Genetic diversity and relationships of indigenous Kenyan camel (*Camelus dromedarius*) populations: implications for their classification

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Summary

The genetic diversity and relationships amongst the dromedary (*Camelus dromedarius*) populations are poorly documented. Four recognized Kenyan dromedary breeds (Somali, Turkana, Rendille, Gabbra) and dromedary from Pakistan and the Arabian Peninsula (Saudi Arabia, United Arab Emirates) were studied using 14 microsatellite loci. Phylogenetic analysis showed that Kenyan dromedaries are distinct from Arabian and Pakistani populations. Expected heterozygosity and allelic diversity values indicate that Kenyan dromedaries are less diverse than non-Kenyan populations. With the exception of the Somali population, the Kenyan dromedaries are poorly differentiated (average $F_{ST} = 0.009$), with only one to two loci separating the Gabbra, Rendille and Turkana populations studied ($P < 0.05$). Individual assignments were performed using the maximum likelihood method. A correct breed assignment of only 39–48% was observed for the Kenyan dromedaries, using an allocation stringency of a log of the odds ratio >2. Our results do not support the present classification of the indigenous Kenyan dromedary into four distinct breeds based on socio-geographical criteria. Instead, our results point to just two separate genetic entities, the Somali and a group including the Gabbra, Rendille and Turkana populations.

Keywords differentiation index value (F_{ST}), dromedary camel, genetic diversity, individual assignment, microsatellite, population differentiation.

Introduction

The family Camelidae comprises the Old World (Camelini) and the New World (Lamini) tribes. The Old World tribe has two species: *Camelus dromedarius,* the dromedary, the Arabian camel or one-humped camel; and *C. bactrianus,* the Bactrian or two-humped camel. The habitat of the Bactrian is mainly in the cold desert regions of Mongolia and China (Stanley *et al.* 1994). The Arabian camel is found from north-western India and the lowlands of Afghanistan to the extremity of the Arabian Peninsula and Somalia to the south and westward across the African deserts. In Australia, there are about 25 000 feral Arabian camels following introduction in the 19th century (http://www.allcamels.com/links/). Worldwide there are about 19.3 million camels, and the largest population (6.2 million) is found in Somalia (FAO Yearbook 2001). Fifty-two different breeds are currently reported in the FAO DAD-IS database (http://www.fao.org/dad-is/). However, this information is based on morphological characteristics and it is largely incomplete. For example, it contains no data from Somalia and only one or two breeds are recognized in major dromedary

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countries like Ethiopia and Mauritania. As in the rest of Africa the only Camelidae represented in Kenya is *C. dromedarius*.

It is widely believed that camel domestication began somewhere in the Arabian Peninsula around 3000 BC (Mikesell 1955; Bulliet 1975). There are dissenting views as to when they were first introduced to North Africa, and dates ranging from the 3rd millennium BC to the 7th century AD have been suggested. In East Africa, it is thought that the camel was introduced following a more direct route through the Horn of Africa during the middle of the 1st millennium BC (Epstein 1971).

According to the FAO Yearbook (2001) there are 0.83 million head of camel in Kenya. Classification of camel breeds in Kenya is based mainly on the ethnic group and geographical distribution of the pastoral communities owning them. In northern Kenya pastoral communities distinguish four local camel breeds, namely Gabbra, Rendille, Turkana and Somali. In the FAO database, some phenotypic characteristics of these local breeds are given, and the Gabbra and Rendille are grouped in a single population. Simpkin (1998) summarizes general phenotypic characteristics for the local Kenyan camel breeds. Somali are in general heavier than the others and show a higher milk yield. Adult males average 600–700 kg live weight and females have a lactation yield of 1000–2000 kg in 10–16 months. Gabbra, Rendille and Turkana camels are smaller and less productive but they have the reputation of being hardy and better adapted to water scarcity. The males have an average live weight of 400–500 kg and females have a lactation yield of 700–1000 kg in 10–12 months.

The extent to which the Kenyan dromedary populations are genetically differentiated is unknown. On one hand local breeding management practices of the pastoralists of the different ethnic groups may favour genetic differentiation (Kaufmann 1998) but on the other hand gene flow also likely exists between the populations.

Microsatellites are currently the markers of choice for the molecular characterization of livestock genetic resources. To date several microsatellite loci have been characterized in South American Camelidae (Lang *et al.* 1996; Obreque *et al.* 1998; Sarno *et al.* 2000) and dromedary (Sasse *et al.* 2000). Recent studies (Jianlin *et al.* 2000; Mburu *et al.* 2001) have demonstrated the usefulness of New World Camelidae microsatellite loci as genetic tools for the study of dromedary and Bactrian camelids. However, there has been no in-depth study on the genetic diversity and relationships amongst populations of these two species using microsatellite DNA markers.

The objectives of this study were to characterize, at the molecular level using polymorphic microsatellite markers, the dromedary breeds from Kenya and to quantify their relationship with dromedary populations indigenous to Asia and the Arabian Peninsula.

Materials and methods

Populations studied

Blood or hair samples were collected from four dromedary populations from Kenya (Somali, $n = 144$; Rendille, $n = 46$; Turkana, $n = 42$; Gabbra, $n = 36$), one population originally from Pakistan ($n = 32$) but sampled in Kenya, one population from Saudi Arabia ($n = 22$) and one population from the United Arab Emirates ($n = 10$). Twenty-eight Chinese Bactrian samples were included as a reference outgroup population for the calculation of genetic distances and generation of a phylogenetic tree. Genomic DNA was extracted from blood following either the method of Sambrook *et al.* (1989) or the salting out procedure of Montgomery & Sise (1990), and from hair as described by Troy *et al.* (2001).

Primers

Nine New World Camelidae microsatellite primer pairs: *VOLP3*, *VOLP8*, *VOLP10* and *VOLP32* (Obreque *et al.* 1998) and *YWLL008*, *YWLLOO9*, *YWLL38*, *YWLL44* and *YWLL59* (Lang *et al.* 1996), and five dromedary-specific primer pairs, *CVRL1*, *CVRL2*, *CVRL5*, *CVRL6* and *CVRL7* (Sasse *et al.* 2000), were used.

DNA amplification by polymerase chain reaction

The Polymerase chain reactions (PCR) were carried out in a total volume of 10 μl containing 20–35 ng genomic DNA, 5 pmol of each primer, 0.3 unit of Ampli*Taq* Gold DNA polymerase (Applied Biosystems, Foster City, CA, USA), 0.125 mM of each dNTP (Boehringer Mannheim, Germany), 1× PCR buffer (10 mM Tris–HCl, pH 8.3) including 50 mM KCl, 0.001% gelatin (Sigma, St Louis, MO, USA), 0.25% nonidet P40 (BDH, Poole, UK) and 2 mM $MgCl_2$. Cycling profile included an initial denaturation step at 95 °C for 10 min, followed by 35 cycles of 45 s at 94 °C, 1 min at 50–65 °C depending on the primer pair used, 1 min at 72 °C and a final step of 15 min at 72 °C using a GeneAmp 9700 (Applied Biosystems) thermal cycler.

Microsatellite genotyping

The PCR fragments were fractionated and sized under denaturing conditions on a 5% polyacrylamide gel using an automated ABI377 DNA sequencer and the internal size standard Genescan 350-TAMRA (Applied Biosystems). Data were collected with the ABI PRISM 377 (version 2.1)

software (Applied Biosystems). Fluorescent DNA fragments were analysed using the GENESCAN (version 3.1) and the GENOTYPER (Version 2.0) softwares (Applied Biosystems). The third order least squares was used for base calling.

Relationships between populations

Nei *et al.*'s (1983) genetic distance (D_A), between pairs of populations was calculated using the DISPAN program (Ota 1993), and a neighbour-joining tree constructed. The reliability of the tree obtained was examined by a bootstrap test with 1000 replicate re-samplings of loci with replacement.

Genetic diversity and population structure

Genetic polymorphism for each population was measured as the mean number of alleles (MNA) per locus and the expected heterozygosity (H_E) assuming Hardy–Weinberg (HW) equilibrium. To remove any sample bias, the MNA for a random sample of 20 individuals, with 99 replicate resamplings of 20 individuals with replacement, was also calculated for each population, except the UAE population where only 10 individuals were available. Expected heterozygosity and associated standard errors were calculated using DISPAN. Observed genotype frequencies were tested for consistency with HW and linkage equilibrium expectations using GENEPOP 3.3 (Raymond & Rousset 1995). To control for type I error associated with multiple comparisons involving single sampling sites, a sequential Bonferroni adjustment (Rice 1989) was performed. Tests for genotypic linkage disequilibrium for all pairs of loci were performed using Fisher's exact test (Raymond & Rousset 1995). F statistics were carried out to partition heterozygosity into a within- and an among-population component using FSTAT 2.9.3 (Goudet 2000).

Population assignment from allele frequency distribution

WHICHRUN 4.1 (Banks & Eichert 2000) program was used to allocate individuals to their most likely source population. The allocation stringency was a log of the odds ratio >2.

Results

Genetic variation

A total of 115 alleles were observed at the 14 loci in the 332 individuals from the seven dromedary populations studied. The total number of alleles per locus ranged from two (*VOLP32*) to 19 (*CVRL1*) with an MNA per locus of 8.21. The largest MNA was found in the Somali camel (MNA = 6.14), while the lowest mean of alleles was found in the UAE with an MNA of 3.57 (Table 1). From the resampling analysis, the Pakistan and Saudi Arabian populations were the most diverse with MNA of 4.70 and 4.83, respectively. All the four Kenyan dromedaries had very close MNA values between 3.89 and 4.29. When pooled the MNA for the Kenyan and non-Kenyan dromedaries were 4.22 and 5.24, respectively. Expected heterozygosity values averaged over loci (H_E) showed an overall pattern similar to that observed for the MNA per locus (Table 1). The highest value, around 59%, was observed within the Pakistan and Saudi Arabian populations. The Kenyan dromedaries had average expected heterozygosity values between 51 and 55%. Raw microsatellite data and allele frequencies are available from the Corresponding author.

Table 1 Expected heterozygosity (H_E) and mean number of alleles per locus (MNA) with their standard error within each of the seven dromedary populations studied.

Population	Country	Sample size	H_E	MNA (all animals)	MNA[1] (20 animals)
Somali	Kenya	144	0.547 ± 0.056	6.14	4.29 ± 0.62
Rendille	Kenya	46	0.513 ± 0.057	4.50	3.89 ± 0.62
Turkana	Kenya	42	0.527 ± 0.057	4.64	4.05 ± 0.58
Gabbra	Kenya	36	0.524 ± 0.059	4.64	4.14 ± 0.69
Kenyan dromedaries	Four populations	268	0.538 ± 0.057	7.00	4.22 ± 0.64
Pakistan	Pakistan[2]	32	0.593 + 0.050	5.00	4.70 + 0.73
Saudi Arabia	Saudi Arabia	22	0.594 ± 0.047	4.93	4.83 ± 0.72
United Arab Emirates	United Arab Emirates	10	0.516 ± 0.058	3.57	–
Non-Kenyan dromedaries	Three populations	64	0.610 ± 0.051	6.64	5.24 ± 0.86

[1]Mean values after 99 sampling.
[2]Sampled in Kenya.

Table 2 Genetic distances (D_A) between the Camelidae populations studied.

	Somali	Rendille	Turkana	Gabbra	Bactrian	Pakistan	Saudi Arabia
Rendile	0.025						
Turkana	0.026	0.025					
Gabbra	0.037	0.027	0.033				
Bactrian	0.784	0.784	0.773	0.767			
Pakistan	0.113	0.147	0.113	0.156	0.775		
Saudi Arabia	0.098	0.122	0.102	0.122	0.787	0.125	
United Arab Emirates	0.189	0.205	0.193	0.211	0.789	0.129	0.164

Genetic distances and relationships between populations

The distance matrix (D_A) showing relationships amongst all pairs of populations is summarized in Table 2. Genetic distances between the Bactrian and the seven dromedary populations were the highest, ranging between 0.767 and 0.789. Distances between the dromedary populations were small, ranging from 0.025 to 0.211. The D_A distances amongst the indigenous Kenyan camel breeds were the smallest, ranging from 0.025 to 0.037.

Figure 1 shows a neighbour-joining tree based on D_A genetic distances of eight Camelidae populations. A clear separation is visible between the Bactrian and the dromedary populations. Within the dromedaries, the Kenyan and non-Kenyan populations are separated, with a moderate bootstrap value of 57%. Among the Kenyan dromedaries, the Gabbra and Rendille populations are the most closely related (bootstrap value of 86%). The Turkana population is linked to these two while the Somali population is separated from the other Kenyan dromedary populations.

Hardy–Weinberg equilibrium

There were a total of 98 HW equilibrium tests (14 loci in seven populations). As a measure of deviation from HW equilibrium the F_{IS} value was calculated and type I error probabilities computed. A total of 13 locus-population combinations gave *P*-values indicating deviation from HW expectations at the level of 5% or lower. There was no global deviation of F_{IS} values of one locus in all populations, and positive and negative values were observed. Application of sequential Bonferroni adjustment for multiple testing reduced the number of significant locus-population combinations to two.

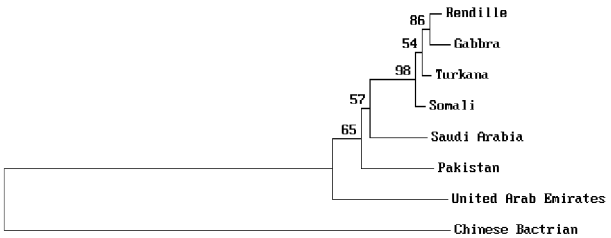

Figure 1 Unrooted neighbour-joining dendogram showing the genetic relationships among one Chinese Bactrian and seven dromedary populations using D_A genetic distance calculated from 14 microsatellite loci. The numbers at the node indicate the percentage of support for each cluster in a bootstrap re-sampling of 1000 trees.

Linkage disequilibrium

Gabbra, Rendille, Turkana and UAE populations had fewer than five pairs of loci (out of 91 comparisons) in linkage disequilibrium ($P < 0.05$). The Somali, Pakistan and Saudi Arabian populations had deviations from linkage equilibrium at 8, 9 and 9 loci pairs, respectively ($P < 0.05$). No comparisons were significant for locus pairs across all populations.

F statistics

Overall, the differentiation index values (F_{ST}) were low with mean values of 0.056 and 0.009 for all dromedary populations and Kenyan dromedaries, respectively. Table 3 indicates the statistical significance of the F_{ST} for each of the 14 loci and for each population pair. This gives a clear illustration of the usefulness of the different markers to distinguish between dromedary populations within a country, Kenya, and between countries. *CVRL1* was the most informative marker with all but two population pairs showing statistically significant differentiation at $P < 0.05$ or lower. At the other end, *YWLL009* did not differentiate any of the population pairs. Within the Kenyan dromedaries no marker was efficient at distinguishing between all four populations. In fact, only one marker was able to distinguish between two of the population pairs Gabbra–Rendille and Gabbra–Turkana, and two markers between the pair Rendille–Turkana. The genetic differentiation between the Somali dromedary and the other Kenyan dromedaries is supported by three to five loci.

Taking all loci together, F_{ST} values between population pairs ranged from 0.0013 for the Gabbra–Turkana pairs to

Table 3 Statistical significance of the F_{ST} for each of the 14 loci and for each population pair.

	VOLP3	*VOLP8*	*VOLP10*	*VOLP32*	*YWLL008*	*YWLL009*	*YWLL38*	*YWLL44*	*YWLL59*	*CVRL1*	*CVRL2*	*CVRL5*	*CVRL6*	*CVRL7*
Rendille & Somali	*	–	*	–	–	–	***	–	–	**	–	**	–	–
Turkana & Somali	–	–	**	*	–	–	–	–	–	–	–	–	–	**
Turkana & Rendille	–	–	*	–	–	–	**	–	–	–	–	–	–	–
Gabbra & Somali	*	–	–	*	–	–	–	–	–	***	–	***	–	**
Gabbra & Rendille	–	–	–	–	–	–	–	–	–	***	–	–	–	–
Gabbra & Turkana	–	–	–	–	–	–	–	–	–	***	–	–	–	–
Pakistan & Somali	***	***	***	*	***	–	***	***	***	***	–	***	–	***
Pakistan & Rendille	***	***	***	–	***	–	***	***	***	***	*	***	–	***
Pakistan & Turkana	***	***	***	–	***	–	***	***	**	***	–	**	–	***
Pakistan & Gabbra	***	***	***	–	***	–	***	***	***	***	–	***	–	***
Saudi Arabia & Somali	***	***	***	–	***	–	***	**	**	***	***	*	–	***
Saudi Arabia & Rendille	***	*	***	–	***	–	***	**	*	***	***	**	–	**
Saudi Arabia & Turkana	***	*	***	–	***	–	***	*	–	***	***	*	–	**
Saudi Arabia & Gabbra	***	**	***	–	**	–	***	*	*	***	***	*	–	**
Saudi Arabia & Pakistan	**	***	*	–	***	–	***	–	–	**	***	***	–	–
United Arab Emirates & Somali	**	***	***	*	***	–	***	–	–	***	–	***	*	***
United Arab Emirates & Rendille	**	**	***	–	***	–	***	–	–	***	*	**	*	***
United Arab Emirates & Turkana	**	***	***	–	***	–	***	–	–	***	–	**	*	***
United Arab Emirates & Gabbra	**	***	***	–	***	–	***	–	–	***	–	*	*	***
United Arab Emirates & Pakistan	*	***	**	–	***	–	–	–	–	*	–	***	–	*
United Arab Emirates & Saudi Arabia	*	–	–	–	***	–	–	–	–	*	*	**	–	–

An unbiased estimate of the *P*-value of a log-likelihood (*G*-based) exact test was performed using GENEPOP (Raymond & Rousset 1995).
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, – Not significant.

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0.1620 between the Rendille and the UAE populations. Tests of significance showed that three population pairs, Gabbra–Rendille, Gabbra–Turkana and Rendille–Turkana were not significant ($P > 0.05$). For all remaining population pairs F_{ST} values are highly significant ($P < 0.001$).

Breed assignment

The lowest type I error was seen in the UAE population where 100% of the individuals were correctly classified. The Saudi Arabia and Pakistan populations also showed a moderate to high accuracy of breed designation with 68 and 81%, respectively, of the animals correctly assigned to the source population. On the other hand, there was a much higher rate of misclassification for the Kenyan dromedaries with the proportion of individuals correctly assigned ranging from 39 to 48% only. When the Kenyan dromedaries were treated as two groups, the Somali and Gabbra–Rendille–Turkana populations, 62% of the former and 76% of the latter were assigned to their respective populations. Interestingly, some Kenyan and Pakistan animals were assigned to the Saudi Arabian Peninsula populations.

Discussion

The Kenyan dromedaries, either as separated populations or when grouped as one, were found to have a lower diversity than the non-Kenyan populations in terms of MNA per locus and expected heterozygosity, excluding the UAE camels where only 10 individuals were analysed (Table 1). The low genetic variation among the Kenyan dromedaries may be due to higher levels of inbreeding or a loss of genetic variation following genetic drift subsequent to migration from a centre of origin. The weak genetic differentiation (F_{ST}) observed between Kenyan dromedary populations, as well as the observed low non-significant F_{IS} values, indicate that inbreeding is an unlikely explanation for the lower heterozygosity within the Kenyan dromedaries.

There were no significant deviations from HW equilibrium expectations in all the populations studied, also the 14 loci analysed may be assumed to be unlinked, as linkage disequilibrium did not yield any significant comparisons for locus pairs across all populations. The slightly higher than expected ($P < 0.05$) deviation from linkage equilibrium observed in the Pakistan, Somali and Saudi Arabian samples could indicate population subdivision, recent introduction of a non-random subset of genotypes or habitat-specific selection (King *et al.* 2001).

Genetic relationships between populations were studied using genetic distances and neighbour-joining tree. As expected for two distinct species, Bactrian and dromedary populations clearly emerged as distinct lineages, and they showed the largest genetic distances. Among the dromedaries, all Kenyan dromedary populations were more closely related to each other than to the non-Kenyan counterparts (Table 2; Fig. 1).

The close relationship amongst Kenyan dromedary populations was further illustrated by the results of the differentiation analysis (F_{ST}). A total of 5.6% of the genetic variation was explained by breed differences, when Kenyan and non-Kenyan populations were analysed together. The figure went down to 0.9% when the analysis was restricted to the four Kenyan dromedary populations only. These differentiation values are much lower compared with those generally recorded in other domestic animal populations [e.g. 8% between Spanish horses (Cañon *et al.* 2000), 9.9% between Spanish dog breeds (Jordana *et al.* 1992), 10% between European cattle (MacHugh *et al.* 1998), and 17% between Swiss goat breeds (Saitbekova *et al.* 1999)]. This result may reflect the more recent domestication and dispersion of the dromedary camels compared with these other domesticated species. Although population differentiation was generally low between the dromedary populations studied, it was highly significant ($P < 0.001$) between all population pairs with the exception of the Gabbra–Rendille, Gabbra–Turkana and Rendille–Turkana pairs.

Breed assignment accuracy was low, especially in the Kenyan dromedaries. The poor success in correct breed assignment could be attributed to the weak genetic differentiation and gene flow between populations. Interestingly, the assignment accuracy was increased considerably when the Kenyan populations were grouped as two separate genetic entities, the Somali and the Gabbra–Rendille–Turkana groups, as suggested by the genetic differentiation results.

The pattern of population differentiation revealed by genetic distances, neighbour-joining tree, differentiation index and assignment test, reflected the evolutionary history and geographical distribution among the camel breeds studied. The present classification of Kenyan dromedary is mainly based on geographical locations and socio-ethnological considerations (http://www.fao.org/dad-is/). Results of the present microsatellite analysis, using autosomal genetic markers, suggest a close genetic relationship of Kenyan dromedary populations. It appears likely that all the Kenyan populations have a common origin and that there is extensive gene flow between the Gabbra Rendille and Turkana populations. Our microsatellite based molecular genetic study does not support the distinction of four Kenyan camel populations. Instead, following the analysis of 14 microsatellite loci, the results indicate two separate genetic entities, the Somali and Gabbra–Rendille–Turkana group.

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