

The effect of inbreeding on birth weight of Saanen goat kids

Utjecaj uzgoja u srodstvu na porodnu masu jaradi sanske pasmine

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ABSTRACT

The study aimed to examine the effect of inbreeding on the birth weight (BW) of Saanen goat kids under the framework of the genetic animal model for maternal traits. The BW of the kids was analyzed as the inherent phenotypic trait of the kid, and not of their mothers (does) which means that the impact of the direct inbreeding (not maternal) was examined. The estimated ratios of variance components for direct genetic, indirect maternal genetic, maternal permanent environmental, and herd effects were 0.127, 0.026, 0.163, and 0.373, respectively. The average coefficient of inbreeding (F) was 2.5%, and 4.2% among the inbreds. The results of the preliminary conducted glm ANCOVA analysis implicated statistically significant inbreeding depression for BW ($\beta_F = -0.0076$, $P < 0.001$). However, when the genetic animal model for maternal traits was applied in the inferential statistical analysis, it turned out that there was no statistically significant effect of F on BW of kids in this population ($\beta_F = 0.0001$; $P > 0.05$).

Keywords: Saanen goat, kids, birth weight, inbreeding

SAŽETAK

Cilj istraživanja bio je utvrditi utjecaj uzgoja u srodstvu na porodnu masu jaradi sanske pasmine koza genetskim "animal" modelom za materinska svojstva. Pritom je svojstvo porodne mase promatrano kao inherentno svojstvo jaradi, a ne njihovih majki (koza) što znači da je analiziran utjecaj direktnog, a ne maternalnog uzgoja u srodstvu. Procijenjeni udjeli komponenti varijance za direktne genske učinke, indirektno materinske genske učinke, trajne materinske učinke te učinke stada bili su redom 0,127, 0,026, 0,163 i 0,373. Prosječni utvrđeni koeficijent uzgoja u srodstvu (F) bio je 2.5%, a inbirdiranih jedinki 4.2%. Rezultati preliminarno provedene glm ANCOVA analize upućivali su na postojanje statistički značajne inbirding depresije za porodnu masu jaradi ($\beta_F = -0,0076$, $P < 0,001$). Međutim, kada je u inferencijalnoj statističkoj analizi primijenjen genetski "animal" model za majčinske osobine, utvrđeno je da uzgoj u srodstvu nije imao statistički značajan utjecaj na porodnu masu jaradi u ovoj populaciji ($\beta_F = 0,0001$; $P > 0,05$).

Ključne riječi: Sanska koza, jarad, porodna masa, uzgoj u srodstvu

INTRODUCTION

There are two major directions of goat farming in Croatia, extensive breeding systems in the karst areas mainly focused on meat production, and semi-intensive breeding systems in continental areas focused on milk production. According to the Annual report of the Ministry of Agriculture, in the year 2018, there were approximately 68000 goats in Croatia, 7395 of which were encompassed by the national selection program (MOA, 2019). Saanen breed was the third most numerous breed in Croatia enrolled in selection program (11.45%). The breed has been predominantly reared in dairy orientated farms in the north-western part of the country. Twenty breeders have been enrolled in selection program with the average herd size of 42 goats and average daily milk gain of approximately 3.3 kg. Selection of dairy goats in Croatia from its earliest days up to now has been directed toward improvement of the economically important traits (milk yield, fat and protein content). The goats enrolled in the national selection program have been subjected to the routine milking controls and recording of reproductive performances for more than two decades now, and recently, breeders have been provided with the BLUP estimated breeding values for the dairy traits. The goat milk is a major source of the income for the breeders of this breed regardless of being sold to the dairies or being processed into cheese on the homesteading. However, a part of the income is obtained by selling replacements and non breeding kids (for meat production). Inbreeding generally refers to the mating of two genetically related individuals and product of such breeding is an inbred animal. The level of inbreeding for an animal can be estimated from the pedigree data and expressed by the coefficient of inbreeding (Wright, 1922). Inbreeding is impossible to avoid in the livestock breeding, and it is particularly hard to keep it under control in populations under a high selection pressure (e.g. Bijma et al., 2001). The main reason is excessive usage of genetically superior sires. Due to its' negative effect on the productivity and viability of animals a.k.a. inbreeding depression (Falconer and Mackay, 1996), great efforts have been made to minify inbreeding in various livestock breeding schemes

(e.g. Bijma et al., 2001; Weigel, 2001). Knowledge about the extent of inbreeding depression for some traits is still very scarce. The phenotypic expression of some traits such as birth weight is influenced by the dam through her direct genetic effects passed to the progeny and through her ability to provide a suitable environment, for example the prenatal nourishment (e.g. Gardner et al., 2007). Such traits are considered as maternal traits and from a genetic point of view require a special statistical approach in the analysis. The application of genetic evaluation models for maternal traits was first presented by Quaas and Pollack (1980). The objective of this study was to evaluate the rate of inbreeding and inbreeding depression for birth weight (BW) in the population of Saanen dairy goats under the framework of the genetic animal model for maternal traits by accounting all the available information contributing to the phenotypic variability of BW.

MATERIAL AND METHODS

Genealogical information, phenotypic records, and all other information used in this study were provided by the Ministry of Agriculture. These data that have been routinely collected in Croatia for about 30 years now, provide a significant basis for breeding activities in the Saanen dairy goat population. Herd affiliation, parity, age of does at kidding, type of birth (a.k.a. litter size), sex, and season of kidding were considered as important environmental sources of phenotypic variability of birth weight (BW) in this study. For the purpose of inferential statistical analysis, litters with three and more kids were considered as the same class, which was from now on referred to as 3+. Parities after 7th were also merged into the same class (7+). Herds with less than ten kiddings within a year were excluded from the data set. Season of kidding was defined as a month within a year and few seasons with small number of records were joined to the adjacent ones to boost the frequency of the classes. Animals with missing any of the above discussed records were omitted from the data set and a total of 17996 BWs were used in the inferential statistical analysis. In the first stage of the study, all genealogical information was used in construction of the pedigree and after that,

some non informative animals were omitted (pruned) from the pedigree. There are always some individuals in the pedigree that jut out. Usually this are older individuals without known ancestors, founders. If such individuals have only one (first) descendant and no phenotype data, then they do not give us any additional information and can be safely removed from the pedigree. Coefficients of inbreeding (F) for the animals in the pedigree were calculated with software CFC (Sargolzaei et al., 2006), and joined to the data set with phenotypic records. Prior to the examination of the impact of the level of inbreeding (F) on the BW with mixed modeling approach, we conducted a preliminary ANCOVA statistical analysis with GLM procedure. Sex, type of birth, parity, age and season were found to have a significant effect on BW. These effects were treated as important sources of phenotypic variability in the inferential statistical analysis pertaining to the estimation of the effect of F on BW. The following statistical genetic animal model for maternal traits was used in the final statistical analysis:

$$Y_{ijklmnopr} = \mu + P_i + L_j + S_k + SE_l + \beta_a (x_i - \bar{x}_i)^2 + \beta_F (z - \bar{z}) + a_m + m_n + h_o + p_p + e_{ijklmnopr} \quad [1]$$

Parity (P_i ; $i = 1, 2, \dots, 7+$), litter size (L_j ; $j = 1, 2, 3+$), sex (S_k ; $k = 1, 2$), and season of the kidding (SE_l ; $l = 1, 2, \dots, 200$) were fitted as class fixed effects. The age of does at kidding was nested within parity as quadratic regression (β_a ; $x = \text{age in months}$, $i = 1, 2, \dots, 7+$). The coefficient of inbreeding (F) was fitted as simple linear regression (β_F , $z = \text{coefficient of inbreeding}$). The random effects in the model were: direct genetic (a_m ; $m = 1, 2, \dots, 21118$), maternal genetic (m_n ; $n = 1, 2, \dots, 21118$), herd (h_o ; $o = 1, 2, 3, \dots, 86$), and maternal permanent environmental effect (p_p ; $p = 1, 2, \dots, 4838$).

The covariance components were estimated by Residual Maximum Likelihood Method (REML) with VCE-6 (Groeneveld et al., 2008). The best linear unbiased estimation (BLUE) of the effect of F on the BW was estimated with the same model and with the same software by using previously obtained components of variance.

RESULTS AND DISCUSSION

After “pruning” of the non-informative individuals, the pedigree contained 21118 animals in total. Summary of the genealogical information for animals under consideration is given in the table 1. Sixty percent of the animals in the pedigree were inbred to some degree. However, the majority of the inbreds (81%) had a really long path ($F < 0.05$) to the common ancestors (Table 2).

Table 1. Structure of the pedigree

Class	Number of animals
Individuals in total	21118
Sires in total (progeny)	833 (20105)
Dams in total (progeny)	5861 (19543)
Inbreds	12770
Non-inbreds	8348
Founders	323
Non-founders	20795
Non founder sires (progeny)	724 (18158)
Non founder dams (progeny)	5698 (18755)

Table 2. Distribution of the coefficient of inbreeding

Coefficient of inbreeding (F)	Number of animals
0.00 < F <= 0.05	10380
0.05 < F <= 0.10	820
0.10 < F <= 0.15	448
0.15 < F <= 0.20	199
0.20 < F <= 0.25	244
0.25 < F <= 0.30	607
0.30 < F	72
Maximum F	0.391
Average F	0.025
Average F in the inbreds	0.041

A higher level of inbreeding ($F > 0.20$) was determined in only 5% of the inbreds. These frequencies, in addition to the average F (0.042 for inbreds and 0.025 for the entire population) implicate that mating of closely related individuals in this population has been under control. It is true that some breeders allow inbreeding in their herds, but they seldom allow inbreds to be used as replacements in their herds. The average BW of kids classified by litter size, sex, and parity and by status of inbreeding (inbreds vs. non-inbreds) is presented in the Table 3. BWs were higher in all analyzed non-inbred categories than in inbreds, except for category of kids being born by first parity does.

For the sake of straightforwardness, it should be noted here that the additive genetic relationship coefficient between individuals with unknown ancestors (founders) was set to 0, which means that F could be underestimated for some animals in the pedigree.

However, even that this had been true, by being far distant from the phenotypic records, this would have had a negligible impact on our inferential statistical analysis and getting the answer about magnitude and direction of the effect of F on BW. Our initial suspicion of the presence of the inbreeding depression based on the results of the descriptive statistical analysis was thoroughly checked, first with the glm ANCOVA approach and later with mixed model ANCOVA approach. The results of the glm ANCOVA analysis suggested statistically significant inbreeding depression with β_F estimated at approximately -0.0076 ($P < 0.001$), depending on the model. The results of the ANCOVA analysis were intentionally not presented in the tabular form in the manuscript in order to minimize the chance for the reader to perceive the obtained result as a trustworthy. Many researchers heavily rely on the glm procedure in their inferential statistical analysis, but there are procedures and approaches in the statistical

Table 3. Descriptive statistics for BW classified by litter size, sex, and parity according to the coefficient of inbreeding

Item	Class	F=0			F>0		
		n	\bar{X}	sd	n	\bar{X}	sd
Litter size	1	2355	3.32	0.72	4633	3.24	0.65
	2	2902	3.27	0.62	5806	3.19	1.39
	3+	927	3.10	0.56	1343	2.99	0.55
Sex	M	2285	3.40	0.68	4127	3.28	0.63
	F	3899	3.19	0.63	7655	3.14	1.25
Parity	1	1837	3.10	0.62	2934	3.12	1.90
	2	1090	3.34	0.62	2976	3.22	0.61
	3	841	3.46	0.64	2262	3.20	0.60
	4	809	3.36	0.64	1509	3.21	0.56
	5	596	3.29	0.63	995	3.20	0.59
	6	348	3.27	0.66	538	3.16	0.60
	7+	663	3.23	0.74	568	3.18	0.55
Overall		6184	3.26	0.66	11782	3.19	1.08

sd = standard deviation, F = coefficient of inbreeding

analysis that provide greater inferential power, such as mixed model approach. This is particularly valuable in genetic studies overwhelmed with unbalanced data so we decided to perform an additional analysis with the genetic animal mixed model for maternal traits as suggested by Mrode (2014). All growth traits in mammals until weaning (including the BW) are not only influenced by the genes of the individual for growth (direct additive genetic effect), but also by the maternal genetic composition (indirect maternal genetic effect) and by non-genetic environment provided by the dams (permanent environment effect). Accounting for these random sources of phenotypic variability were particularly important for the final outcome of this study pertaining to the estimated effect of F on BW. The estimated ratios of variance components for direct genetic effects, indirect maternal genetic effects, maternal permanent environment, and herd were 0.127, 0.026, 0.163, and 0.373, respectively. (Table 4).

The estimated correlation between animal and the maternal genetic effect was negative (-0.967), which is in general agreement with prevailing results on this issue. For example, this correlation for BW in Boer (Zhang et al., 2008), Creole (Menendez-Buxadera et al., 2003), and Angora (Snyman, 2012) breeds were all negative.

Table 4. Estimates of variance components for BW with animal model for maternal traits

Class	Component	Symbol	(Co)variance	Ratio
Genetic	Animal (direct additive)	σ_a^2	0.160	0.127
	Maternal (indirect additive)	σ_m^2	0.033	0.026
	Covariance between animal and indirect genetic effects	σ_{am}	-0.070	-0.967
Non-genetic	Maternal permanent environment	σ_p^2	0.205	0.163
	Herd	σ_h^2	0.469	0.373
Residual	Residual	σ_e^2	0.529	0.421

Due to the prevalence of determined negative correlations between direct and maternal genetic effects for BW in all livestock species, this correlation is among the researchers prevalently perceived as negative.

Finally, and the most importantly for this study, when all the available sources of the phenotypic variability of BW were accounted for with the appropriate statistical model, it was found that inbreeding did not statistically affect BW of Saanen goat kids ($\beta_F = 0.0001$, $P > 0.05$). The result is in general agreement with numerous previous reports on this issue in sheep and goats where there was no significant inbreeding depression on BW (e.g. Dorostkar et al., 2012, Mokhtari et al., 2014, Rashidi et al., 2015). Albeit it seems that inbreeding is not very detrimental for the BW of goats, generalization of this effect based on the results of this and previous studies should be avoided, or at least performed with great caution because inbreeding depression could have been masked by positive responses to selection and/or imbalance of the non-experimental field data. Likewise, comparisons of the results between the studies have to be conducted with great precaution, not only due to large discrepancy in analyzed data sets, but also due to different analytical approaches applied in different studies.

CONCLUSIONS

The results underpin scientific claims that Inbreeding is not unconditionally detrimental, and that the effects of Inbreeding heavily depend upon: genetic makeup of the population, genetic architecture of the trait, and genetic effects on causal loci. Inbreeding did not affect BW of Saanen goat kids which might be the reflection of the correlated response to selection on the dairy traits in this population. However, more scientific evidence is needed to generalize the absence of this effect, especially in the goat populations that had never been systematically bred.

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