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Genetic Structure and Differentiation of Three Indian Goat Breeds

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ABSTRACT : Gene flow, genetic structure and differentiation of Kutchi, Mehsana and Sirohi breeds of goat from North-Western India were evaluated based on 25 microsatellite markers so as to support breed conservation and improvement decisions. The microsatellite genotyping was carried out using an automated DNA sequencer. The gene diversity across the studied loci for the Kutchi breed varied from 0.57 (ILST 065) to 0.93 (OarFCB 304, OMHC 1, ILSTS 058) with an overall mean of 0.79±0.02. The corresponding values for Mehsana and Sirohi breeds were 0.16 (ILST 008) to 0.93 (OMHC 1, ILSTS 058) with an average of 0.76±0.04, and 0.50 (ILSTS 029) to 0.94 (ILSTS 058) with an average of 0.78±0.02, respectively. The Mehsana breed had lowest gene diversity among the 3 breeds studied. All the populations showed an overall significant heterozygote deficit (F_{is}). The F_{is} values were 0.26, 0.14 and 0.36 for Kutchi, Mehsana and Sirohi goat breeds, respectively. Kutchi and Mehsana were more differentiated (16%) followed by Mehsana and Sirohi (13%).The measures of standard genetic distance between pairs of breeds indicated that the lowest genetic distance was between Kutchi and Sirohi breeds (0.73) and the largest genetic distance was between Mehsana and Kutchi (1.0) followed by Sirohi and Mehsana (0.75) breeds. Mehsana and Kutchi are distinct breeds and this was revealed by the estimated genetic distance between them. All measures of genetic variation revealed substantial genetic variation in each of the populations studied, thereby showing good scope for their further improvement. (**Key Words :** Microsatellite Loci, Genetic Variation, Genetic Distance and Breed Assignment, Goat)

INTRODUCTION

Kutchi, Mehsana and Sirohi breeds of goat are found in semi-arid to arid regions of North-Western India. These breeds had previously been described on the basis of phenotype and/or geographical distribution (Acharya, 1982). They are highly adapted to their environment and are an important economic resource especially to farmers of the region. The classification of these breeds based on phenotype and/or geographical distribution may not actually characterize the genetic structure of population because genetically similar individuals might be labeled differently because of distinct geography and/or phenotype. On the other hand, geographic overlap or phenotypic similarity may mask underlying genetic variation. Moreover, they share their breeding area and there may be intermixing of these breeds/populations which may cause dilution of genetic structure.

Genetic variation within and between breeds is warranted to differentiate them on a genetic basis. The resulting genetic information may assist in choosing the best conservation and improvement options for these genetic resources. The need for conservation of livestock diversity and for characterization of breeds and populations, including their genetic differentiation and relationships, has been highlighted (FAO, 1995a; b). Microsatellite markers are best suited to characterize the genetic variability within and between populations because of their high variability, distribution throughout the genome, co-dominant inheritance and neutrality to selection (Boyce et al., 1996).

The present investigation was undertaken to evaluate gene flow, genetic structure and differentiation of these goat populations of North-Western India based on microsatellite loci. The individual animals were also assigned to their breed on the basis of estimated microsatellite allele frequencies.

MATERIALS AND METHODS

Molecular techniques

Blood samples (10 ml each) of 46-52 unrelated animals of each of the three breeds, namely Kutchi, Mehsana and

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Sirohi, were collected from their respective breeding area. The genomic DNA was isolated from these samples using a standard phenol-chloroform extraction method (Sambrook et al., 1989). A battery of 25 microsatellite markers based on the guidelines of ISAG & FAO's DADIS program was utilized to generate allelic data. Each forward primer was tagged on the 5′ end with one dye out of four dyes (FAM, PET, VIC, NED) as supplied by Applied Biosystems, UK.

Polymerase Chain Reaction (PCR) was carried out using about 50-100 ng genomic DNA in a 25 µl reaction volume on a PTC-200 PCR machine (M J Research). The reaction mixture consisted of 200 µM each dNTP, 50 nM KCl, 10 mM Tris-HCl (pH 9.0), 0.1% Triton X-100, 2.0 mM $MgCl_2$, 0.75 unit Taq DNA polymerase and 0.4 µM of each primer. The thermal cycling conditions employed were initial denaturation at 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. At the end of the reaction, 5.0 µl of stop dye (95% formamide, 0.25% bromophenol blue and 0.25% xylene cyanol) was added to terminate the reaction. 6 µl of PCR products were run onto a 2% agarose gel, electrophoresed and visualized over UV light after ethidium bromide staining to detect the amplification.

The microsatellite genotyping was carried out using an ABI 3100 prism (Avant genetic analyzer) with LIZ 500 as internal lane standard. The data were collected and analyzed using Gene Mapper Software (Version 3.0, Applied Biosystems software).

Statistical analysis

To determine the genetic variation within and between breeds, parameters such as Nei's (1978) unbiased heterozygosity and Wright's (1978) F-statistics (F_{st}, F_{is} and F_{it}) were calculated. Heterozygosity is defined as the probability that a given individual randomly selected from a population will be heterozygous at a given locus. The statistics F_{st}, is an estimate of variation due to differences among populations, which is the reduction in heterozygosity of a sub-population due to genetic drift. The statistics F_{is} is an estimate of variation within populations that measures the reduction in heterozygosity in an individual due to non-random mating within its subpopulations. The statistics F_{it} is the overall reduction in heterozygosity in an individual relative to the total population. This includes the contribution due to non-random mating within sub-populations (F_{is}) and that due to population subdivision (F_{st}). The Popgene (version 3.1) program (Yeh et al., 1999) was employed to calculate the number of alleles; effective number of alleles (Kimura and Crow, 1964); observed and expected heterozygosity at each locus within and across the populations under study.

A number of statistics have been developed to summarize genetic differentiation at microsatellite loci while taking into account the incremental stepwise mutation model (Goldstein et al., 1995; Slatkin, 1995; Barbujani et al., 1997). We have chosen not to use these new measures as recent analyses have shown that microsatellite allele frequency drift and not mutation seems to play a more important role in genetic differentiation among closely related populations (Takezaki and Nei, 1996). The drift based classical measure of degree of genetic differentiation such as F_{st} was calculated using the FSTAT program (Version 2. 9.3.2) (Goudet, 2002). The level of significance ($p<0.05$) of F_{is} was determined by permutation test with sequential Bonferroni procedure applied over all loci (Goudet et al., 1996) to test Hardy-Weinberg equilibrium within breeds. The test for pair-wise linkage (genotypic) disequilibrium among the microsatellite loci was also done using the FSTAT program. The level of significance for genotypic equilibrium based on 18,000 permutations was calculated and the adjusted p value for 5% nominal level was 0.000056.

The effect of migration and gene flow on the genetic structure of the analyzed population was estimated between each pair of populations according to an Island model under neutrality and negligible mutation (Slatkin, 1993). N_{em} value indicates the average number of effective migrants per generation to produce the observed F_{st} under the Island model. The private allele method as applied in the Genepop program (Raymond and Rousset, 1995) was used to calculate N_{em} estimate and private alleles.

An unweighted pair group method with arithmetic mean (UPGMA, Sneath and Sokal, 1973) was used to construct the phylogenetic tree based on Nei's (1972) standard genetic distance using the DISPAN program (Ota, 1993).

It has previously been demonstrated that the set of alleles an organism carries for a control panel of microsatellite loci can be used to identify the source population. Using the allele frequency across 25 studied loci from three breeds of goat, the individuals were assigned to their source population (breed) on the basis of simulated data based on a coalescent process by different methods using the GeneClass program (Cornuet et al., 1999). This program includes two types of methods for assigning individuals to populations. Likelihood based methods (frequency and Bayesian) assign individuals to the population in which the likelihood of their genotype is highest. Nei's (1972) genetic and shared allele (DAS) distances were used to assign individuals to the genetically closest population.

RESULTS

The various measures of genetic variation across the

Table 1. Measures of genetic variation across Kutchi, Mehsana and Sirohi breeds of goat

Locus	Sample size	Observed number of alleles	Effective number of alleles	Shannon's information index	Heterozygosity	
					Observed	Expected
ILST008	258	12	5.34	1.87	0.11	0.81
ILSTS059	254	24	10.58	2.68	0.75	0.90
ETH225	196	14	4.65	1.93	0.09	0.78
ILST044	258	30	13.10	2.88	0.69	0.92
ILSTS002	252	23	12.10	2.75	0.65	0.92
OarFCB304	260	47	26.76	3.51	0.85	0.96
OarFCB48	262	35	19.34	3.18	0.77	0.95
OarHH64	258	24	11.49	2.74	0.51	0.91
OarJMP29	200	16	9.96	2.50	0.21	0.90
ILSTS005	274	19	9.97	2.50	0.36	0.90
ILSTS019	280	22	13.89	2.77	0.75	0.93
OMHC1	260	38	21.89	3.32	0.86	0.95
ILSTS087	268	29	18.16	3.07	0.42	0.94
ILSTS30	276	28	12.24	2.87	0.56	0.92
ILSTS34	290	19	5.65	2.18	0.37	0.82
ILSTS033	206	32	11.58	2.90	0.61	0.91
ILSTS049	274	27	13.50	2.87	0.72	0.92
ILSTS065	284	12	6.90	2.08	0.48	0.85
ILSTSO58	280	50	31.23	3.62	0.79	0.97
ILSTSO29	280	19	6.29	2.14	0.61	0.84
RM088	264	24	9.85	2.54	0.69	0.90
ILSTS022	274	16	8.74	2.34	0.50	0.88
OARE129	292	27	10.90	2.65	0.82	0.91
ILSTS082	276	33	16.29	3.03	0.84	0.94
RM4	292	17	6.46	2.22	0.43	0.84
Mean±SE	263	25.48±1.98	12.68±1.32	2.69±0.09	0.58±0.04	0.90±0.02

three breeds of goat, namely Kutchi, Mehsana and Sirohi, investigated at each locus are presented in Table 1. A total of 637 alleles were observed among 146 assayed animals across the three breeds. The observed and effective number of alleles across the studied loci for the 3 breeds varied from 12 (ILST 008, ILSTS 065) to 50 (ILSTS 058), and from 4.65 (ETH 225) to 31.23 (ILSTS 058) with an overall mean of 25.48±1.98 and 12.68±1.32, respectively. The proportion of diagnostic alleles in Kutchi, Mehsana and Sirohi breeds was 0.053, 0.057 and 0.037, respectively. However, there were two private alleles with allele frequency of ≥0.08 in Kutchi (ILSTS 019, ILSTS 30) and one each in Mehsana (ILSTS 082) and Sirohi (RM 088) breeds. The proportion of low frequency (<0.05) alleles observed at different loci in these breeds varied from 0.10 to 0.91. Shannon's information index (Lewontin, 1972), a measure of polymorphism, across these loci for the populations varied from 1.87 (ILST 008) to 3.62 (ILSTS 058) with an average of 2.69±0.09. All the studied microsatellite loci were polymorphic, which indicates that the microsatellites used were suitable for genetic diversity analysis. The observed heterozygosity and unbiased expected heterozygosity over the studied loci across all three populations ranged from 0.09 (ETH 225) to 0.86 (OMHC 1) with an overall mean of 0.58±0.04 and from 0.78 (ETH 225) to 0.97 (ILSTS 058) with an average of 0.90±0.02, respectively.

The gene diversity across the studied loci for the Kutchi breed varied from 0.57 (ILST 065) to 0.93 (OarFCB 304, OMHC 1, ILSTS 058) with an overall mean of 0.79±0.02 (Table 2). The corresponding values for Mehsana and Sirohi breeds were 0.16 (ILST 008) to 0.93 (OMHC 1, ILSTS 058) with an average of 0.76±0.04, and 0.50 (ILSTS 029) to 0.94 (ILSTS 058) with an average of 0.78±0.02, respectively. These populations were the same based on heterozygosity. There was no differentiation between these statistics (0.76-0.79). Although varying among populations, the observed heterozygosity was lower than expected based on overall microsatellite loci (Table 1) for all the populations and for the pooled data across the populations. Significant deviations from Hardy-Weinberg equilibrium were detected in all the populations for most of the loci studied. Out of 25 studied loci, 22 loci showed positive deviations (observed heterozygote deficiency) in the Sirohi breed, while 13 different loci showed positive deviations in Kutchi and Mehsana breeds. Heterozygote excess (negative

Table 2. Gene diversity and heterozygote deficiency (F_{is}) across studied loci in three breeds of Indian goats

Locus	Kutchi		Mehsana		Sirohi	
	Gene diversity	F_{is} value	Gene diversity	F_{is} value	Gene diversity	F_{is} value
ILST008	0.64	0.76*	0.16	0.65*	0.52	0.76*
ILSTS059	0.78	-0.05	0.79	0.10	0.89	0.18*
ETH225	0.72	0.71*	0.33	0.72*	0.69	0.96*
ILST044	0.89	-0.02	0.79	0.06	0.77	0.43*
ILSTS002	0.78	0.27*	0.85	0.13	0.89	0.23*
OarFCB304	0.93	-0.04	0.92	-0.04	0.92	0.27*
OarFCB48	0.90	-0.01	0.90	0.13*	0.91	0.26*
OarHH64	0.80	0.41*	0.90	0.24*	0.84	0.49*
OarJMP29	0.83	0.83*	0.82	0.80*	0.77	0.64*
ILSTS005	0.82	0.68*	0.77	0.48*	0.82	0.50*
ILSTS019	0.88	0.02	0.76	0.05	0.88	0.25*
OMHC1	0.93	0.08	0.93	0.01	0.91	0.08
ILSTS087	0.91	0.68*	0.90	0.19*	0.82	0.73*
ILSTS30	0.61	0.53*	0.91	0.19*	0.88	0.23*
ILSTS34	0.68	0.77*	0.77	0.14*	0.54	0.46*
ILSTS033	0.86	0.09	0.57	-0.14	0.89	0.51*
ILSTS049	0.82	0.03	0.88	-0.01	0.79	0.32*
ILSTS065	0.57	-0.08	0.46	0.34*	0.77	0.30*
ILSTSO58	0.93	0.18*	0.93	0.04	0.94	0.23*
ILSTSO29	0.71	-0.12	0.58	-0.03	0.50	0.14
RM048	0.81	-0.21*	0.81	-0.14	0.83	0.74*
ILSTS022	0.76	0.38*	0.78	0.25*	0.73	0.36*
OARE129	0.82	-0.04	0.78	-0.23*	0.81	0.16*
ILSTS082	0.90	0.16*	0.90	0.11*	0.86	-0.12*
RM4	0.76	0.83*	0.84	0.16*	0.58	0.24*
Mean±SE	0.79±0.02	0.26*	0.76±0.04	0.14*	0.78±0.02	0.36*

* $p<0.05$.

F_{is}) was also observed for one locus in each of the populations (Table 2).

Significant linkage disequilibrium ($p<0.05$) was detected in the overall microsatellite data for 33 locus pairs out of 300 pairs (data not shown). For individual populations, the number of tests that were significant after Bonferroni correction was: Sirohi (17), Kutchi (18), Mehsana (15). Overall means of the F-statistics obtained from jackknifing over all loci were significantly different from zero based on 't' test (Table 3). The global deficit of heterozygotes across populations (F_{it}) amounted to 35.9%. An overall significant deficit of subpopulation heterozygosities (F_{is}) of 26.0% occurred in analyzed loci. The overall genetic differentiation among the breeds (F_{st}) was 13.4%.

The estimates of pair-wise F_{st} between each population pair revealed that Kutchi and Mehsana were more differentiated (16%) followed by Mehsana and Sirohi (13%). Kutchi and Sirohi were least differentiated (11%) among all the population pairs. The overall N_{em} value of 1.95 indicated the genetic flow between the populations. F_{st} values indicated a moderate level of genetic differentiation among these populations (11-16%). Takezaki and Nei (1996) showed that Nei's (1978) DA distance was generally best for inferring the correct topology for the infinite mutation (IAM) model. Thus, DA was used to derive a dendrogram of genetic relationship among the populations, constructed as a neighbor joining tree (Saitou and Nei, 1987). However, the tree nodes had very low bootstrap values (9-16%) and consequently the tree collapsed.

The measures of standard genetic distance between pairs of breeds indicated that the lowest genetic distance was between Kutchi and Sirohi (0.73) and that the largest genetic distance was between Mehsana and Kutchi (1.0) followed by Sirohi and Mehsana (0.75). With the aid of prior population information, 25 microsatellite markers could assign the individuals to their respective breed 65 to 83% of the time using likelihood based methods of breed assignment (Table 4). The test, in essence, resolved whether an individual of a particular breed possessed a genotype that is typical of its own breed or whether it better reflected the genetic characteristic of another breed. On the other hand, genetic distance-based methods could assign the individuals to their respective breed 44 to 91% of the time.

DISCUSSION

All measures of genetic diversity revealed that there was substantial genetic variation within and across the three breeds studied. The substantial genetic variation has also

Table 3. F-statistics per locus across three breeds of Indian goat

Locus	F (F_{it})	θ (F_{st})	f (F_{is})
ILST008	0.871	0.482	0.751
ILSTS059	0.173	0.095	0.086
ETH225	0.893	0.330	0.841
ILST044	0.271	0.136	0.157
ILSTS002	0.273	0.071	0.218
OarFCB304	0.112	0.039	0.077
OarFCB48	0.153	0.013	0.142
OarHH64	0.435	0.073	0.391
OarJMP29	0.770	0.126	0.736
ILSTS005	0.582	0.060	0.556
ILSTS019	0.181	0.081	0.109
OMHC1	0.071	0.016	0.056
ILSTS087	0.547	0.062	0.518
ILSTS30	0.399	0.147	0.295
ILSTS34	0.543	0.188	0.438
ILSTS033	0.368	0.185	0.224
ILSTS049	0.226	0.116	0.125
ILSTS065	0.453	0.315	0.202
ILSTSO58	0.173	0.026	0.151
ILSTSO29	0.302	0.317	-0.022
RM048	0.224	0.090	0.147
ILSTS022	0.409	0.113	0.334
OARE129	0.069	0.094	-0.027
ILSTS082	0.079	0.040	0.041
RM4	0.503	0.166	0.403
Mean±SE	0.359±0.047	0.134±0.023	0.260±0.044

been observed in many other breeds of goat (Barker et al., 2001; Kim et al., 2002; Li et al., 2002; Behl et al., 2003; Chenyambuga et al., 2004; Jandurova et al., 2004; Kumar et al., 2005; Iamartino et al., 2005; Takahashi et al., 2008). Although varying among populations, observed mean heterozygosity was lower than the expected mean heterozygosity for all the populations. The majority of the loci (>50%) in each population showed heterozygote deficiency, which may be due to presence of low frequency alleles segregating at many of the loci and the significant genotypic linkage disequilibrium observed in these breeds.

The moderate level of genetic differentiation (F_{st}) among the three breeds (13.4%) under study implied that 86.6% of the total genetic variation corresponded to differences among individuals within breed and 13.4% of the total genetic variation corresponded to the breed. This level of differentiation among the populations is within the range of F_{st} values reported in the literature. A value of 0.146 was found in indigenous goats of sub-Saharan Africa (Chenyambuga et al., 2004); 0.105 in 12 Chinese indigenous goat populations (Li et al., 2002); 0.17 in Swiss goat breeds (Saitbekova et al., 1999); 0.073 in Italian goat populations (Iamartino et al., 2005); 0.202 in goats from Korea and China (Kim et al., 2002); and 0.227 in Asian goats (Barker et al., 2001). The overall F_{is} value (0.26) was higher and significantly different from zero indicating departure from random mating and suggested that some of the studied loci were homozygous in the populations. Some

Table 4. Breed assignment using 10,000 simulated genotypes from 25 microsatellite loci

Breed/method	Kutchi	Mehsana	Sirohi	More than one breed	Unclassified
Kutchi breed					
Likelihood based methods					
Frequency method	83	-	-	-	17
Bayesian method	76	-	-	2	22
Genetic distance based methods					
Nei DA	57	-	-	-	43
Nei standard	83	-	-	-	17
Shared allele distance (DAS)	91	-	-	-	9
Mehsana breed					
Likelihood based methods					
Frequency	-	75	-	-	25
Bayesian	-	65	-	20	15
Genetic distance based methods					
Nei DA	-	58	-	-	42
Nei standard	-	75	-	-	25
DAS	-	81	-	-	19
Sirohi breed					
Likelihood based methods					
Frequency	-	-	71	-	29
Bayesian	-	-	69	4	27
Genetic distance based methods					
Nei DA	-	-	44	-	56
Nei standard	-	-	71	-	29
DAS	-	-	77	-	23

of these homozygous loci could be undergoing natural selection or linked to other loci affecting morphological, productive or adaptive traits undergoing natural selection. The measures of genetic differentiation revealed that the different populations remained genetically distinct, despite the fact that there is no breeding policy to create breeds or maintain the breed purity.

With prior information, the assignment of individuals to the rightful breed based on 25 microsatellite markers revealed that different methods used could not effectively discriminate individuals with a moderate level of differentiation among the breeds determined by their history of development, breeding and management practices to their rightful populations. Our results are in accordance with the results of Awemu and Erhardt (2005) for zebu cattle breeds.

In conclusion, all the measures of genetic variation revealed substantial genetic variation in each of the studied populations and thereby there is good scope for their further improvement. The measures of F-statistics differentiated the breeds moderately on a genetic basis and revealed a significant level of heterozygote deficit in the populations at some of the studied loci. The measurement of gene flow showed immigration of new genes from other populations and thereby intermixing of the populations; hence, this may pose a danger to the purity of the breed in the long run. Therefore, suitable breeding strategies are required for maintaining breed purity and improving these breeds.

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