Microsatellite Variation in Two Populations of Free-Ranging Yellow Baboons (*Papio hamadryas cynocephalus*)

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*We investigated genetic variation at six microsatellite (simple sequence repeat) loci in yellow baboons (*Papio hamadryas cynocephalus*) at two localities: the Tana River Primate Reserve in eastern Kenya and Mikumi National Park, central Tanzania. The six loci (D1S158, D2S144, D4S243, D5S1466, D16S508, and D17S804) were all originally cloned from and characterized in the human genome. These microsatellites are polymorphic in both baboon populations, with the average heterozygosity across loci equal to 0.731 in the Tana River sample and 0.787 in the Mikumi sample. The genetic differentiation between the two populations is substantial. Kolmogornov–Smirnov tests indicate that five of the six loci are significantly different in allele frequencies in the two populations. The mean F_{ST} across loci is 0.069, and Shriver's measure of genetic distance, which was developed for microsatellite loci (Shriver et al., 1995), is 0.255. This genetic distance is larger than corresponding distances among human populations residing in different continents. We conclude that (a) the arrays of alleles present at these six microsatellite loci in two geographically separated populations of yellow baboons are quite similar, but (b) the two*

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populations exhibit significant differences in allele frequencies. This study illustrates the potential value of human microsatellite loci for analyses of population genetic structure in baboons and suggests that this approach will be useful in studies of other Old World monkeys.

KEY WORDS: *Papio*; microsatellite loci; DNA polymorphism; population structure.

INTRODUCTION

Previous surveys of genetic variation in baboons showed substantial variability both in proteins (Buettner-Janusch and Olivier, 1970; Shotake, 1981; Williams-Blangero *et al.*, 1990) and in DNA (Rogers and Kidd, 1996). Analyses of the distribution of that variation within and between populations suggest that baboons exhibit genetic substructure at several hierarchical levels. Subspecies share many alleles in common but may differ significantly in the frequencies of specific alleles (Williams-Blangero *et al.*, 1990). Less is known about genetic differentiation among local populations within a subspecies, but there is evidence that local populations can also vary substantially in allele frequencies (Olivier *et al.*, 1986). More data are required before it will be possible to describe how taxonomic—subspecific—differences and geographic distances are correlated with genetic differentiation among populations of *Papio*.

Analyses of genetic differentiation in baboons and other cercopithecines have suffered from a lack of highly informative genetic markers in the nuclear genome. While >30 genetic polymorphisms have been described in baboons (VandeBerg 1992), most of the loci have only two or three alleles and exhibit a rather low heterozygosity in any given population. Recently, researchers have begun to utilize microsatellite loci (also called simple sequence repeats or short tandem repeats) in genetic studies of nonhuman primates. Microsatellites are short sequences of DNA consisting of tandem arrays of nucleotide repeats 2 to 5 base pairs in length (Weber and May, 1989; Bruford and Wayne, 1993). They are highly susceptible to mutations that alter the number of repeat units (Edwards *et al.*, 1992; Weber and Wong, 1993); consequently, the loci accumulate high levels of intrapopulation variability. Recent evidence suggests that, in humans, mutations at these loci typically add or delete one repeat unit at a time (Valdes *et al.*, 1993).

Microsatellite loci that were cloned from the human genome, and first studied in human populations, have been used in population genetic analyses of hominoids (Morin *et al.*, 1994; Deka *et al.*, 1994; Deinard and Kidd, 1995) and in genetic linkage analyses of baboons (Rogers *et al.*, 1995; Perelygin *et al.*, 1996). Altmann *et al.* (1996) used microsatellites in combination

with two protein polymorphisms to investigate paternity and kinship statistics within a troop of yellow baboons in Amboseli National Park. Morin *et al.* (1997) described microsatellite variation among rhesus macaques. The successful analysis of human microsatellite loci in studies of the population genetics of baboons and other Old World monkeys will dramatically increase the number of potentially informative genetic markers, since >8000 polymorphic microsatellites have been isolated from the human genome (Genome Data Base, Baltimore, MD). We used six microsatellite loci originally cloned from the human genome as markers for studies of genetic variation within and between two free-ranging populations of yellow baboons.

STUDY SITES

We investigated subjects from two distinct populations: Mikumi National Park, Tanzania, and the Tana River Primate Reserve, Kenya. These localities are separated by approximately 650 km. All subjects included in the study are yellow baboons, *Papio hamadryas cynocephalus* (Jolly, 1993). The Tana River Reserve is located in eastern Kenya, and consists of riverine forest (Marsh, 1986). In 1986, E. O. Smith initiated a survey of baboon troops in the reserve. Over the next 3 years, observers followed and habituated individual troops and began behavioral research (Bentley-Condit, 1995). In 1992, the total population size of baboons in the 171-km^2 Tana River Reserve was approximately 700, with an average group size of between 75 and 100 (V. Bentley-Condit, personal communication). We obtained blood samples from one troop, which consisted of 83 animals.

Research on the baboons of Mikumi National Park began in 1974, under the supervision of Rhine (1986). Our Mikumi subjects are drawn at random from seven troops that inhabit the central portion of the 3300-km^2 park. These troops have been assayed for restriction fragment length polymorphisms in five nuclear loci (Rogers and Kidd, 1993, 1996). The total census size of these seven troops is between 300 and 350 baboons. Adult males migrate among the troops, and consequently all the Mikumi study subjects are considered to be members of a single, large interbreeding population (Rogers and Kidd, 1996). The total baboon population of Mikumi Park is large, probably >20,000. The region surrounding Mikumi Park also supports substantial numbers of baboons, so the animals within the park are inferred to be part of an even larger network of local populations. The average size of social groups in Mikumi National Park at the time of sampling was estimated to be between 45 and 60 baboons (Rogers, 1989).

MATERIALS AND METHODS

To obtain the Tana River sample, we trapped, tranquilized, bled from the femoral vein, and released members of a single troop. We drew between 3 and 10 ml of blood per individual, depending on age and body weight, into Vacutainers containing EDTA as anticoagulant. In order to keep the whole blood samples cool during shipment to the U.S., we transported them on wet ice. Genomic DNA was extracted from white blood cells by treating them with lysis buffer (0.32 *M* sucrose, 10 m*M* Tris, 5 m*M* $MgCl_2$, 1% Triton-X-100, 0.02% sodium azide), then centrifuging and recovering nuclei. Lysis of nuclei used a buffer of 50 m*M* Tris, 20 m*M* EDTA, and 2% SDS. We extracted genomic DNA by incubating samples with proteinase at 55°C for 1 hr, followed by incubation with RNase at 37°C for 15 min. The DNA was precipitated with ethanol and resuspended in Tris–EDTA buffer. For the Mikumi population Rogers and Kidd (1993; Rogers, 1989) have described procedures used in the field collection of blood and the laboratory preparation of genomic DNA. For the present study of microsatellites, we randomly selected DNA samples from 42 Mikumi baboons from the available material collected from the seven study groups.

To analyze baboon microsatellites, we used standard polymerase chain reaction (PCR) amplification methods. The amplification reactions were 25 μl in total volume and contained 50–80 ng of template DNA, a 0.25 μ*M* concentration of each primer, 1 U of Taq polymerase, and standard PCR buffers. We followed either touchdown PCR (Don *et al.,* 1991) or standard three-temperature PCR routines using a Perkin Elmer Model 9600 thermal cycler. One primer in each reaction was radiolabeled via ^{32}P. To score genotypes among the baboons, we analyzed radiolabeled PCR products using denaturing polyacrylamide gel electrophoresis in sequencing gels with standard electrophoretic buffers. To produce autoradiographs we exposed dried gels to Kodak X-OMAT X-ray film for 4–24 hr in autoradiography cassettes with intensifying screens. Genotypes were scored independently by two investigators and compared for concordance. We ran DNA samples from baboons with known genotypes—selected from the large colony at the Southwest Foundation—on each gel as positive controls. Sample sizes for allelic frequency calculations differ across loci because not all samples produced reliable genotypes for every locus.

We typed individuals from each of the two populations for six polymorphic microsatellite loci (Table I). These loci were selected for study in the free-ranging baboons because they are known to be polymorphic and to exhibit Mendelian inheritance in a multigeneration pedigree of baboons at the Southwest Foundation (Rogers *et al.,* 1995; Rogers and Witte, unpublished data). The alleles have alphabetical designations from the longest

Table I. Allelic Frequencies and Standard Errors for Six Microsatellite Loci in the Tana River and Mikumi Baboons

Locus	Allele	Size (bp)[a]	Tana River	Mikumi
D1S158	B	145	—	0.028 ± 0.019
	C	143	—	0.083 ± 0.033
	D	141	—	0.111 ± 0.037
	E	139	0.236 ± 0.050	0.069 ± 0.030
	F	137	0.375 ± 0.057	0.042 ± 0.024
	G	135	—	0.056 ± 0.027
	H	133	—	0.056 ± 0.027
	I	131	—	0.153 ± 0.042
	J	129	0.056 ± 0.027	0.167 ± 0.044
	K	127	0.333 ± 0.056	0.069 ± 0.030
	L	125	—	—
	M	123	—	—
	N	121	—	—
	O	119	—	—
	P	117	—	0.167 ± 0.044
			(n = 72)[b]	(n = 72)
D2S144	A	179	0.012 ± 0.012	—
	B	177	0.105 ± 0.033	0.024 ± 0.017
	C	175	0.291 ± 0.049	0.037 ± 0.021
	D	173	0.256 ± 0.047	0.110 ± 0.035
	E	171	—	0.061 ± 0.026
	F	169	0.116 ± 0.035	0.256 ± 0.048
	G	167	—	0.280 ± 0.050
	H	165	0.186 ± 0.042	0.183 ± 0.043
	I	163	0.035 ± 0.020	0.037 ± 0.021
	J	161	—	—
	K	159	—	—
	L	157	—	0.012 ± 0.012
			(n = 86)	(n = 82)
D4S243	A	180	0.038 ± 0.021	0.068 ± 0.029
	B	176	0.050 ± 0.024	0.095 ± 0.034
	C	172	0.125 ± 0.036	0.149 ± 0.041
	D	168	0.138 ± 0.039	0.162 ± 0.043
	E	164	0.225 ± 0.047	0.189 ± 0.046
	F	160	0.287 ± 0.051	0.054 ± 0.026
	G	156	0.038 ± 0.021	0.176 ± 0.044
	H	152	0.013 ± 0.013	0.081 ± 0.032
	I	148	0.087 ± 0.032	0.027 ± 0.019
			(n = 80)	(n = 74)
D5S1466	A	315	—	0.016 ± 0.016
	B	311	0.013 ± 0.013	—
	C	307	0.038 ± 0.021	0.113 ± 0.040
	D	303	0.050 ± 0.024	0.129 ± 0.043
	E	299	0.150 ± 0.040	0.242 ± 0.054
	F	295	0.225 ± 0.047	0.210 ± 0.052
	G	291	0.363 ± 0.054	0.194 ± 0.050
	H	287	0.162 ± 0.042	0.048 ± 0.027
	I	283	—	0.048 ± 0.027
			(n = 80)	(n = 62)

Table I. Continued

Locus	Allele	Size (bp)[a]	Tana River	Mikumi
D16S508	A	105	0.139 ± 0.040	—
	B	103	0.028 ± 0.019	—
	C	101	—	0.095 ± 0.035
	D	99	0.042 ± 0.023	0.122 ± 0.035
	E	97	—	0.243 ± 0.051
	F	95	0.389 ± 0.057	0.095 ± 0.035
	G	93	0.181 ± 0.045	0.189 ± 0.046
	H	91	0.014 ± 0.014	0.203 ± 0.047
	I	89	—	—
	J	87	0.208 ± 0.047	0.027 ± 0.019
	K	85	—	0.027 ± 0.019
			(n = 74)	(n = 72)
D17S804	A	167	—	0.088 ± 0.034
	B	165	0.029 ± 0.020	0.029 ± 0.020
	C	163	0.086 ± 0.034	0.176 ± 0.046
	D	161	0.329 ± 0.056	0.662 ± 0.057
	E	159	0.557 ± 0.059	0.044 ± 0.025
			(n = 70)	(n = 68)

[a]Length estimates are ±2 base pairs.
[b]n = the number of chromosomes sampled per locus; the number of individual animals sampled is $n/2$.

PCR product to the shortest. We determined allele frequencies via gene counting, calculated standard errors using the method of Edwards *et al.* (1992), and computed average heterozygosity per locus (H) as $H=1-\Sigma q_i^2$, in which q_i is the frequency of the ith allele. The observed genetic variance was partitioned into intra- and interpopulation variance using Wright's F statistics (1969), incorporating modifications proposed by Nei (1973) for multiple alleles. We calculated both Nei's standard genetic distance (1987) and Shriver's genetic distance statistic, which is designed for use with data from microsatellites (Shriver *et al.*, 1995), from observed allele frequencies.

RESULT

All six loci are polymorphic in the Tana and Mikumi populations. Allele frequencies are graphically represented in Fig. 1. Table I lists the estimated frequency of each allele, the standard error for each estimate, and the estimated lengths of alleles in base pairs. Most alleles are present in both population samples. We observed a total of 54 alleles with 34 present at both localities. None of the loci shows significant deviation from Hardy–Weinberg equilibrium expectations in either population sample. Average heterozygosity

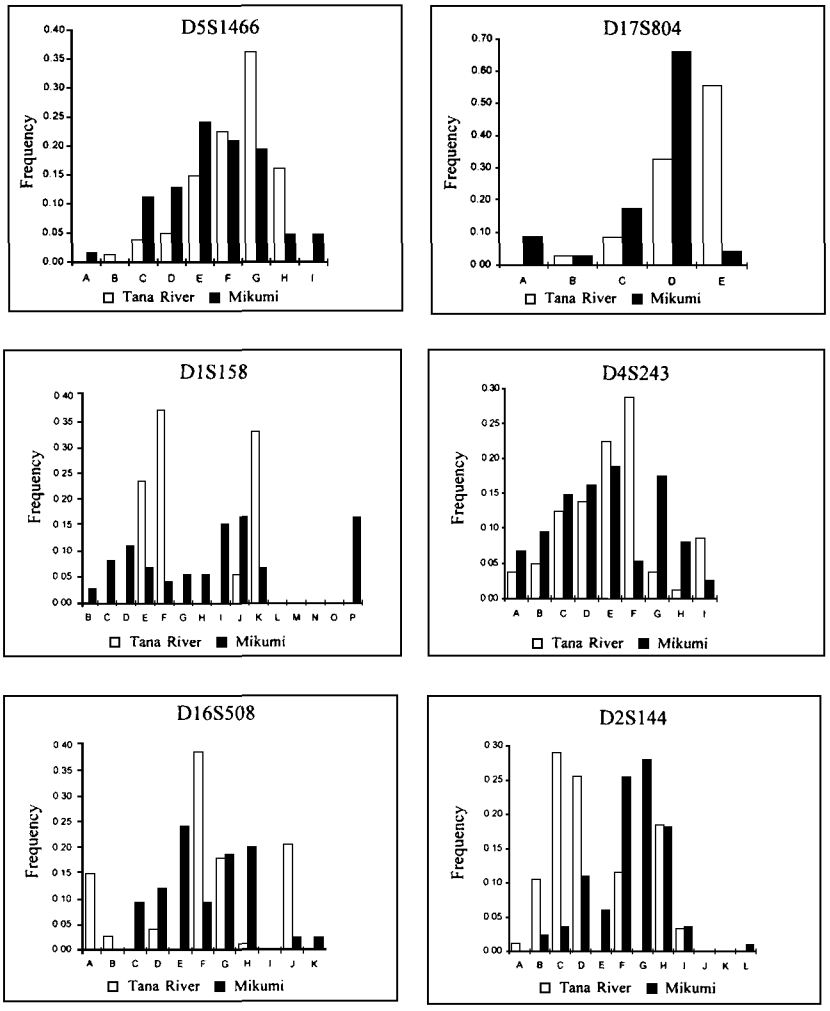

Fig. 1. Allelic frequencies for six microsatellite loci in the Tana River and Mikumi baboon populations.

per locus ranges from 0.520 for D17S804 in the Mikumi sample to 0.883 for D1S158 in Mikumi baboons. All six heterozygosity estimates for the Tana River sample fall within that range. Average heterozygosity across these loci is 0.731 for Tana and 0.787 for Mikumi (Table II). While most alleles are shared by the two populations, we observe substantial differences in the frequency of specific alleles between localities. For each locus, a different allele

Table II. Heterozygosity of Microsatellite Loci in Yellow Baboons

Locus	Tana River	Mikumi
D1S158	0.690	0.883
D2S144	0.789	0.803
D4S243	0.819	0.861
D5S1466	0.765	0.826
D16S508	0.751	0.830
D17S804	0.573	0.520
Mean	0.731	0.787

Table III. F_{ST} and Genetic Distances Using Microsatellites

Locus	F_{ST}	Shriver's distance	Nei's distance
D1S158	0.087	0.317	1.084
D2S144	0.057	0.618	0.649
D4S243	0.026	0.034	0.309
D5S1466	0.021	0.131	0.161
D16S508	0.073	0.131	0.888
D17S804	0.152	0.298	0.561
Mean	0.069	0.255	0.609

is predominant in the two populations. Kolmogorov-Smirnov tests of differences in alleleic frequencies are significant for five loci (D1S158, $p<0.01$; D2S144, $p<0.001$; D5S1466, $p<0.05$; D16S508, $p<0.05$; D17S804, $p<0.01$). The F_{ST} statistics (Table III) also illustrate this differentiation. The mean F_{ST} across loci is 0.069, with a range of 0.026–0.152. Table III also lists the results of the two genetic distance calculations.

DISCUSSION

Little is known about genetic differentiation among baboon populations of the same subspecies because few researchers have surveyed the same genetic markers in more than one locality. In addition, few highly informative genetic markers have been available for this type of comparative analysis. However, recent advances in molecular genetics provide new opportunities for detailed analyses of population differentiation. Our investigation of microsatellite variation in these two populations of yellow baboons indicates that primers for human microsatellite loci can detect

highly informative markers for the analysis of genetic structure in baboon populations.

The results of this genetic survey can be viewed from alternative perspectives. On the one hand, the two population samples show important similarities. Most of the observed alleles occur in both baboon populations. This sharing of alleles may be the result of either recent gene flow between the two localities or the retention of polymorphisms that predate the genetic separation of the populations. On the other hand, the observed allelic frequencies are statistically different between the two localities at five of the six loci studied, and such clear genetic differentiation also requires explanation. The value for Shriver's distance statistic is 0.255, which is higher than analogous estimates of genetic distance between human populations sampled from different continents (Jorde *et al.,* 1995; Watkins *et al.,* 1995). The parameter estimates obtained for F_{ST}, Nei's standard distance, and Shriver's genetic distance should be taken as preliminary, since six loci do not constitute a large enough sample to generate highly reliable estimates. Nevertheless, these results indicate that there is substantial genetic differentiation between these two baboon populations.

Genetic drift among geographically isolated (or semiisolated) populations is the most likely cause of the differentiation between the Mikumi and the Tana River populations. Previous work has demonstrated that baboon populations <500 km apart can exhibit statistically significant differentiation (Olivier *et al.,* 1986). The number and population density of baboons in southeast Kenya and central and eastern Tanzania are substantial, and it may be that male-mediated dispersal could, through complex interconnections among populations, maintain effective gene flow between the Tana River and Mikumi sites. The magnitude of genetic differences between the two sites suggests that gene flow, if it has occurred recently, was not strong enough to resist significant local differentiation. Until more genetic information is available from additional localities across this region of eastern Africa, it is not possible to develop detailed inferences about the demographic or genetic processes that produced and maintain the current level of genetic differentiation. Altmann *et al.* (1996) also found significant allelic variation at microsatellite loci in the baboons of Amboseli National Park, Kenya. There is no overlap in the microsatellites they studied and those investigated here, so it is not possible to calculate genetic distances among the Amboseli, Tana River, and Mikumi.

Our population sample from the Tana River is not ideal for analyses of genetic differences between local populations. An optimal study would compare allele frequencies across sets of unrelated individuals, with each set drawn at random from several social groups representing one locality. The Mikumi sample is structured this way, but all the Tana subjects were

members of one social group. Sampling from additional groups is not possible. We note that the Mikumi sample contains a larger number of alleles (49) across all loci than the Tana sample. The greater variability in the Mikumi sample may be due in part to the larger number of social groups sampled, but we do not believe that this has had a major effect. The observed array of alleles found in the Tana sample is likely to be a reasonable reflection of the overall genetic composition of the Tana population, since any one baboon social group generally exhibits all or nearly all the alleles present in the surrounding population (Byles and Sanders, 1981; Rogers, 1989, Rogers and Kidd, 1993, 1996). The process of obligate male dispersal in yellow baboons probably results in the rapid transfer of new mutations to most or all of the social groups in a locality.

Rubinsztein *et al.* (1995) proposed that microsatellite alleles at a given locus are longer on average in humans than in nonhuman primates and that this is due to a difference in the mutational process that produces microsatellite variation in humans. The range of allele sizes observed here for baboons overlaps the range of human allele sizes for all six loci (Genome Database, Baltimore, MD; http://gdbwww.gdb.org). It is not possible to test directly the hypothesis of Rubinsztein *et al.* (1995) with our data because the baboon alleles have not all been sequenced, and thus it is not possible to determine the exact length of the di- or tetranucleotide repeat arrays. If the total lengths of PCR products are compared, there are four cases out of the six loci (D1S158, D2S144, D4S243, and D5S1466) in which the average size of baboon alleles is shorter than the apparent average for humans. However, this is best explained as the result of a bias for long alleles in the original clone selection during the isolation of microsatellite loci from the human genome, as opposed to a directionality of mutation rate or a difference in the process of mutation in humans versus baboons.

In summary, first, we find that microsatellite loci which were cloned from the human genome can provide informative genetic markers for studies of population structure and genetic differentiation among *Papio*. The immediate availability of several thousand such loci makes this a powerful approach to the development of genetic markers for cercopithecines and other Old World monkeys. Second, we find that the two study populations show similar arrays of alleles at the six loci. Third, a significant level of allele frequency differentiation between the populations exists. Analysis of additional loci in the Tana River, Mikumi, and other baboon populations is necessary to determine whether this level of differentiation is typical for local populations of baboons classified in the same subspecies. The use of microsatellite markers may also be valuable in studies of genetic differentiation among more distantly related populations, such as comparisons

between subspecies of baboons or among closely related congeneric species, e.g., macaques and guenons.

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