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Genetic variability and bottleneck analysis of Barbari goat population using microsatellite markers

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ABSTRACT

Genetic variation at 24 microsatellite loci and genetic bottleneck hypothesis were examined for Barbari goat population found in Uttar Pradesh, India. The estimates of genetic variability such as effective number of alleles and gene diversities revealed substantial genetic variation. Shannon's information index as indicator of polymorphism across studied loci, and Nei's expected heterozygosity were 1.183 and 0.58±0.191, respectively. The population was observed to be significantly differentiated into different groups, and showed heterozygote deficiency (f=0.202±0.044). The population has not suffered bottleneck in recent past. The study revealed that the Barbari goat breed needs genetic management for its conservation and improvement.

Key words: Barbari, Bottleneck, Genetic variation, Goat, Microsatellite markers

Barbari, a dual purpose (milk and meat) dwarf goat breed, evolved and adapted around Agra, Aligarh, Etah, Etawah, Hathras and Mathura districts of Uttar Pradesh, India (Acharya 1982). Its origin was traced to the city of Berbera, Somalia in East Africa (Singh 1966, Jindal 1984). The breed is highly prolific and non-seasonal (Devendra 1985) and well suited for rearing under restrained and stall-feeding conditions. An investigation for genetic variation within the breed, and its structure may help to evaluate how likely various factors responsible for change in its foundation genetic structure are operating.

Of the many genetic markers now available, microsatellite loci are best suited for answering these questions (Goldstein and Pollock 1997) due to high variability and mutation rate, large numbers, distribution throughout the genome, codominant inheritance and neutrality with respect to selection (Boyce *et al.* 1996). The aim of this study was to estimate genetic variability in the Barbari breed of goat using microsatellite markers.

MATERIALS AND METHODS

Molecular techniques

Blood sampling was done as per the guidelines of FAO's MoDAD (Measurement of Domestic Animal Diversity) programme. Thus, 50 blood samples (25 each from Mathura and Agra districts) were collected from breeding tract of Barbari to make them representative of population. As far as could be ascertained, unrelated animals were chosen. Samples were taken from different villages, and owners were questioned in detail in order to avoid close relationships. Genomic DNA was isolated by the method described by Pandey *et al.* (2002). A battery of 24 microsatellite markers (Table 1) was selected based on the guidelines of ISAG and FAO's DADIS programme. Polymerase chain reaction (PCR) was carried out on about 50-100 ng genomic DNA in 25 µl reaction volume. The reaction mixture consisted of 200 µM each of dATP, dCTP, dGTP and dTTP, 50mM KCl, 10mM tris-HCl (pH 9.0), 0.1% Triton X-100, 2.0 mM $MgCl_2$, 0.75 unit *Taq* DNA polymerase and 4 ng/µl of each primer using PTC-200 PCR machine. The "touchdown" PCR protocol used with initial denaturation of 95°C for 1 min, 3 cycles of 95°C for 45 sec and 60°C for 1 min, 3 cycles of 95°C for 45 sec and 57°C for 1 min, 3 cycles of 95°C for 45 sec and 54°C for 1 min, 3 cycles of 95°C for 45 sec and 51°C for 1 min, 20 cycles of 95°C for 45 sec and 48°C for 1 min. PCR products were loaded on 2% agarose gel, electrophoresed and visualized over UV light after ethidium bromide staining to detect the amplification.

The PCR products were resolved on 6% denaturing polyacrylamide gels 10 bp ladder was used as a size standard. To visualize the PCR products gels were stained using silver staining (Bassam *et al.* 1991). The genotypes were scored manually.

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Table 1. Microsatellite markers, their sequences, type of repeat, location and accession numbers

Locus	primer sequence	Type of repeat	Ch. No. repeat	Gene Bank Acc. Number
OarHH64	cgttcctcactatggaaagttatatatgc cactctatthtaagaatttgaatgagagc	-	4	212*
ILSTS34	aagggtctaagtccactggc gacctggtttagcagagagc	$(GT)_{29}$	5	L37254
ILSTS 05	ggaagcaatgaaatctatagcc tgttctgtgagtttgtaagc	$(nn)_{39}$	10	L23481
OarFCB304	ccctaggagctttcaataaagaatcgg cgctgtcaactgggtcaggg	$(CT)_{11}(AC)_{15}$	Ann	L01535
ILSTS008	gaatctggatttctgggg tagcagtgatgaggttggc	$(CA)_{12}$	14	L23483
ILSTS044	agtcacccaaaagtaactgg acagttgtattccaaagtgc	$(GT)_{20}$	Ann	L37259
ILSTS019	aagggacctcatgtagaagc actttggaccctgtagtgc	$(TG)_{19}$	Ann	L23492
ILSTS087	agcagacatgatgactacagc ctgcctcttttcttgagagc	$(CA)_{14}$	Ann	L37279
ILSTS30	ctgcagttctgcatatgtgg cttagcaacaggggtttgg	$(CA)_{33}$	2	L37212
RM4	cagcaaaatatcagcaaacct, ccacctgggaaggccttta	$(CA)_{13}$	15	U32910
ILSTSO49	caatttcttgtctctcccc gctgaatcttgtcaaacagg	$(CA)_{26}$	11	L37361
ILSTS002	tctatacacatgtgctgtgc cttagggtgaagtgacacg	$(CA)_{17}$	Ann	L23479
ETH225	gatcaccttgccactatttcct,cccatgacagccagctqctact	$(CA)_{18}$	14	Z14043
ILSTS033	tattagagtggctcagtgcc atgcagacagttttagaggg	$(CA)_{12}$	12	L37213
ILSTS022	agtctgaaggcctgagaacc cttacagtccttggggttgc	$(GT)_{21}$	Ann	L37208
ILSTS058	gccttactaccatttccagc catccgactttggctgtgg	$(GT)_{15}$	17	L37225
OMHC1	atctggtgggctacagtccatg gcaatgctttctaaaattctgaggaa	-	Ann	228*
OarFCB48	gagttagtacaaggatgacaagaggcac gactctagaggatcgcaaagaaccag	$(GT)_{10}$	17	M82875
ILSTS029	tgtttgatggaacacagcc tggatttagaccagggttgg	$(CA)_{19}$	3	L37252
ILSTS065	gctgcaaagcttgaacacc aactattacaggaggctccc	$(AC)_{22}$	24	L37269
ILSTS059	gctgaacaatgtgatatgttcagg gggacaatactgtcttagatgctgc	$(CA)_4(GT)_2$	13	L37266
RM088	gatcctcttctgggaaaaagagac cctgttgaagtgaaccttcagaa	$(CA)_{14}$	4	U10392
OarAE129	aatccagtgtgtgaaagactaatccag gtagatcaagatatagaatatttttcaacacc	$(CA)_{14}$	7	L11051
ILSTS082	ttcgttcctcatagtgctgg agaggattacacaccaatcacc	$(GT)_{17}$	2	L37236

*Accession number of Arkdob base (htt://www.thearkdb.org).

Statistical analysis

Observed and expected heterozygosity estimates were calculated after Levene (1949) and Nei (1973) as implemented in POPGENE software (Yeh *et al.* 1999). The observed and effective numbers of alleles (Kimura and Crow 1964) were also calculated using POPGENE software.

The tests for deviation from Hardy-Weinberg equilibrium were derived using the exact tests of POPGENE. Heterogeneity of deviations from Hardy-Weinberg equilibrium among the microsatellite loci was examined by treating the deviations as correlation coefficient and tested accordingly (Barker *et al.* 2001). As samples were obtained from different localities (districts), deviations from Hardy-Weinberg equilibrium in the population could be due to genetic differences between subpopulations and a consequent Wahlund effect. Given the observed allele frequencies in each subpopulation, the expected heterozygote deficit due to Wahlund effect can be computed (Li 1976). Expressing this as a percentage of observed heterozygote deficit then measures the contribution of Wahlund effect to the observed heterozygote deficit. Heterozygote deficiencies were expressed as $D=[H_0-H_e]/H_E$ where H_0 and H_E are the observed and expected frequency of heterozygotes, respectively.

Tests for pair-wise linkage (genotypic) disequilibrium among the microsatellite loci were done using F-STAT version 2.9.3 an update version 1.2 (Goudet 1995). F-statistics were determined after Weir and Cockerham (1984) as used in F-STAT software with Jackknifing procedure applied over loci in deriving significance levels. These parameters of population structure are defined as the correlations between pairs of genes (i) within individuals (F), (ii) between individuals in the same population (θ), and (iii) within individuals within populations (f), and are analogous to Wrights (1978) F_{IT}, F_{ST} and F_{IS}, respectively.

Finally the bottleneck hypothesis was investigated using BOTTLENECK 1.2.01 (Cornuet and Luikart 1996). The BOTTLENECK test for the departure from mutation drift equilibrium based on heterozygosity (not hetrozygote), excess or deficiency. Bottleneck compares heterozygosity expected (H_E) at Hary-Weinberg equilibrium to the heterozygosity expected (H_{eq}) at mutation drift equilibrium in same sample, that has the same size and the same number of alleles. All the 3 models of mutation were used to calculate H_{eq}. The strict one-step mutation model of mutation was used to calculate H_{eq}. The strict one-step mutation model (Ohta and Kimura 1973), the infinite allele model (Kimura and Crow 1964) and two-phase model (Di Rienzo *et al.* 1994).

RESULTS AND DISCUSSION

The number of alleles observed across the studied microsatellite loci varied from 2 (ILST 044, ILSTS059 and ETH225) to 10 (OarFCB304, OarHH41) with an overall mean of 5.542±2.167 (Table 2). The observed number of

Table 2. Measures of genetic variation and heterozygote deficiency in Barbari goat

Locus	Observed number of alleles	Size range (base pairs)	Effective number of alleles	Shannons information index	PIC	Observed	Heterozygosity[a] expected	Neis	Heterozygote deficiency[b]	f-value[c]
OarHH64	4	124-130	2.661	1.096	0.559	0.250	0.631	0..624	-0.604	0.600*
ILSTS034	5	151-171	1.514	0.755	0.327	0.250	0.343	0.339	-0.271	0.263*
ILSTS005	4	172-190	1.539	0.654	0.313	0.426	0.354	0.350	0.203	-*
OarFCB304	10	150-178	4.037	1.646	0.714	0.738	0.761	0.752	-0.30	-
ILSTS008	5	171-181	1.833	0.933	0.428	0.512	0.460	0.455	0.113	-
ILSTS044	2	155-157	1.207	0.313	0.157	0.135	0.174	0.171	-0.224	-
ILSTS019	5	148-156	2.804	1.254	0.601	0.317	0.651	0.643	-0.513	0.507*
ILSTS087	6	145-159	4.346	1.599	0.735	0.676	0.781	0.770	-0.134	-
ILSTS030	6	153-171	3.379	1.446	0.668	0.694	0.714	0.704	-0.113	-
RM4	5	115-123	1.855	0.950	0.434	0.500	0.466	0.461	0.072	-
ILSTS49	5	170-178	3.316	1.343	0.647	0.548	0.707	0.698	-0.225	0.216
ILSTS002	7	114-128	5.172	1.730	0.778	0.561	0.817	0.807	-0.313	0.305
ETH225	2	151-153	1.366	0.439	0.232	0.234	0.271	0.268	-0.137	-
ILSTS033	6	170-182	2.003	1.076	0.475	0.525	0.507	0.501	0.036	-*
ILSTS022	6	190-204	4.026	1.459	0.708	0.689	0.760	0.52	-0.093	-
ILSTS058	6	139-181	2.761	1.283	0.560	0.433	0.649	0.638	-0.332	0.321
OMHC1	7	189-201	3.627	1.576	0.696	0.463	0.733	0.724	-0.368	0.360
OarFCB48	7	15-179	5.387	1.794	0.789	0.500	0.825	0.814	-0.394	0.386
OarCP34	4	120-128	2.171	0.890	0.446	0.643	0.546	0.539	0.178	-
ILSTS029	4	153-167	1.448	0.623	0.288	0.333	0.313	0.309	0.064	-
OarHH41	10	127-151	3.769	1.677	0.705	0.652	0.743	0.735	-0.122	-
ILSTS059	2	155-157	1.867	0.657	0.357	0.200	0.472	0.464	-0.576	0.569
OarAE129	9	140-176	4.164	1.714	0.727	0.512	0.769	0.760	-0.334	0.327
ILSTS072	6	154-170	3.678	1.490	0.693	0.585	0.737	0.728	-0.206	0.196*
Mean	5.542		2.914	1.183	0.543	0.474	0.591	0.584		
-										
St. error	2.167		1.246	0.448		0.174	0.193	0.191		-

Effective number of alleles [Kimura and Crow (1964)].

Shannons information index [Lewontin (1972)].

a, Expected heterozygosity were computed using Levene (1949) and Nei's (1973) expected heterozygosity;

b, heterozygote deficiencies were expressed as D=(Ho-He)/He, refer the text for symbols used;

c, f-values (Weir and Cockerham 1984) given for significant tests after Bonferroni corrections;

*Wahlund effects varied from 0.9% to 65.76%; PIC (polymorphic information content).

Table 3. F-statistics analyses for 24 microsatellite loci in Barbari goat population

Locus	f(F_{IS})	0 (F_{ST})	F(F_{IT})	Relatc	Relatc	R_{st}
OarHH64	0.602	0.025	0.611	0.032	-3.147	0.021
ILSTS034	0.274	0.001	0.274	0.002	-0.753	-0.012
ILSTS005	0.214	0.015	0.196	0.038	0.328	-0.023
OarFCB304	0.028	-0.006	0.033	-0.011	-0.069	-0.008
ILSTS008	-0.096	0.029	0.029	0.064	0.228	0.019
ILSRS044	0.259	0.084	0.191	0.134	-0.471	0.084
ILSTS019	0.510	-0.023	0.521	-0.031	-2.177	-0.012
ILSTS087	0.144	0.018	0.128	0.032	-0.294	0.023
ILSTS030	0.019	-0.017	0.035	-0.033	-0.073	-0.027
RM4	-0.079	-0.010	-0.068	-0.022	0.128	-0.002
ILSTS049	0.261	0.078	0.199	0.124	-0.496	0.007
ILSTS002	0.304	-0.031	0.325	-0.047	-0.962	-0.034
ETH225	0.219	0.175	0.054	0.286	-0.115	0.175
ILSTS033	-0.032	0.008	-0.040	0.016	0.076	0.051
ILSTS022	0.111	0.035	0.079	0.063	-0.172	0.025
ILSTS058	0.333	-0.007	0.337	-0.011	-1.018	-0.040
OMHC1	0.391	0.058	0.353	0.083	-1.091	-0.024
OarFCB48	0.390	-0.022	0.402	-0.031	-1.347	-0.015
OaeCP34	-0.193	-0.020	-0.170	-0.049	0.290	-0.005
ILSTS029	-0.076	-0.018	-0.057	-0.038	0.108	-0.004
OarHH41	0.138	0.033	0.109	0.057	-0.247	-0.014
ILSTS059	0.589	0.037	0.573	0.046	-2.684	0.037
OarAE129	0.331	-0.017	0.342	-0.026	-1.042	0.006
ILSTS72	0.206	-0.005	0.210	-0.008	-0.531	0.042
Mean[a]	0.202	0.018	0.888	0.028	-0.648	0.011
(SE)	(0.044)	(0.008)	(0.045)	(0.013)		

Relat, an estimator of the average relatedness of individuals within samples when compared to whole (Queller and Goodnights 1989) Relate estimates the inbreeding corrected relatedness (Pamilo 1985).

[a] Standard error-estimate from Jackknife over loci and significance from t-test using these estimates, $P<0.05$.

alleles across the loci was more than the effective number of alleles (1.207 to 5.387). The Shannon information index and polymorphic information content (PIC) showed that most of the loci were highly informative indicating the high polymorphism across the loci with an overall mean of 1.183 and 0.543, respectively. The average observed heterozygosity (0.74±0.174) was less than the expected (0.591±0.193). The average expected gene diversity (Nei 1973) within the population ranged from 0.171 (ILSTS044) to 0.807 (ILSTS002) with an overall mean of 0.584±0.191. Eleven out of 24 loci showed significant deviations from Ha Weinberg Equilibrium. All 11 loci showed significant heterozygote deficiency in the Barbari goat population. Wahlund effects accounted for 1 to 66% of the observed hetrozygote deficiency at 6 loci.

Significant linkage disequilibrium was detected in the overall microsatellite data for 15 out of 276 loci pairs. The overall means for the F-statistics were significantly different from zero. The relatedness among the individuals in the given sample was also significantly different from zero. The over all Rst, an estimator of genetic differentiation among these samples was 0.011 (Table 3). Rst and θ (Fst) were of the same magnitude (0.011 and 0.018, respectively).

The Barbari breed of goat had substantial genetic variation based on its gene diversity and average number of alleles per locus. The average genetic variation (0.585) observed in this study was in the range of the values (0.54-0.59) reported for other Indian breeds of goat, viz. Black Bengal, Chegu, Jamnapari, Sirohi, Marwari and Jakhrana (Behl *et al.* 2003, Ganai *et al.* 2001, Gaur *et al.* 2006, Kumar *et al.* 2005, 2005b). The average genetic variation observed in this population was more than the average gene diversity among populations of Asian goats and Sub-saharan African goats (Barker *et al.* 2001, Chenyambuga *et al.* 2004).

The f (F_{IS}) estimates across 11 out of 24 studied loci were significantly positive (significant heterozygote deficit) based on table wide randomizations ($P<0.05$). The f estimates ranged from 0.019 to 0.602 with an average of 0.202±0.044 (Table 3). Similar high estimates were also reported for Asian goat populations (Barker *et al.* 2001). Significant hetrozygote deficiencies were also reported in some studies of goats (Luikart and Cornuet 1998, Barker *et al.* 2001). The significant hetrozygote deficiency found in Barbari breed of goat could be due to one or more of the reasons: segregation

Table 4. Mutation-drift equilibrium, heterozygosity excess/deficiency under different mutation models in Barbari goat population

Methods	Models	Sign test	Standardized	Wilcoxon test
A Frequency method	IAM	Hee=13.76 Hd=19 H=5 P=0.00028	T2=-5.508 P=0.00000	P(one tail for H deficiency): 0.00005 P (one tail for H excess): 0.99995 P (Two tails for H excess and deficiency): 0.00011
	TPM	Hee=13.91 Hd=23 He=1 P=0.00000	T2=-10.249 P=0.00000	P (one tail for H deficiency): 0.00000 P (one tail for H excess): 1.00000 P (two tails for H excess or deficiency): 0.00000
	SMM	Hee=13.88 Hd=23 He=1 P=0.00000	T2=-18.292 P= 0.00000	P (one tail for H deficiency): 0.00000 P (one tail for H excess): 1.00000 P (Two tails for H excess or deficiency): 0.00000
B Heterozygosity method	IAM	Hee=13.71 Hd=11 He=13 P = 0.46097	T2=0.530 P=0.29815	P (one tail for H deficiency): 0.75460 P (one tail for H excess): 0.25438 P (two tails for H excess and deficiency): 0.50877
	TPM	Hee=13.96 Hd=12 He=12 P=0.27027	T2 =2.108 P=0.01750	P (one tail for H deficiency): 0.07999 P (one tail for H excess): 0.92425 P (two tails for H excess or deficiency): 0.15999
	SMM	Hee=13.93 Hd=16 He=8 P=0.01262	T2=-6.301 P=0.00000	P (one tail for H deficiency): 0.00326 P (one tail for H excess): 0.99705 P (two tails for H excess or deficiency): 0.00652

Parameters for TPM: Variance=30.00 Proportion of SMM in TPM = 70.00%; Extimation based on 1000 replications; Hee: heterozygosity excess expected; Hd: heterozygosity deficiency; He: heterozygosity excess; P: probability; IAM: infinite allele model, TPM: two phase model, SMM: step-wise mutation model.

of non-amplifying (null) alleles, Wahlund effects, scoring biases (heterozygotes scored incorrectly as homozygotes) or inbreeding. Distinguishing among these is generally difficult (Christiansen *et al.* 1974). However, null alleles are most unlikely to be segregating at all the loci. Similarly, scoring bias may be possible for a few loci but not for all loci. Wahlund effects do account for 1 to 66% of the observed heterozygote deficit for >50% of the loci showing significant heterozygote deficiency. There is inbreeding in the population as indicated by f estimate (0.202), presumably resulting from the unplanned and indiscriminate mating prevalent in the breeding track leading to small effective population size/or mating between relatives and consequent genetic drift. The general practice of breeding in the region was to allow a few bucks for the whole village. Therefore, inbreeding and Wahlund effects may be most reasonable causes of heterozygote deficit. The non-random association of alleles across the loci was also compatible with genotypic disequilibrium observed in the population. Both the samples (taken from different localities) were substantially differentiated from each other as indicated by the theta (θ) and Rst estimates. These estimates are also in accordance with measures of Wahlund effect in the study. F_{IT} estimates revealed significant deviations (heterozygote deficit) from Hardy-Weinberg equilibrium across most of the loci studied. These estimates showed global heterozygote deficit in the population after applying the Bonferroni corrections to different tests.

The Sign, Standardized differences and Wilcoxon tests under bottleneck hypothesis detected significant departure from mutation-drift-equilibrium in the population for most of the loci studied (allele frequency method, Table 4). However, based on heterozygosity, standardized differences test indicated significant departure of the population from the mutation drift equilibrium under 2 phase and single step mutation models whereas other 2 tests indicated the significant departure under SMM model only.

Bottleneck test and L-shaped mode-shift curve indicated that the population had not undergone bottleneck in the recent past (15-20 generations). When a population goes through a bottleneck, rare alleles tend to be lost and the average number of alleles per locus, or allelic diversity is reduced. However, heterozygosity is not proportionately reduced as rare alleles contribute little to the heterozygosity. The microsatellite alleles were classified into 10 frequency classes, which allow checking whether the distribution followed the normal L-shaped form, where alleles with low frequencies (0.01-0.1) are the most abundant.

Our results indicated that there was substantial genetic variation and polymorphism across studied loci in the Barbari breed of goats and population was neither in Hardy-Weinberg equilibrium nor in mutation drift equilibrium. The population appears to be divided into small subpopulations, which resulted in mating among close relatives leading to inbreeding in the population. Appropriate breeding strategies should therefore be designed under field conditions for its conservation and improvement.

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