0 & \mathbf{C} \otimes \mathbf{I_c} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I_n} \end{vmatrix},$$

where $\otimes$ is the Kronecker product; $\mathbf{A}$ is the numerator relationship matrix; $\mathbf{I_t}$, $\mathbf{I_c}$, and $\mathbf{I_n}$ are identity matrices; and $\mathbf{G}$, $\mathbf{C}$, and $\mathbf{R}$ denote variance-covariance matrices among the 12 traits for the additive genetic, random HYS, and the residual effects, respectively.

The THRGIBBS1F90 program (Tsuruta and Misztal, 2006) was used for estimating (co)variance components using Gibbs sampling. Residual variance for WT was fixed at 1.0 on the liability scale. A flat prior was used for fixed effects, and an inverted Wishart distribution was used as prior for the random effects. For each analysis, 300,000 samples (saving every 100th sample after discarding a burn-in of 50,000 iterations) were drawn. Convergence was determined from a visual inspection of trace plots.

The posterior mean was used as a point estimate of (co)variance components and related parameters. Lower and upper bounds of the 95% highest posterior probability density regions (**HPD**) for heritability and additive genetic correlations were estimated from the Gibbs samples.

Heritability (h^2) was computed as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{hys}^2 + \sigma_e^2},$$

where σ_a^2 is the additive genetic variance, σ_{hys}^2 is the HYS variance, and σ_e^2 is the residual variance. Intraherd heritability $\left(h_{ih}^2\right)$ was calculated as

$$h_{ih}^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}.$$

Genealogical Data Analysis

A genealogical data analysis was also implemented, including genealogical data completeness, inbreeding, and identification of possible most recent common ancestors (**MRCA**). The pedigrees used for both breeds were the same as the one used for genetic parameter estimation. Identification of MRCA was stratified by year of birth. All the analyses were conducted using OptiSel (Wellmann, 2019) and GENLIB (Gauvin et al., 2015), which are R packages for the analysis of genealogical data.

RESULTS

Genetic Parameters

Posterior means of heritabilities, HYS, and additive and residual variances for the 12 observed traits in the 2 breeds are in Table 3. Heritability for WT was 0.27 and 0.26 for Saanen and Alpine, respectively. Overall heritability estimates ranged from a minimum of 0.02 for SCS in Alpine to a maximum of 0.38 for TL in Alpine. Intraherd heritability had a similar pattern, ranging from a minimum of 0.03 for SCS in Alpine to a maximum of 0.49 in Alpine. The HYS variances ranged from a minimum of 15% for udder floor position in Saanen to a maximum of 59.2% for MY in Alpine.

Genetic and phenotypic correlations among WT, MY, and SCS are in Table 4. The observed phenotypic correlations were all close to zero. Genetic correlation between MY and WT was −0.16 in Saanen and 0.43 in Alpine. However, HPD was very large for both breeds. Only for Alpine did the interval from lower to upper bound of the 95% highest posterior density not include zero, suggesting that the correlation was actually positive. The genetic correlation between MY and SCS had a similar pattern, with a negative value (−0.13) for Saanen and a positive value for Alpine (0.19). Further-

Table 3. Posterior means of heritability, intraherd heritability (lower and upper bounds of the 95% highest posterior density region in parentheses), and herd-year-season of kidding (HYS) variance for WT, MY, SCS, and udder traits in Saanen and Alpine primiparous goats

Trait[1]	Heritability	Intraherd heritability	HYS variance
WT			
Saanen	0.27 (0.06–0.46)	0.42 (0.14–0.70)	38.4
Alpine	0.26 (0.11–0.42)	0.38 (0.18–0.57)	32.4
MY			
Saanen	0.10 (0.03–0.18)	0.16 (0.04–0.27)	39.2
Alpine	0.11 (0.06–0.16)	0.28 (0.17–0.38)	59.2
SCS			
Saanen	0.05 (0.01–0.11)	0.06 (0.01–0.14)	22.1
Alpine	0.02 (0.00–0.06)	0.03 (0.02–0.08)	26.9
UA			
Saanen	0.29 (0.20–0.39)	0.31 (0.22–0.41)	6.1
Alpine	0.13 (0.09–0.19)	0.16 (0.10–0.22)	15.2
UP			
Saanen	0.22 (0.14–031)	0.25 (0.16–0.35)	12.8
Alpine	0.37 (0.28–0.45)	0.41 (0.32–0.50)	11.5
UFP			
Saanen	0.12 (0.07–0.17)	0.15 (0.09–0.21)	22.4
Alpine	0.20 (0.12–0.29)	0.28 (0.18–0.39)	29.1
TL			
Saanen	0.23 (0.19–0.27)	0.27 (0.23–0.31)	14.7
Alpine	0.38 (0.31–0.46)	0.49 (0.41–0.57)	23.6
TF			
Saanen	0.20 (0.13–0.29)	0.27 (0.17–0.37)	27.5
Alpine	0.17 (0.10–0.23)	0.20 (0.13–0.28)	18.7
TA			
Saanen	0.16 (0.11–0.21)	0.20 (0.14–0.26)	23.6
Alpine	0.26 (0.17–0.35)	0.35 (0.24–0.46)	24.2
TO			
Saanen	0.22 (0.14–0.29)	0.26 (0.17–0.35)	18.4
Alpine	0.24 (0.18–0.30)	0.28 (0.21–0.36)	15.5
RU			
Saanen	0.25 (0.16–0.33)	0.32 (0.22–0.43)	27.6
Alpine	0.23 (0.16–0.29)	0.32 (0.24–0.40)	28.0
RUA			
Saanen	0.20 (0.15–0.27)	0.31 (0.23–0.39)	40.8
Alpine	0.23 (0.15–0.31)	0.35 (0.24–0.45)	37.6

[1]WT = weeping teats; MY = milk yield (kg/d); UA = udder attachment; UP = udder profile; UFP = udder floor position; TL = teat length; TF = teat form; TA = teat angle; TO = teat orientation; RU = rear udder; RUA = rear udder attachment.

more, the genetic correlation between SCS and WT was negative in both Saanen (-0.03) and Alpine (-0.31), whereas HPD was larger for Saanen than Alpine.

Phenotypic correlations among WT and udder traits ranged from -0.07 (teat orientation) to 0.06 (teat form) in Saanen breed and from -0.07 (teat orientation) to 0.12 (udder profile) in Alpine breed (data not shown). Genetic correlations among WT and udder traits are shown in Table 5 and range from a minimum of -0.44 for rear udder in Alpine to a maximum of 0.68 for TL in Saanen.

Genealogical Data Analysis

Genealogical data completeness, average inbreeding, number of MRCA, and number of individuals related to MRCA per WT and normal does by breed and year of birth are shown in Table 6. The average number of fully traced generations in WT does was 2.6 and 2.0 in Alpine and Saanen. respectively. It ranged from 1.58 (Saanen goats born in 2010) to a maximum value of 3.1 (Alpine goats born in 2009). Fully traced generations in normal does ranged from a minimum of 1.83 (Saanen goats born in 2007) to a maximum value of 2.8 (Alpine goats born in 2008). Average pedigree completeness was 0.8 and 0.7 irrespective of the presence of WT in Alpine and Saanen, respectively. The highest mean inbreeding was observed in WT Alpine ($F = 5.1$), with a maximum value of 7.12 for Alpine goats born in 2009. Average inbreeding of WT does was higher than inbreeding of normal does in Alpine goats (5.1 vs. 3.4). An opposite relationship was observed in Saanen goats, where the average inbreeding of normal does was higher (2.9 vs. 2.4). The total number of MRCA was 5 and 4 for WT does in Alpine and Saanen, respectively. Only 1 MRCA in Saanen was found for normal does.

DISCUSSION

In their review of the principal diseases of the mammary gland in sheep and goats, Plummer and Plummer (2012) relate the possibility of having milk-secreting tissue in the wall of the teat. In such a situation, according to the authors, 3 outcomes could be possible:

Table 4. Phenotypic and genetic correlations among MY, WT, and SCS in Saanen and Alpine breeds

	Saanen				Alpine			
			HPD95%[2]				HPD95%	
Trait[1]	Phenotypic correlation	Genetic correlation	Lower	Upper	Phenotypic correlation	Genetic correlation	Lower	Upper
MY–WT	0.05	−0.16	−0.98	0.78	0.00	0.43	0.03	0.75
MY–SCS	0.02	−0.13	−0.88	0.92	−0.05	0.19	−0.97	0.76
SCS–WT	0.04	−0.03	−0.84	0.80	0.02	−0.31	−0.86	0.49

[1]MY = milk yield (kg/d); WT = weeping teats.

[2]Lower and upper bounds of the 95% highest posterior density region.

Table 5. Genetic correlation among weeping teats and udder traits in Saanen and Alpine breeds

	Saanen			Alpine		
		HPD95%[2]			HPD95%	
Trait[1]	Correlation	Lower	Upper	Correlation	Lower	Upper
UA	−0.13	−0.26	0.00	0.13	−0.02	0.26
UP	−0.04	−0.17	0.09	0.34	0.19	0.48
UFP	−0.13	−0.28	0.00	−0.11	−0.25	0.02
TL	0.68	0.59	0.78	0.48	0.34	0.61
TF	0.05	−0.07	0.18	0.01	−0.14	0.15
TA	0.27	0.12	0.43	0.15	0.01	0.28
TO	0.16	0.03	0.30	0.54	0.39	0.68
RU	0.14	0.02	0.26	−0.44	−0.58	−0.30
RUA	−0.35	−0.48	−0.19	0.15	0.02	0.27

[1]UA = udder attachment; UP = udder profile; UFP = udder floor position; TL = teat length; TF = teat form; TA = teat angle; TO = teat orientation; RU = rear udder; RUA = rear udder attachment.

[2]Lower and upper bounds of the 95% highest posterior density region.

(1) the milk comes back into the teat cistern with no evidence of any defect; (2) the milk is released onto the skin surface, resulting in a WT; or (3) the milk is accumulated at the base of the teat, eventually causing the development of a teat cyst. The same authors classify this abnormality as "congenital" but do not present any data or statistics about its incidence. The only peer-reviewed article reporting statistics about a similar disease is Yeruham et al. (2005). In this study, 19 does (5.6% of the total) are reported to exhibit subcutaneous cysts in the region of the teat. In France, WT scoring is part of the type appraisal routine evaluation, but no official statistics are available. Generally, WT females are excluded from selection paths. The incidence of WT in the present study was low to moderate depending on the breed. However, if we consider that some potential WT goats are not evaluated because of voluntary culling or are not identified as WT because of an inaccurate defect evaluation, we can speculate that the observed proportion can be considered an underestimate. Martin et al. (2018) considered the same issue when analyzing supernumerary teats, an additional disease of the mam-

Table 6. Genealogical data completeness, average inbreeding, number of most recent common ancestor (MRCA), and number of individuals related to MRCA per WT or normal does[1] by breed and year of birth

		WT does					Normal does				
Breed	Year	Full gen[2]	PCI[3]	F[4]	MRCA	Individuals[5]	Full gen	PCI	F	MRCA	Individuals
Alpine	2007	2.3	0.77	6.90	2	4	2.1	0.67	1.02	0	0
	2008	2.8	0.84	6.76	1	14	2.7	0.83	4.34	0	0
	2009	3.1	0.90	7.12	1	26	2.8	0.82	3.58	0	0
	2010	2.9	0.87	2.28	1	46	2.6	0.83	4.66	0	0
	2011	2.1	0.67	2.87	0	0	2.6	0.80	3.59	0	0
	2012	2.4	0.77	4.78	0	0	2.5	0.78	3.30	0	0
	Mean	2.6	0.80	5.1	0.8	15	2.6	0.79	3.4	0.0	0.0
Saanen	2007	—	—	—	—	—	1.83	0.62	1.69	0	0
	2008	2.00	0.65	7.15	0	0	2.43	0.75	2.54	0	0
	2009	2.00	0.76	0.34	0	0	2.47	0.78	2.48	0	0
	2010	1.58	0.58	0.83	4	12	2.18	0.73	2.23	0	0
	2011	2.37	0.79	2.38	0	0	2.31	0.74	2.65	0	0
	2012	2.25	0.76	1.36	0	0	2.67	0.84	5.69	1	24
	Mean	2.0	0.70	2.4	0.8	2.4	2.3	0.75	2.9	0.2	4

[1]WT does = does showing weeping teat; normal does = does not showing weeping teats.

[2]Number of fully traced generations.

[3]Index of pedigree completeness (MacCluer et al., 1983).

[4]Inbreeding coefficient × 100.

[5]Individuals related to the MRCA.

mary gland, in French Alpine and Saanen dairy goats. The observed frequency was 4%, below that reported in the available literature by Brka et al. (2007), who found a frequency of 17% for goats. Daily milk production and daily SCS are in the range of values usually reported in dairy goats (Bergonier et al., 2003; Rupp et al., 2011; Brito et al., 2018).

Genetic Parameters

To the authors' best knowledge, no studies reporting heritability estimates for WT are available today. Yeruham et al. (2005), in their paper regarding cases of teat cystic dilation in an Israeli dairy goats herd, speculated that one possible reason is "the genetic fault in one or more of the bucks." However, in their case no genealogical information was available, and, consequently, genetic parameter estimation was not feasible. In the present study the estimated heritability for WT was greater than 0.25 in both Alpine and Saanen breeds, with a highest posterior density interval ranging from 0.06 to 0.46 (Table 3). Although our results cannot be compared with any previous studies, the estimates are in the range of results obtained in disease-related traits in goats (Martin et al., 2018), beef (Inoue et al., 2015), or dairy cattle (Pryce et al., 2016). Indeed, these estimates indicate the existence of a genetic component for WT. Intraherd heritabilities differed from heritabilities only when there was a strong HYS effect. The model used to estimate the genetic parameters included an HYS random effect. The inclusion of a random HYS effect had a double purpose. Fitting HYS as a random effect reduces the loss of information due to small contemporary group size (Visscher and Goddard, 1993), and a random HYS effect helps take into account the nongenetic covariance between individuals producing in the same herd. Indeed, contemporary groups are generally used to identify group of animals that are the same sex, born or producing in the same period, or raised in the same condition or that received the same management care (Schaeffer, 2018). In this way, the model should better reflect any characteristic that affects all responses for that particular herd. In the present study, the observed proportion of WT phenotypic variance due to the HYS effect was 38.3 and 32.5% for Saanen and Alpine, respectively. Those results seem to confirm the hypothesis that some aspect related to management, such as an inappropriate milking routine or an incorrect setting of the milking machine, might exacerbate the incidence of WT within farm (Pierre Guy Marnet, Department of Animal and Food Sciences, Agrocampus Ouest, France, personal communication).

An additional objective of the present study was to identify the possible genetic relationship between WT and other important traits, such as milk production or udder traits. The genetic correlation between MY and WT was −0.16 and 0.43 in Saanen and Alpine, respectively. However, HPD interval in Saanen is extremely large, spanning from −0.98 to 0.78. A different situation can be observed for Alpine, where HPD, even if still large, is always positive. However, this result is not sufficient to confirm the hypothesis by Plummer and Plummer (2012) that the possibility of having milk-secreting tissue in the wall of the teat is related to selection for high milk production. A similar pattern was observed for the genetic relationship between WT and SCS, which was negative in both Saanen (−0.03) and Alpine (−0.31) and with a large HPD. Moreover, the phenotypic correlations among WT and MY or SCS were near zero (0.05 and 0.04, respectively). As Lynch and Walsh (1998) pointed out, the difference in absolute magnitude between phenotypic and genetic correlations, with the latter exceeding the former, can arise with small sample sizes. This is particularly true when the "effective number of families" (Nh_1h_2, where N is the actual number of families and h_1 and h_2 are the heritabilities of the observed traits) is less than 50. In the current study, the effective number of families was less than 20 in both Saanen and Alpine when evaluating MY and WT and less than 10 when evaluating SCS and WT. Positive (unfavorable) genetic correlations were also observed among WT and teat characteristics in both Saanen and Alpine. In Saanen breed, the higher correlation was between WT and TL (0.68). In Alpine, the genetic correlation between WT and TL was still positive but not of the same magnitude (0.48 vs. 0.68). In both breeds, the observed HPD were smaller than that observed for MY and SCS. According to the scoring system used in Italy, a larger score for TL identifies longer teats. Teat orientation in Alpine also showed a medium to large genetic correlation with WT (0.54). In this case, teats pointing outward, away from each other, are scored as 1, whereas those pointing inward, toward each other, are scored as 9; a score of 5 is given to teats pointing straight down. A divergent result was observed for genetic correlation between rear udder attachment and WT (−0.35 and 0.15 in Saanen and Alpine, respectively). Based on empirical experiences, breeders have defined an optimum intermediate score for rear udder attachment between 4 and 5, and it might partially explain the observed result. Heritabilities for milk production (0.10 and 0.11 for Saanen and Alpine, respectively) were estimated using a single test day per each goat, adjusting for the stage of lactation at sampling. On average, the production was recorded at 127 and 119 DIM in Saanen and Alpine, respectively. Estimates obtained from a single test day are generally lower than those obtained from a repeatability model

or from a lactation model. Indeed, residual variances can be larger, as expected when observing the variability of a single day. Such a pattern is typical of a random regression model, which actually tries to cope with the nonconstant variation of the genetic, environmental, and residual components. Brito et al. (2018), using different random regression models in primiparous Alpine goats, related that milk heritability ranged from 0.15 to 0.40 throughout the lactation. The same authors observed that the heritability estimates were lower in early and late lactation, particularly before 120 and after 150 DIM. Menéndez-Buxadera et al. (2010), in primiparous Spanish Murciano-Granadina goats, using a random regression model, found values ranging from 0.21 to 0.14 from wk 1 to wk 40. Thepparat et al. (2015), fitting random regression models with different covariance functions in an admixture population of Thailand goats, found that MY heritability ranged across lactation from 0.13 to 0.23. As expected, intraherd heritabilities were higher, reflecting the true additive genetic variability. The SCS showed the lowest heritability value, smaller than that reported by Rupp et al. (2011) in the French population.

Genealogical Data Analysis

In recent years, many studies have been conducted to connect certain diseases to inbreeding (Miglior et al., 1995; Falconer and Mackay, 1996; Smith et al., 1998; Thompson et al., 2000a,b). Traditionally, pedigree-based relationship coefficients have been used to estimate inbreeding even if now the widespread incorporation of genomic information in livestock management allows for the opportunity to develop and implement methods to manage populations at the genomic level (Howard et al., 2017). Nevertheless, when genomic information is not available, inbreeding estimation still depends on the quality of the genealogical information. Indeed, pedigree completeness, a parameter that describes the quality of available pedigree information, is of great importance in assessing inbreeding. A low degree of completeness can eventually cause bias in the estimation of an individual inbreeding coefficient. The observed average pedigree completeness index, first described by MacCluer et al. (1983), was 0.8 and 0.7 for Alpine and Saanen breeds, respectively (Table 5). Those values correspond to an average number of fully traced generations of 2.6 and 2.3. Martin et al. (2018), in their study about supernumerary teats in French Saanen and Alpine, report that the total number of complete generations was 4. No differences were observed between WT and normal does within breeds. The average inbreeding was actually higher in WT does

than in normal does but only in Alpine (5.1 vs 3.4). In Saanen breed, the opposite was observed. However, it must be noted that the Saanen WT group has the lowest pedigree completeness index value, especially in goats born in 2010. We can speculate that the inbreeding estimation in this group might be biased downward.

Retrospective studies can be very useful when coping with inherited disorders, and experiences in dairy cattle are quite informative (Agerholm, 2007). Indeed, the most interesting results from the genealogical data analysis regard the number of MRCA. If we consider the WT group in Alpine, the algorithm by Gauvin et al. (2015) identified 2 MRCA in goats born in 2007 and 1 in goats born from 2008 until 2010. Interestingly, both MRCA were 2 bucks born in 1979 and 1997, respectively. A different situation was observed in Saanen breed. In the WT group, 4 MRCA have been identified, all in goats born in 2010. Even in this case the MRCA are bucks born from 1975 to 1982. It is worthwhile to observe that 2010 is the year with the lowest pedigree completeness index. This could be due to some pedigree gaps on the maternal side.

CONCLUSIONS

The present study reported genetic parameters for the WT udder defect in Alpine and Saanen primiparous goats and their relationship with MY, SCS, and udder traits. Estimates of heritability for WT were moderate to high, suggesting a possible genetic background. Genetic correlation between WT and MY or SCS was generally uninformative due to the large standard error. Only in the Saanen breed was a positive genetic correlation between WT and MY observed. Positive (unfavorable) genetic correlations were observed among WT and teat characteristics. Using a genealogical data analysis, 2 and 4 common ancestors were found in Alpine and Saanen WT does, respectively. A valuable step forward in elucidating the genetic architecture of this defect would be the use of genomic information. Indeed, a national project that includes massive genotyping of the Italian Saanen and Alpine goat population coupled with an accurate phenotype collection, including possible defects, is currently ongoing. This approach will eventually provide valuable data to allow the investigation of possible regions of the genome related to the observed defect.

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