



Population structure and effect of inbreeding on milk yield of Saanen goats in Brazilian production systems

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ABSTRACT

The aim of this study was to evaluate the history of a population of Saanen goats based on the population structure and the effect of inbreeding on accumulated 305-d milk yield (*MY305*) and lactation length (*LL*). Pedigree records of 7640 individuals born between 1997 and 2014 were analyzed and population parameters were estimated based on the probability of gene origin, effective population size (*Ne*), average inbreeding coefficient (*F*), flock classification according to origin and use of breeding animals, average relatedness coefficient (*AR*), pedigree completeness and number of generations using the ENDOG v4.8 program. A total of 79.57 %, 50.73 %, 29.10 % and 11.60 % of the examined individuals had pedigrees in the first, second, third and fourth ascendancy, respectively. The total number of founders and ancestors was 123 and 101, respectively, and 39 of the latter explained 50 % of the genetic variability in the population, which indicates a loss of original genes. The *AR* and *F* coefficients were 0.78 % and 1.48 %, respectively. There was no significant inbreeding effect on *LL*. The *MY305* was significantly affected by inbreeding, with a reduction of 2.31 kg per 1% increase in the individual inbreeding coefficient. The *LL* and *MY305* exhibited heritability of 0.03 and 0.18 respectively, with a genetic correlation of 0.97.

1. Introduction

The genetic structure of the population can be defined as a function of the distribution of genetic variability between and within populations as a result of the combination among mutation, genetic flow, selection and genetic drift (Malhado et al., 2010). The main objective of studying the structure of populations is to estimate the parameters which characterize them, such as inbreeding and effective population size, in order to develop strategies to adequately manage genetic resources for conservation and take advantage of maximum diversity (Oliveira et al., 2011).

Inbreeding occurs in a breeding stock when mating occurs between related individuals. Therefore, its intensity is a direct function of the degree of relationship between the mated animals. This type of mating is mainly practiced by purebred breeders in order to ensure greater

breed uniformity and establish certain traits of interest. However, Falconer and Mackay (1996) show that an inbreeding level above 10 % has harmful effects on animals, mainly by compromising traits related to reproduction and viability, in addition to milk yield and animal growth. These authors defined inbreeding depression as a reduction in mean phenotypic value of traits associated with reproductive ability or physiological efficiency as a result of high inbreeding, which may also have a negative impact on other economic traits under selection.

The literature contains several reports on the significant influence of inbreeding depression on economically important traits in a number of animal species, such as cattle (Curik et al., 2014; Scraggs et al., 2014), buffaloes (Santana et al., 2011) and sheep (Pedrosa et al., 2010; Mokhtari et al., 2014; Eteqadi et al., 2015). Despite its importance, there are still few studies aimed at assessing population structure and especially the effects of inbreeding on traits under selection in goats

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(Barros et al., 2011; Rashidi et al., 2015). Brazilian goat herds use a wide variety of breeds, however the Saanen breed and its various crosses with other breeds is undoubtedly the most used in milk production systems. There are no precise statistical data, but in characterizing the goat milk production systems in *Cariri* region in *Paraíba* state (the country's main goat milk region, in northeastern of Brazil), Costa et al. (2010) reported that between 40 % and 50% of herds used Saanen bucks and does. The use of the Saanen breed is even greater in the southeastern region of Brazil, being characterized by more intensive production systems. Thus, the objective of the present study was to investigate the population structure and effect of inbreeding on accumulated 305-d milk yield (*MY305*) and lactation length (*LL*) of Saanen goats in Brazil.

2. Material and methods

Pedigree records and *MY305* and *LL* data were obtained from Saanen goats born between 1997 and 2014, in 26 flocks enrolled in the Dairy Goat Breeding Plan (Capragene®) conducted by *Embrapa Caprinos e Ovinos (Empresa Brasileira de Pesquisa Agropecuária)*, in partnership with the *Associação dos Criadores de Caprinos e Ovinos de Minas Gerais (Caprileite/ACCOMIG)*, Brazil. These flocks are distributed in the following states: one in Ceará, two in São Paulo, two in Rio de Janeiro, one in Espírito Santo and twenty in Minas Gerais. We used information from 3548 lactations obtained from 2154 goats distributed into 238 groups of contemporaries. The herds are generally kept on an intensive diet, receiving the total diet directly in the troughs installed in masonry and/or wood structures, except the herd from Ceará state which also received a concentrated diet and was allowed to graze a few hours a day.

The ENDOG 4.8 program (Gutiérrez and Goyache, 2005) was used to analyze pedigree and estimate population parameters based on the probability of gene origin, effective population size (*Ne*), average inbreeding coefficient (*F*), flock classification according to origin and use of breeding animals, average relatedness coefficient (*AR*), pedigree completeness and number of generations. The flocks were classified as “nucleus”, “multiplier”, “commercial” or “disconnected” according to the way the breeding animals were obtained and interchanged among the flocks. Pedigree completeness was assessed considering the amount and depth of the information contained in the records (Vassallo et al., 1986).

The number of complete generations, maximum number of generations and number of equivalent complete generations were traced. The first is defined as the number of generations that separate the progeny from the most distant generation in which all the individual's ancestors are known. The second indicates the number of generations that separate an individual from its most distant ancestor; and the third is obtained from the sum of all known ancestors in terms calculated under the condition of $(1/2)^n$, in which *n* is the number of generations that separate the individual from each known ancestor (Maignel et al., 1996).

Animals without known parents are called founders. Thus, based on the number of founders, the effective number of founders (*fe*) was calculated according to the equation:

$$fe = \frac{1}{\sum_{k=1}^f q_k^2} \quad (1)$$

in which *fe* is the effective number of founders and *q_k* is the *AR* of founder *k* (varying from 1 to *f*).

The effective number of ancestors (*fa*), which represents the minimum number of animals (founders or not) necessary to explain total genetic variability found in the population (Boichard et al., 1997), was estimated by the equation:

$$fa = \frac{1}{\sum_{j=1}^a q_j^2} \quad (2)$$

in which *fa* is the effective number of ancestors and *q_j* is the marginal contribution of ancestor *j* (varying from 1 to *a*).

Wright's *F*-statistics were obtained by the fixation coefficients *F_{ST}*, *F_{IS}* and *F_{IT}*. *F_{ST}* estimates the loss of heterozygosity in subpopulations compared to the total population; *F_{IS}* estimates the loss of heterozygosity within subpopulations; and *F_{IT}* estimates the loss of heterozygosity of the entire population. These coefficients can be estimated applying:

$$F_{ST} = \frac{\tilde{f} - \bar{f}}{1 - \bar{f}} \quad F_{IS} = \frac{\tilde{F} - \bar{f}}{1 - \bar{f}} \quad F_{IT} = \frac{\tilde{F} - \tilde{f}}{1 - \tilde{f}} \quad (3)$$

in which, \tilde{f} and \tilde{F} are the *AR* and *F*, respectively, for the total population, and \bar{f} is the *AR* for the subpopulation, such that $(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST})$.

Falconer and Mackay (1996) reported that the *F* coefficient in a determinate generation *t* could be estimated using the following equation:

$$F_t = 1 - (1 - \Delta F)^t \quad (4)$$

where ΔF corresponds to the inbreeding rate of a generation for the next or new inbreeding. González-Recio et al. (2007) proposed changing the above equation aiming to define the inbreeding rate for each individual, as represented below:

$$\Delta F_i = 1 - \sqrt[t]{1 - F_i} \quad (5)$$

where *F_i* is the individual inbreeding coefficient and *t* is the number of equivalent complete generations of the individual.

The *Ne* represents the relationship between the number of males and females that are genetically contributing to the population, and is therefore inversely proportional to the inbreeding rate. This was estimated as a function of the increase in inbreeding by the formula:

$$N_e = \frac{1}{2\Delta F} \quad (6)$$

The values of ΔF_i were used to estimate the effect of inbreeding on *MY305* and *LL*. The derivative-free restricted maximum likelihood (DFREML) method with a two-trait model (*MY305* and *LL*) was applied for this estimate, using the Multiple-Trait Derivative Free Restricted Maximum Likelihood (MTDFREML) program (Boldman et al., 1995). The following model was adopted for each trait:

$$Y_{ijklm} = X_{ij}\beta_j + Z_{ik}\alpha_{ik} + W_{il}p_{il} + e_{ijklm} \quad (7)$$

in which *Y_i* corresponds to the vector of observations of trait *i*; β , the vector of fixed effects *j*; α , the vector of additive genetic values *k*; *p*, the vector of permanent environmental effects *l*; and *e*, the vector of residual effects; and *X*, *Z* and *W* are incidence matrices for the aforementioned effects.

The model included the fixed effects of the contemporary group (*CG*) composed of goats with deliveries in the same season and year, the covariable age at delivery (linear and quadratic for *MY305* and linear for *LL*) and the individual increase in inbreeding (linear); and the direct additive genetic and permanent environmental random effects of the goat. The significance of the inbreeding effect was assessed using the *t*-test by contrasting in a subroutine of MTDFREML.

3. Results

3.1. Population parameter

The population parameters were determined from the base population, which means from the number of founders and ancestors which are responsible for the genetic variability found in the entire population (Table 1). A total of 1882 of the 7640 animals in the population under study had at least one unknown parent. Thus, the reference population in which both parents are known contained 5758 individuals.

Table 1
Population parameters of Saanen goats.

Population parameters	Number
Total population	7640
Base population (with at least one unknown parent)	1882
Number of animals in the reference population	5758
Average inbreeding (<i>F</i> , %)	1.48
Average relatedness coefficient (<i>AR</i> , %)	0.78
Number of animals that explain 50 % of the variability	39
Number of founders	1087
Number of ancestors	1036
Effective number of founders (<i>fe</i>)	123
Effective number of ancestors (<i>fa</i>)	101

3.2. Pedigree structure

Analysis of pedigree structure (Fig. 1) shows that 79.57 % of the 7640 animals studied exhibited pedigree in the first ascendancy (obtained from the average number of known parents); 50.73 % in the second; 29.10 % in the third; and 11.60 % in the fourth. Pedigree completeness (*I*) is the average percentage of the complete pedigree of each generation per year. If all the ancestors of an individual in a specific generation are known, then *I* = 1. If one of the parents is unknown, then *I* = 0. There was loss of information from the first to second generation, since 28.84 % of the animals had no information on their father or mother in the pedigree (obtained from the difference of the known parents), and 50.47 % showed no information on grandparents. The low value observed for the average number of complete generations traced (1.21) suggest the need to broaden the knowledge of ancestors in higher-order generations. However, a larger average number of remote ancestors were found for the maximum number of generations traced (Table 2).

The *AR* of individuals in the whole population showed significant changes across generations, with the lowest value in generation zero (0.15 %); it exhibited gradual increases in the following period, reaching value of 2.76 % in the fourth generation. Given the relationship between *AR* and *F*, it was found that the *F* estimated for the four generations showed increasing behavior, from 0.74 % in the first generation to 9.49 % in the fourth. Similarly, the percentage of inbred individuals, which was 4.58 % in the first generation, reached 100 % in the fourth generation (Table 3).

The *N_e* values were obtained in different ways in the present study (Tables 2 and 3) and ranged from 10 to 96. The Food Agricultural Organization (FAO, 1992) indicates that improvement nuclei must have a *N_e* of at least 50. If we consider the value calculated based on an increase in inbreeding per equivalent generation (*N_e* = 39.69), this number is below that recommended by the FAO.

Wright's *F*-statistics for the population under study showed values of 0.0011 for parameter *F_{IT}*; 0.028 for *F_{ST}* and -0.017 for *F_{IS}*. *F_{IS}*, which measures the deviation from random mating, was negative and close to zero, indicating low mating occurrence between relatives in the sub-populations (Carneiro et al., 2009), which contributed to reducing inbreeding.

Most flocks (69.0 %) were classified as multiplier flocks, in which

Table 2
Average number of generations traced, increase in inbreeding (ΔF) and effective size (*N_e*) by type of generation considered in Saanen goats.

Type of generation	Average number	ΔF (%)	<i>N_e</i>
Maximum	3.24	0.52	96.21
Complete	1.21	1.66	30.08
Equivalent complete	1.82	1.26	39.69

Table 3
Number of animals (*N*), average inbreeding coefficient (*F*), percentage of inbred individuals (%), average relatedness coefficient (*AR*) and effective size (*N_e*) of Saanen goats based on the complete generation.

Generation	<i>N</i>	<i>F</i> (%)	% inbred	<i>AR</i> (%)	<i>N_e</i>
0	1882	0	–	0.15	–
1 st	2967	0.74	4.58	0.63	67.7
2 nd	2168	2.6	37.27	1.21	26.6
3 rd	539	4.98	76.62	1.84	20.4
4 th	84	9.49	100	2.76	10.5

breeders also sell the breeding animals in addition to using their own and external sires. The other 31 % were classified as commercial flocks, since they use external breeding animals and their own, but do not sell them. None of the flocks were classified as a nucleus (flock which does not use external breeding animals). The use of purchased breeding animals in 100 % of the flocks may have contributed to maintain inbreeding at an acceptable level in the studied population (Table 4).

Average *MY305* was 753.10 ± 359.74 kg, while average *LL* was 312 ± 127.30 days. The effect of inbreeding on *LL* was not significant (*P* > 0.05). These great variations are explained by the diversity of environments and by the managerial decisions which are often made by the breeders to extend or shorten the lactations according to the conditions of the milk and/or breeding market. The *MY305* was significantly affected by inbreeding (*P* < 0.05), with a reduction of 2.31 kg of milk per 1% increase in individual inbreeding (ΔF_i) (Fig. 2).

The estimates of heritability for *MY305* and *LL* were 0.18 and 0.03, respectively (Table 5). Considering the milk yield, such heritability value was of moderate magnitude indicating the existence of genetic variability which can be exploited via selection and mating plans to obtain genetic progress.

4. Discussion

There was a difference between the average number of founders (*fe*) and ancestors (*fa*), such that the *fe/fa* ratio calculated was 1.22, which is lower than the ratio of 1.32 obtained by Rashidi et al. (2015). These authors report that the *fe/fa* ratio expresses the bottleneck effect and results from a decline in the number of breeding animals used between periods. The *fe/fa* ratio in our study suggests that almost all founders were also ancestors, given that the value was near 1.0, and that some of these founders stopped contributing effectively to the current population. According to Boichard et al. (1997), the effective number of ancestors makes it possible to assess the bottlenecks found in the pedigree,

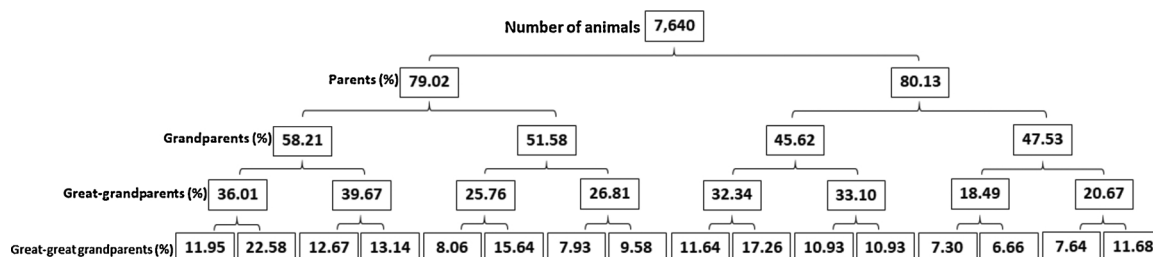


Fig. 1. Pedigree structure of the Saanen goats with percentage of known parents, grandparents, great-grandparents and great-great-grandparents.

Table 4
Flocks classification of Saanen goats according to the origin and ways of using the breeding animals.

Type of flock	Use external parents	Use own parents	Sell breeding animals	Number of flocks	Percentage of external parents
Nucleus	No	Yes	Yes	0	0.00
Multiplier	Yes	Yes	Yes	17	37.91
Multiplier	Yes	No	Yes	1	100.00
Commercial	Yes	Yes	No	5	55.81
Commercial	Yes	No	No	3	100.00
Disconnected	No	Yes	No	0	0.00

such that f_e will always be greater than or equal to f_a .

A small number of ancestors (39) belonging to the reference population explained 50 % of the genetic variability in the entire population. This indicates the disproportionate use of some breeding animals, since all the animals should ideally contribute equally across the generations. The value obtained for the effective number of ancestors (f_a) indicates the intense use of few breeding animals. The f_a observed in the present study was 101, higher than that found by Oravcová (2013) with White Shorthaired goats (45), and by Rashidi et al. (2015) with the Markhoz goats (37).

The F found (1.48 %) is acceptable, since according to Falconer and Mackey (1996) only values above 10 % are harmful. A higher inbreeding coefficient was observed in goats by Rashidi et al. (2015), who sustain that controlling F -values would be one of the ways to maintain the within-breed genetic variability. The AR and F values have been used to assess the loss of intra-breed diversity. The AR value indicates the likelihood of an allele randomly taken from the population belonging to a given animal, such that the higher its value, the closer the relatedness with the current population. Emphasis must be given to using breeding animals with the lowest AR values in order to control inbreeding.

The estimates of effective population size in different types of generations (Table 2) considering pedigree completeness are useful in indicating the upper (maximum number of generations traced), lower (complete generations traced) and real limit (equivalent generations traced) of the N_e in populations in which genealogical information is scarce (Gutiérrez et al., 2005).

With this, ΔF which is the approximation rate to the complete inbreeding in each generation depends on the value of the N_e , meaning that the lower the N_e in previous generations, the higher the number of

Table 5
Estimates of variance, heritability and repeatability for accumulated 305-d milk yield (MY305) and lactation length (LL) in Saanen goats.

Trait	MY305	LL
Additive genetic variance (σ^2_a)	11178.40	242.06
Permanent environmental variance (σ^2_{pe})	13185.80	653.75
Residual variance (σ^2_e)	38110.68	7626.47
Phenotypic variance (σ^2_p)	62474.88	8522.28
Direct heritability (h^2_d)	0.18	0.03
Repeatability (t)	0.39	0.10

common ancestors. Thus, the value of ΔF will also be higher. The lower average number of complete generations (1.21) indicates that a small number of ancestors were known, which therefore raised the probability of a greater increase in inbreeding (1.66) within the three types of generations given the lower N_e (30.08). On the other hand, a larger average number of remote ancestors were observed for the maximum generations when compared to their complete (most remote ancestors) and equivalent (all known ancestors) counterparts. Thus, the probability of obtaining high inbreeding rates was lower; a fact reinforced by the lower ΔF and higher N_e for the maximum generations.

The values found for equivalent complete generations were intermediate, since the calculation considered all known ancestors, and not only the most remote. However, N_e values oscillated according to the inbreeding rate, given that N_e is calculated as a function of ΔF for equivalent generations, which displays an inversely proportional relationship. A consistent increase in F and the percentage of inbred animals across generations can be explained by the fact that the more complete generations of an individual are known, the greater the probability of an important ancestor having contributed to the pedigree more often. The absence of some values in generation 0, symbolized by a dash, is due to the lack of information on inbreeding in the previous generation, formed by the founding population.

The low AR values observed resulted from the small number of known generations. The AR can show different tendencies and evolution across generations as a function of the amount of information regarding the pedigree (Oravcová and Margetín, 2011).

The large number of animals in this population of Saanen goats and the modern reproduction techniques that allow introducing genes from other populations make it possible to increase the N_e to more acceptable levels once again. However, it is generally expected that populations submitted to genetic improvement programs decrease their effective size due to the smaller proportion of animals selected for

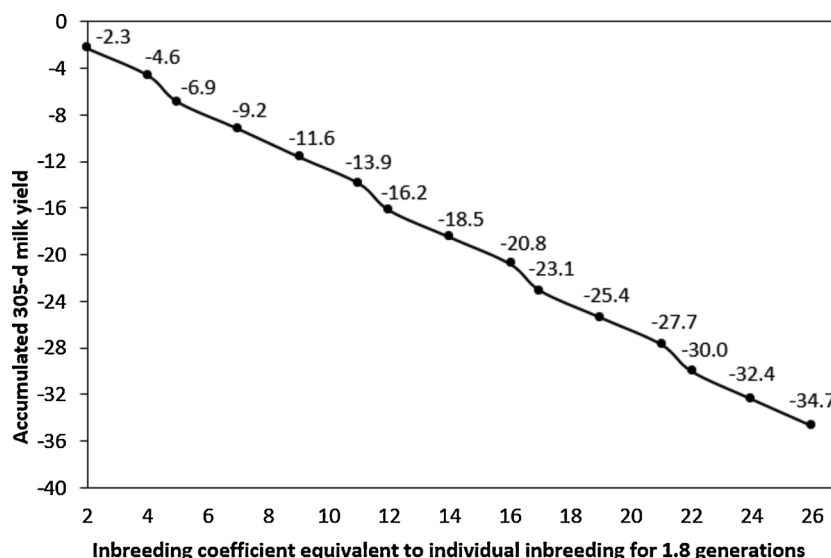


Fig. 2. Inbreeding depression effect on accumulated 305-d milk yield in Saanen goats.

reproduction, leading to an increased intensity of the selection, and in turn to a greater probability of loss of variability.

Barros et al. (2011) defined F_{IS} , F_{ST} and F_{IT} statistics as a reduction in heterozygosity within subpopulations, between subpopulations and in the entire population, respectively. F_{ST} values between 0.05–0.15; 0.15–0.25; and over 0.25 in this sequence indicate a moderate, high and very high magnitude of difference between subpopulations (Malhado et al., 2010). The low F_{ST} value reveals an absence of population structure, demonstrating intergroup genetic exchanges, given that no division occurred in the population. The low F_{ST} value is likely associated with the fact that 100 % of the flocks used external breeding animals, and 69 % sold their own. The intensive use of some animals added to their low flow between flocks may have led to the formation of subpopulations; however, F-statistics show that this is not occurring at the moment in the studied population. Given that interpreting ΔF_1 is not simple, this parameter was transformed to the inbreeding coefficient for animals with average pedigree depth using the equation proposed by Falconer and Mackey (1996) for the F and fixing $t = 1.82$ equivalent complete generations to illustrate the effect of individual inbreeding rate on the traits.

An increase of 1% in ΔF_1 (equivalent to a traditional inbreeding coefficient of 1.81 % when 1.82 equivalent generations are known in the pedigree) reduced *MY305* by 2.31 kg. Thus, there was a decline of 1.3 kg/% F. According to González-Recio et al. (2007), the F coefficient depends on the known depth of the pedigree, with ΔF_1 being an alternative parameter that relates an increase in inbreeding in the population and represents the amount of known pedigree. This property is an advantage of ΔF_1 over F, when a large amount of pedigree is unknown.

The results show that a female descending from the mating between a father and its daughter will therefore exhibit an inbreeding coefficient of 25 %, and considering 1.82 equivalent generations known in its pedigree, it will produce 34 kg less milk than a non-inbred female up to 305 days. Therefore, inbreeding depression may compromise the sustainability of production systems, leading to significant economic losses. According to Leroy (2014), inbreeding depression is assessed in species by measuring the decrease rate in the trait of interest with an increase in the inbreeding coefficient.

Deroide et al. (2016) studied inbreeding depression in Murciano-Granadina goats for total milk yield, showing the significant linear and quadratic effects of inbreeding, differing from our investigation, in which only a significant linear effect was found. They estimated the negative effects up to an inbreeding level of 10.59 %, which caused a decline in total milk yield of 19.02 kg of milk. Khan et al. (2007) studied the effect of inbreeding on the growth and reproduction traits of Beetal goats, applying regression analysis. They found a significant effect of inbreeding on birth weight, weaning weight, and pre and post-weaning average daily gain. Pedrosa et al. (2010) investigated the effect of inbreeding depression on birth weight, weight at 60 days and 180 days of Santa Inês sheep, observing a significant inbreeding depression effect on all the traits.

The moderate estimate of the heritability for *MY305* (0.18) indicated for existing genetic variability which could be exploited by genetic selection and mating plans aiming at genetic progress for milk yield. Irano et al. (2012) studied Saanen and Alpina goats and estimated heritability of 0.29 for *MY305*. They considered it to be of moderate magnitude which should provide a response to selection, as we observed herein. In the same study, the repeatability for *MY305* was 0.36, also of moderate magnitude, suggesting the possibility of using the first lactations of goats as an indication of future production, thereby serving as a parameter to select the females which will continue producing in the flock. The low magnitude heritability of *LL* (0.03) demonstrates the significant effect that the environment had on this trait. Thus, the selection for *LL* should not have significant effects. It is important to underscore that the *LL* observed in this population is already satisfactory, dispensing efforts to improve it.

Lôbo and Silva (2005) studied Saanen and Anglo-nubiana goats,

estimating the genetic parameters for milk yield and lactation length. Heritability values of 0.12 and 0.03, respectively, were found in Saanen; and of 0.10 and 0.07, respectively, in the Anglo-nubiana. The heritability estimates indicated small additive genetic variability to be exploited in these populations. In this study a genetic correlation of 0.97 was estimated between *MY305* and *LD*. The high magnitude for this correlation was expected, given that animals with greater productive potential show tendency of stabilizing their production and increasing the *LL*.

5. Conclusions

There is no population subdivision considering the population structure of the evaluated Saanen flocks. The *F* and *AR* are under control and serve as a starting point to establish a future genetic management plan for flocks. Nevertheless, there is an inbred depression effect on *MY305* reducing significantly the averages assessed.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

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