Ecology, Demography, and Population Genetics of Barbary Macaques in Algeria

WOLFGANG SCHEFFRAHN,
Universität Zürich

NELLY MÉNARD, DOMINIQUE VALLET,
Centre National de la Recherche Scientifique, France

and BELKACEM GACI
Djurdjura National Park, Algeria

ABSTRACT. Over a 9-year period from 1982 to 1990 ecological and demographic data were collected on two genetic isolates of Barbary macaques (*Macaca sylvanus*) in Algeria, from the deciduous oak-forest of Akfadou and from the evergreen cedar-oak forest of the National Park Djurdjura. Macaques at Djurdjura profit from more suitable ecological conditions and have a higher rate of population increase as well as a higher male migration rate than those at Akfadou. Genetic data, gained from 23 genetic markers (blood proteins), proved to be highly influenced by the demographic structure of the groups. The macaque populations of Akfadou and Djurdjura have become genetically differentiated. Group fission, coupled with founder effect (genetic drift) and kin-structured (matrilineal) separation, resulted in a priori genetic diversity between one newly-established group and its parent group.

Key Words: *Macaca sylvanus*; Ecology; Demography; Migration; Group fission; Population genetics.

INTRODUCTION

The Neo-Darwinian evolutionary concept is the most plausible explanation for the genetic differentiation in biological systems. Recent field studies of non-human primates contribute new insights into this core concept of evolution by elucidating the causal chain between ecology, demography, and population genetics: a further possible pathway of ongoing evolutionary processes in wild populations. These studies demonstrate that different ecological conditions can govern demographic features such as group size, natality, mortality, migration, etc. (ALTMANN et al., 1985; CHAPMAN, 1990; CHENEY, 1983; CHENEY & SEYFARTH, 1983; CROCKETT & EISENBERG, 1987; DITTUS, 1988; FUKUDA, 1988; MÉNARD et al., 1990; SOUTHWICK & SIDDIQI, 1988; STRUHSAKER, 1976; SYMINGTON, 1987). To date, however, only a few studies have focussed on demographic characteristics as determinants of genetic structure (MELNICK, 1987; MELNICK & HOELZER, 1992; MELNICK & KIDD, 1983; PHILLIPS-CONROY et al., 1992; POPE, 1990). On the other hand, a growing number of longitudinal field studies are starting to reveal further evidence of microevolutionary processes within non-human primate societies and to postulate models for the interpretation of certain evolutionary processes in human evolution (CAMPERIO CIANI et al., 1989; MELNICK, 1988; NOZAWA et al., 1982; PHILLIPS-CONROY et al., 1992; POPE, 1992; DE RUITER et al., 1992; SCHEFFRAHN & DE RUITER, in press; SHOTAKE, 1981; TURNER et al., 1984).

The prime goal of the current paper is to outline the relationship between ecological

constraints, demographic parameters, and genetic structure in two populations of the Barbary macaque (*Macaca sylvanus*) in Algeria, from Akfadou and Djurdjura. The specific aims of the study were: 1) to describe the genetic structure of the two populations; 2) to determine their degree of genetic relatedness; 3) to report on their genetic differences in relation to ecological and demographic conditions; 4) to consider the microevolutionary change over generations in subdivided populations and their dependence on demographic dynamics; and 5) to discuss the genetic consequences of group fission.

The results of longitudinal study (1982 – 1990) of the ecology and demography of Algerian Barbary macaques living in different habitat types have been described elsewhere (MÉNARD & VALLET, 1988, 1993, in press). Evidence for the influence of ecological characteristics on the demography of social groups will be taken into closer consideration here.

MATERIAL AND METHODS

Algerian Barbary macaques live in seven "genetic isolates," defined here as populations, without any gene flow between them. Our study was carried out in two populations: in a deciduous oak-forest in Akfadou (36°43'N; 4°33'E) and in an evergreen cedar-oak forest in the Djurdjura National Park (36°27'N; 4°8'E) (Fig. 1).
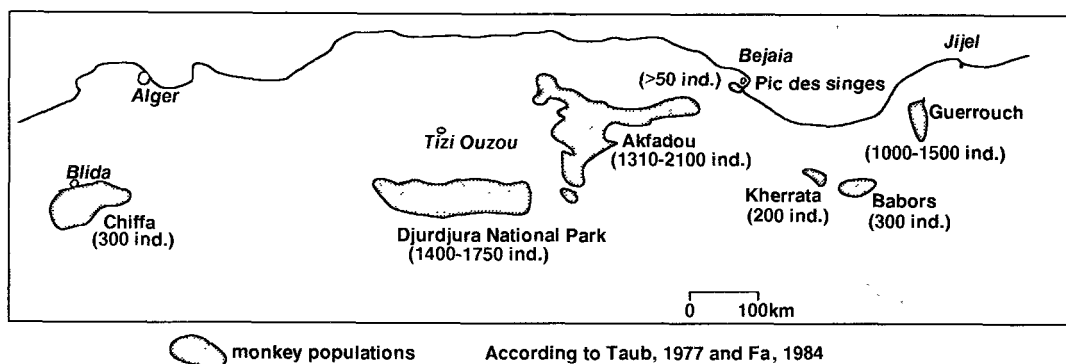

Fig. 1. Map showing the distribution of the seven populations (genetic isolates) of *Macaca sylvanus* in Algeria; numbers in brackets refer to the estimated size of populations; note the total geographical separation of Akfadou and Djurdjura.

The ecological characteristics of these two habitats as well as the dietary selectivity of the monkeys have been quantitatively analyzed. Results suggest that monkeys encounter more suitable conditions in the cedar-oak forest of Djurdjura than in the deciduous oak-forest of Akfadou (MÉNARD & VALLET, 1988).

DEMOGRAPHIC CHARACTERISTICS

Demographic subdivisions within the populations are regarded as "social groups." A longitudinal study has been carried out since 1982 to analyze demographic parameters such as group size, birth and mortality rates, and migration rates. The studies essentially

concentrated on one "focal group" (resident animals) at each site. All the animals belonging to these units have been individually identified on the basis of physical characteristics, such as pigmentation patterns of face, or coloured ear tags. The Barbary macaque groups studied exhibit the typical pattern of multimale-multifemale structure.

In Djurdjura, the mean annual rate of population increase was more than three times higher than that in Akfadou (18.6% vs. 5.1%), mainly due (more than 75%) to differences between natality and mortality rates, whilst migrations had a weaker effect. The intrinsic rate of increase was three times higher in Djurdjura than in Akfadou (14.6% vs. 4.8%) due to a greater recruitment of adult females, a greater number of births and fewer infant deaths, especially of females (MÉNARD & VALLET, 1993).

The demographic status of the Djurdjura group, which increased from 37 to 76 individuals, developed into a group fission resulting in the foundation of three new stable groups of 50, 24, and 13 individuals, in 1989. Moreover, individuals were not distributed randomly in the new groups after fission. Adult females and immatures were grouped together according to relatedness and matrilineages, respectively (MÉNARD & VALLET, 1993).

Males emigrate to other groups whereas females remain in the natal group. There was no difference between Akfadou and Djurdjura as far as the emigration rate was concerned (0.16 and 0.14/year). On the other hand, the immigration rate was very much higher in Djurdjura (0.20/year) than Akfadou (0.08/year). Fifty-four percent of the migration events observed between 1983 and 1990 occurred during the process of group fission between the years 1987 to 1989 (MÉNARD & VALLET, in press).

To summarize, it can be stated in general terms that annual group increase was higher in Djurdjura than in Akfadou, leading to a more frequent group fission favouring in turn an increase in the male migration rate. On the other hand, it seems reasonable to assume that the demographic characteristics encountered in the cedar-oak forest in Djurdjura are linked with the more favourable ecological conditions in this habitat type. The group fission event in Djurdjura in 1989 clearly suggests, on the basis of demographic data, that at the initial step of subgrouping a founder effect, based on kin-structured dispersion, took place.

GENETICS

EDTA blood samples were collected from 119 animals (70 in Djurdjura and 49 in Akfadou) that were present in the populations at any time between 1983 and 1991 (Table 1). The animals originated from three to four different groups, but the majority of them (73% in Djurdjura and 78% in Akfadou, respectively) belonged to the resident animals. In order to test to what extent dynamic events such as births, deaths, and migrations could induce modifications of the genetic structure of the groups over time (years), genetic parameters of the resident animals have been compared between 1983 and 1988 in Djurdjura and between 1983 and 1990 in Akfadou. In Djurdjura, 60.9% and 59.1% of the animals present in the group in 1983 and 1988, respectively, have been sampled; in Akfadou, 54% and 51% of the animals present in the group, in 1983 and 1990, respectively, have been sampled. After group fission in 1989, the process of genetic differentiation between the parent (focal) group of Djurdjura in 1987 and the three newly established groups (SM, LO, and UL) from 1989 to 1991 has been considered in a sample of 26 (52%) and 20 (51%) individuals of the new group "SM" and of 19 (79%) and 21 (72%) individuals of the group "LO" (Table 1). The sample of the third group "UL" has been regarded as being too small for comparison.

Table 1. Groups, polymorphic systems, number of individuals, and allele frequencies at Akfadou and Djurdjura.

	Akfadou Total	Akfadou 1988	Djurdjura Total	Djurdjura 1987	SM89	SM91	LO89	LO91
Transferrin								
n	49	33	70	46	26	20	19	21
TF*1	0.920	0.939	0.607	0.620	0.519	0.500	0.684	0.595
TF*2	0.080	0.061	0.393	0.380	0.481	0.500	0.316	0.405
PI								
n	44	33	69	45	26	20	18	20
PI*1	1.000	1.000	0.949	0.956	0.962	1.000	1.000	0.975
PI*2	0.000	0.000	0.051	0.044	0.038	0.000	0.000	0.025
C3								
n	6	6	28	11	10	10	11	14
C3*1	0.167	0.167	0.661	0.455	0.500	0.600	0.727	0.750
C3*2	0.833	0.833	0.339	0.545	0.500	0.400	0.273	0.250
Amylase 2								
n	44	33	69	46	26	20	19	21
AMY*1	0.875	0.894	0.819	0.859	0.865	0.875	0.763	0.738
AMY*2	0.125	0.106	0.181	0.141	0.135	0.125	0.237	0.262
Haemoglobin								
n	35	24	51	31	20	16	15	19
HB*1	0.714	0.688	0.706	0.774	0.750	0.750	0.800	0.737
HB*2	0.286	0.312	0.294	0.226	0.250	0.250	0.200	0.263

Immunglobulin systems (IgGM, IgKM, and IgBM) have been typed by J. M. DUGOUJON and colleagues (Toulouse, France) following the methods described elsewhere (DUGOUJON et al., 1981). Some other plasma proteins, the haemoglobin (HB), the pancreatic amylase (AMY2), and protease inhibitor (PI) have been screened after extended modifications of conventional methods of isoelectric focussing techniques which were necessary to reveal protein variability and genetic polymorphism, respectively. In the present paper a gene locus is defined as being polymorphic if the frequency of the most common allele does not exceed 0.99. A good selection of enzyme systems has been analyzed by J. ARNAUD (Toulouse, France). For detailed description of electrophoretic methods see SCHEFFRAHN (1992). Twenty-three blood protein markers (10 plasma proteins: ALB, DBP, PI, TF, C3, BF, GM, KM, BM, and AMY2; haemoglobin (HB), 12 red blood cell enzymes; 6-PGD, ADA, AK, CA1, CA2, ESD, ACP, GLO, PGM1, PGM2, DIA1, and DIA2) have been typed. The protein-based comparison of genetic data between Akfadou, Djurdjura and their groups has been performed with the help of a variety of statistical procedures for the analysis of allele frequencies and genetic variability measures (mean heterozygosity as unbiased estimate, using corrections in the case of small sample size, LEVENE, 1949; NEI, 1978), chi-square goodness-of-fit test of Hardy-Weinberg equilibrium (HWE), genetic similarity and distance (NEI, 1978, unweighted pair group method), F-statistics (WRIGHT, 1965; NEI, 1977), significance probabilities etc., available in the computer package *Biosys-1* (SWOFFORD & SELANDER, 1989).

RESULTS

GENETICS

Akfadou and Djurdjura: Of 23 blood protein loci considered, 18 markers (mentioned above) were found to be monomorphic; only 5 (PI, TF, C3, HB, and AMY2) of the total

Table 2. Nei matrix of coefficients of genetic identity (above diagonal) and genetic distance (below diagonal).

	1	2	3	4	5	6	7	8	9
1 Akfadou 1988	–	0.816	1.000	0.950	0.870	0.952	0.923	0.893	0.781
2 Akf neighb.	0.203	–	0.828	0.891	0.962	0.893	0.888	0.963	0.964
3 Akf resid. animals	0.000	0.188	–	0.953	0.877	0.955	0.927	0.901	0.794
4 Djurdjura 1987	0.051	0.115	0.048	–	0.962	1.000	0.996	0.974	0.886
5 Djur. neighb.	0.139	0.038	0.131	0.039	–	0.962	0.969	0.986	0.931
6 Djur. resid. animals	0.049	0.113	0.046	0.000	0.038	–	0.996	0.974	0.887
7 SM Djur. 1989	0.080	0.119	0.076	0.004	0.031	0.004	–	0.973	0.883
8 LO Djur. 1989	0.114	0.037	0.105	0.027	0.014	0.026	0.027	–	0.964
9 Kintzheim Bal	0.247	0.037	0.230	0.121	0.072	0.120	0.125	0.037	–

set of genetic markers applied have proven to be polymorphic. Allele frequency data for the five polymorphic loci for all individuals of different units from Akfadou and Djurdjura are given in Table 1. At Djurdjura five genetic markers (PI, TF, C3, HB, and AMY2) are variable, in contrast to only four (TF, C3, HB, and AMY2) at Akfadou. The relatively low rates of polymorphism (at Djurdjura about 0.217, at Akfadou about 0.174) seem to throw light upon the often mentioned phenomenon of reduced genetic variation of protein loci encountered in the Barbary macaques and they can be considered in the framework that the variable markers uniformly represent diallelic systems in this species. Only ten alleles have been identified at five polymorphic loci (Djurdjura), i.e. the average number of alleles at Djurdjura is 2.0, in contrast to 1.8 alleles at Akfadou. In this context it seems worth mentioning that after the fission of the Djurdjura group in 1989 and the foundation of three new stable groups, the PI locus of the LO group also became monomorphic, as a consequence of genetic drift.

A careful look at the allele frequency distributions reveals striking differences in the allelic variation of the two populations (Table 1): the C3 system appears divergent, for example the C3 *2 allele is the most common in Akfadou, whereas the C3 *1 is the most common in Djurdjura. As for the transferrin alleles, the frequencies of the TF *1 allele are markedly distinct between the two populations. The PI *1 allele is fixed in Akfadou; in Djurdjura it exhibits polymorphism. Only the frequencies of the alleles of the AMY2 and HB loci are very much alike in both populations. This overall evidence is well expressed in Nei's genetic distance value of 0.051 (Table 2) between the two populations (Akfadou 1988/Djurdjura 1987), which clusters them into different branches of the relatedness dendrogram (Fig. 2a, c). The F_{ST} value as a measure of the degree of genetic differentiation between the two populations is 0.113 (Table 3), indicating that about 11% of the total variation is responsible for the genetic difference between the macaques of Akfadou and Djurdjura. All phenotype frequencies are in Hardy-Weinberg equilibrium (HWE, $p < 0.05$), except that of the PI in Djurdjura.

Table 3. F-statistics at all loci TF, AMY2, HB, C3, and PI.

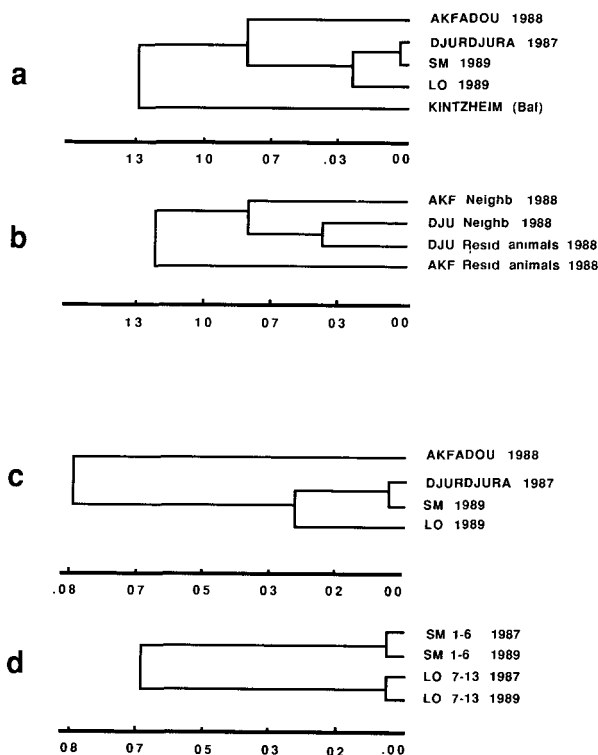|	F_{IS}	F_{IT}	F_{ST}
Algerian macaques	− 0.054	0.108	0.153
AKF total − DJU total	− 0.005	0.109	0.113
DJU resid. animals − DJU neighb.	0.040	0.073	0.035
AKF resid. animals − AKF neighb.	− 0.206	− 0.178	0.024
DJU 1987 − SM 1989	− 0.025	− 0.021	0.004
DJU 1987 − LO 1989	0.049	0.075	0.028
SM 1989 − LO 1989	0.000	0.029	0.028

Fig. 2. Dendrograms of *Macaca sylvanus* populations (see text).

The demographic data collected by two of the authors (NM and DV) in a long-term study provide a unique possibility to judge the influence of demographic dynamics (such as asymmetrical migration by males, births, and deaths) on the gene pool composition of subsequent generations. The expectation is that the allele frequencies should not have changed over the years under identical or rather similar conditions. This holds in Djurdjura where no sharp breaks of allele frequencies have occurred from 1983 to 1988 and the degree of genetic variation has remained almost unchanged, as measured by the mean heterozygosity which has stabilized around 0.340 over all these years (Table 4), without any dramatic change in rates of migration, births, and death cases. In Akfadou, however, an increase in the mean heterozygosity is noticeable from 1983 to 1986; then a small break occurs in 1987, followed by another increase in the period 1988 – 1989. Moreover these data on heterozygosity underline the general tendency that the degree of genetic variation was consistently greater in Djurdjura than in Akfadou.

Akfadou: The mean heterozygosity (H) at four variable loci (TF, C3, AMY2, and HB) in

Table 4. Mean heterozygosity at Akfadou (4 loci) and Djurdjura (5 loci).

	1983	1984	1985	1986	1987	1988	1989	1991
Akfadou	0.136±0.068	0.122±0.057	0.147±0.081	0.213±0.077	0.189±0.069	0.210±0.076	0.212±0.078	
Djurdjura	0.349±0.076	0.346±0.077	0.338±0.078	0.332±0.080	0.337±0.079	0.346±0.074		
SM							0.347±0.085	0.326±0.097
LO							0.312±0.080	0.345±0.076

Table 5. Mean heterozygosity in species of macaques.

Species	Mean H	Author
Asian macaques	0.018 – 0.108	NOZAWA et al., 1977
Macaca mulatta	0.053	MELNICK et al., 1984
Macaca fuscata	0.001 – 0.033	NOZAWA et al., 1982
Macaca fascicularis	0.012 – 0.054	KAWAMOTO et al., 1981
Macaca nigra ssp.	0.033 – 0.107	KAWAMOTO et al., 1982
Macaca sinica	0.068 – 0.088	SHOTAKE & SANTIAPILLAI, 1982
Macaca sylvanus	0.031 – 0.083	
Akfadou	0.031 – 0.051	Present study
Djurdjura	0.073 – 0.083	Present study
LO Djurdjura 1989	0.0679	Present study
SM Djurdjura 1989	0.0753	Present study

the total population of Akfadou ($n = 49$) was 0.215 (HWE expected, S.E. 0.071), estimated over all 23 loci, 0.047 (Tables 4 and 5). The population of Akfadou can be subdivided into two, those individuals which belonged to the focal group since 1982 and their offspring (resident animals) and those which were present in the neighbouring groups at any time between 1982 to 1988 (neighbouring animals, $N = 11$). Surprisingly, the resident animals exhibited a mean heterozygosity value of 0.031 (HWE expected, over 22 loci without the C3 marker) in 1988 ($N = 35$), the neighbouring animals a value of 0.051 (Table 5), indicating an existing genetic heterogeneity in the overall population. In addition to this observation the fixation index, measuring the effect of population subdivision, shows an excess of heterozygotes, especially in the neighbouring animals (Table 6).

Djurdjura: The mean heterozygosity (H) at five variable loci (TF, C3, AMY2, HB, and PI) of the total population of Djurdjura ($n = 70$) was 0.350 (HWE expected, S.E. 0.071), estimated over all 23 loci 0.076 (Table 5). In 1988, the H value at the five variable loci in the resident animals of Djurdjura was 0.335 (HWE expected, S.E. 0.080, over all 23 loci 0.073), of the "neighbouring animals" 0.380 (HWE expected, S.E. 0.064, over all 23 loci 0.083).

In June 1989 a fission of the Djurdjura group occurred and led to the foundation of three stable groups (SM, LO, and UL). We have compared (Tables 1 – 5): 1) the two groups SM 1989 and LO 1989 with the parental Djurdjura group of 1987, before intensified migration of males took place in connection with the fission event; 2) the group SM 1989 to LO 1989; and 3) the groups SM and LO in their population development from 1989 to 1991. Firstly, in all the parameters chosen in the current study for such a population genetic comparison, the group SM 1989 remained very similar to the parent Djurdjura group of 1987. There is no significant difference between the mean H value of SM and Djurdjura in 1987.

Table 6. Fixation index (coefficients for heterozygotic deficiency or excess).

	TF	AMY2	HB	C3	PI
Akfadou total	– .079	– .129	– .020	– .200	– .000
Akfadou resid. animals 1988	– .049	– .103	.236	– .250	– .000
Akfadou neighb. 1988	– .125	– .385	– .556	.000	.000
Djurdjura total	.072	.072	.056	– .036	.248
Djurdjura resid. animals 1988	– .043	.259	.098	.100	– .041
Djurdjura neighb. 1988	.375	– .019	– .048	.333	.640
Djurdjura 1987	.032	.194	.077	– .100	– .047
Djurdjura SM 1989	– .310	– .156	– .067	.200	– .040
Djurdjura SM 1991	– .200	– .143	– .333	.167	.000
Djurdjura LO 1989	.269	.272	.167	– .375	.000
Djurdjura LO 1991	.308	.138	.186	– .333	– .026

Although a difference in the allele frequencies can be observed (and in particular in the TF), Nei's index of genetic similarity of about 0.996 demonstrates the close genetic relatedness between the parent group Djurdjura 1987 and the filial group SM 1989. As a consequence of these findings, the F_{ST} value of 0.004 is very low. If we compare the filial group LO 1989 to the parent group Djurdjura 1987, the allele frequency distribution of AMY2, C3, and PI appears to be widely different. It should be pointed out again that the allele PI *1 has been fixed in the gene pool of the group LO as a consequence of the fission event. This event partly contributes to the lower mean H of 0.312 (over 4 Loci, S.E. 0.080) of the LO group. The Nei similarity is reduced to 0.974, the genetic differentiation slightly marked (F_{ST} 0.028) between the filial group of LO and the parental group of Djurdjura 1987. Secondly, the question arises as to whether a genetic distinction has developed between the filial groups SM and LO in 1989, caused uniquely by fission and governed by founder principle, genetic drift, and matrilineal grouping. This is to stress that the gene pool composition of the two new groups is characterized by rather remarkable deviations from the expected allelic frequency distribution of the genetic markers TF, AMY2, C3, and PI. In addition, the Nei similarity has diminished to 0.973 and the degree of genetic differentiation has reached the figure of almost 3% (F_{ST} 0.028). It is noteworthy that the mean H of the group LO has fallen to a relatively low value (0.312). Finally, neither the gene pool of the group SM nor that of the group LO has drastically changed in the two years after fission, from 1989 to 1991. All the observed phenotypic numbers have been compared to those expected assuming HWE in Djurdjura groups 1989 − 1991; no significant difference has been found between the observed and expected numbers.

DISCUSSION

The current paper is the first announcement on electrophoretically revealed blood proteins of Barbary macaques (*Macaca sylvanus*) from Algeria, the only non-Asian macaque species. The paper attempts to present an overview of the causal chain between ecological and demographical correlates as well as their influence on the genetic structure of populations from two Algerian localities, Akfadou and Djurdjura (Fig. 1). One of the prime concerns of the current paper centres on group fission and its genetic implications.

Blood protein systems which are genetically variable in different populations/groups of *Macaca sylvanus* are summarized in Table 1. SOCHA et al. (1981) have determined several serological blood groups of Barbary macaques of Moroccan descent at the captive colony at Kintzheim (France); the authors detected a genetic polymorphism only in the D[rh] graded blood group system with a species-specific allele frequency distribution. Plasma proteins (BIEDERMANN, 1979) and erythrocytic enzymes (SCHEFFRAHN, unpubl. observ.) of animals of the same colony and their descendants in the sanctuary of Salem (Germany) have been electrophoretically analyzed and only the genetic markers TF, DBP (one animal was heterozygous), and AMY2 were found to be polymorphic and variable, respectively. SCHMITT et al. (1981) published results on genetic polymorphism of the systems ABO, TF, GOTs (soluble glutamic oxaloacetic transaminase), and AMY2 of Barbary macaques of the Rheine Zoo, Westfalia, Germany, which also originated from Morocco (Middle Atlas region). Incidentally, this paper and that by SMITH (1980) were the first papers which, to the best of our knowledge, not only highlighted the issue of verification of paternity in non-human primates but, furthermore, coupled the genetic findings with sociobiological concerns (differential reproduction and Darwinian fitness). In contrast to the findings of

Table 7. Polymorphic systems in *Macaca sylvanus* populations of Moroccan descent and from Algeria.*

	ABO	D^{rh}	PI	TF	DBP	C3	AMY2	GOT	HB
Morocco	pol[1]	pol[2]	mon[3]	pol[1][5]	var[4]	mon[3][5]	pol[1][3]	pol[1]	mon[3]
Algeria	n.t.	n.t.	pol[3]	pol[3]	mon[3]	pol[3]	pol[3]	n.t.	pol[3]

*Data from Akfadou and Djurdjura combined. mon: Monomorphic; pol: polymorphic; n.t.: not tested; var: variable. 1) SCHMITT et al. (1981); 2) SOCHA et al. (1981), SOCHA & RUFFIE (1983); 3) present paper; 4) SCHEFFRAHN, unpubl.; 5) BIEDERMANN (1979).

Moroccan Barbary macaques, the present study on the genetic markers of Algerian populations has revealed genetic polymorphisms in the blood proteins PI, TF, C3, AMY, and HB while the DBP (GC) appears to be monomorphic (Table 7). At the time being, it still remains undecided by the scarce genetic information available whether the Moroccan macaques are genetically very distinct from the Algerian populations of Akfadou and Djurdjura. But further support for a greater genetic distance between Moroccan and Algerian Barbary macaques comes from the extended comparison of Akfadou and Djurdjura groups to one colony of Moroccan descent (Kintzheim), as cautiously judged from the dendrogram (Fig. 2a). Some real genetic differences between the Moroccan and the Algerian Barbary macaques may actually exist, but the issue will remain unanswered until the forthcoming genetic screening of wild Moroccan macaques has been completed.

The genetic data obtained so far lead to the assumption that the populations of Akfadou and Djurdjura have differentiated genetically at a relatively high level. Certainly, it remains debatable how large the degree of genetic differentiation has to be before it can be concluded that two groups are genetic isolates. But in the current study we gain support from the findings on geographic barriers, on many substantial ecological and demographic differences and, consequently, we are willing to suggest that the macaques of Akfadou and Djurdjura have taken the first steps towards a sharper genetic differentiation and can be viewed as genetic isolates on the basis of an F_{ST} value of 0.113. Although both populations still have 89% of the total Algerian macaque variation in common, they have reached a genetic differentiation on the level of approximately 11%. The most plausible explanation for this degree of differentiation is that these two sets of Barbary macaque populations have experienced decreased gene flow over a long time period. FOODEN and LANYON (1989) evaluated the degree of genetic differentiation of macaques at various hierarchical levels and mentioned mean values of "populations within country" of F_{ST} 0.0816. The F_{ST} between Akfadou and Djurdjura is considerable above that observed for Asian macaques of this hierarchical level and the degree of differentiation, therefore, can be viewed as relatively advanced on the comparative basis of other macaques.

The reference by all authors to the existence of only a few variable/polymorphic and only diallelic systems in *Macaca sylvanus* led to the assumption that this species was characterized by little variation of protein loci, compared to other species of macaques. MÉNARD et al. (1992) have warned that the size of genetic variation of this species cannot be assigned by protein markers alone and have shown that at the nuclear DNA level a huge variability exists in the form of RFL polymorphisms (fingerprints). Over and above this, it has been argued, that the smaller degree of genetic variability in *Macaca sylvanus* might be the result of passing through different bottlenecks during withdrawal from a wider Pleistocene expanse to its contemporary areas of dispersal. If we summarize (Table 2) all information about the variability of protein loci it can be confirmed that at least the following nine markers exhibit some kind of variability in the species *Macaca sylvanus*: ABO, D^{rh}, PI,

DBP (GC), TF, C3, AMY2, GOT, and HB, i.e. a considerable array out of about 30 systems so far tested. In addition, J. M. DUGOUJON (pers. comm.) has shown a genetic variability of the immunoglobulins (IgGM 13, IgBM 5, and IgBM 8). The overall picture leads to the conclusion that the magnitude of variable genetic markers of the Barbary macaques falls almost into the range of the Asian macaques. From this view, it should be stressed that the detection of genetic polymorphisms heavily depends on the facilities and preferred interests of a laboratory as well as on the geographical area where the animals have been originally captured and on the founder principle effects.

To recapitulate, it has been outlined in the present paper that the locus PI is mono-morphic in all the groups of Akfadou macaques. After fission, the PI locus became also monomorphic in the Djurdjura group LO in 1989, but remained polymorphic in the group SM (Table 1). Two years later, in 1991, we observe that the PI locus is polymorphic in the group LO, apparently due to immigration, but became monomorphic in the group SM, probably caused by microevolutionary effects. These examples impressively demonstrate how the gene pool can rapidly change in groups of special structure or of limited size. On the other hand, the observation of the existence of only diallelic and not multiallelic loci very much testifies that the species has lost some part of its original genetic variation dur-ing recent evolution or, in other words, the decreased number of alleles at a single locus as well as the diminished number of polymorphic systems indicates that possible bottleneck effects may have occurred during the phylogeny of this species.

The average heterozygosity (H) over all 23 loci is 0.047 at Akfadou and 0.076 at Djurd-jura, respectively. The Akfadou value represents a relatively low value compared to other wild species of macaques, whereas the Djurdjura value comes closer to the average H values of other wild macaque species (Table 5).

The genetic differentiation between populations/groups of Algerian Barbary macaques is well expressed, judged on the basis of the F_{ST} value of 0.153 (Table 3, Fig. 2a, b, c, & d), the highest value of genetic differentiation found so far in Algerian populations. As shown in Table 2 the Nei distance value is remarkably greater between the neighbouring animals and the resident animals at Akfadou than at Djurdjura, indicating more genetic heterogeneity at Akfadou. This observation fully fits the statement of FOODEN and LANYON (1989) who found that F_{ST} values can vary enormously between neighbouring populations. This finding might be regarded in the light of demographic structure pecu-liarities of Akfadou which, as outlined above, is characterized by less migration so that greater genetic differences between groups are more likely to occur. The cluster dendrogram (Fig. 2), which summarizes the relatedness between the groups on the basis of genetic-distance measures, demonstrates that the resident animals and the neighbouring animals of Akfadou cluster separately, whereas all Djurdjura groups join the same cluster indicating more homogeneity at this locality due to more migration as documented by demographic data. The genetic analysis indicates significant differences between Akfadou and Djurdjura also in terms of the genetic variation within populations. Interestingly, the mean heterozygosity is higher in Djurdjura than in Akfadou and always greater in the neighbouring animals than in the resident animals.

To summarize, due to more appropriate ecological conditions for Barbary macaques at Djurdjura we observe a higher rate of population increase which favours a higher demographic pressure to fission and migration of males (in particular during the process of group fission) in this area. The larger genetic variation and the smaller genetic distance between groups at Djurdjura might be regarded as being in accordance with the specific ecological and demographic characteristics.

Table 8. Values of F_{ST} and genetic distance (Nei) in the matrilineages SM and LO at Djurdjura (1987, 1989).

Matrilineages	Nei distance	F_{ST}
SM 1987 > < LO 1987	0.075	0.085
SM 1989 > < LO 1989	0.054	0.061

One evolutionary-genetic interest in group fissions in non-human primates lies in the sudden formation of groups with diverged gene pools. But, after the publication by MELNICK and KIDD (1983), it remained questionable whether fission accelerates subpopulation genetic differentiation due to division along matrilineal relatedness as previously described for semifree-ranging groups of *Macaca mulatta* at Cayo Santiago (OBER et al., 1979; OLIVIER et al., 1978, 1981) or not as argued for a wild population of *Macaca mulatta* from Pakistan (MELNICK, 1987; MELNICK & KIDD, 1983). As for *Macaca sylvanus*, group fissions have been described for semifree-ranging groups (PAUL & KUESTER, 1988; PRUD'HOMME, 1991) and, very recently, for wild Barbary macaques from Algeria (MÉNARD & VALLET, in press).

The differences in genetic effects of group fission in populations of the same species lie according to MELNICK and KIDD (1983) in the dissimilar demographic structure, patterns of paternity and in the degree to which matrilines are genetically divergent before split. The current paper aims at emphasizing the genetic data for fission products at Djurdjura where three new groups came into existence in June 1989 of which groups SM ($N=50$) and LO ($N=24$) were large enough to be genetically compared to the parent group 1987. Certainly, the genetic distance between the parent group 1987 and the two new groups is a result of a specific allele distribution. The genetic difference between the parent group and LO reached almost 3%, only due to this fission happening, whereas that between the parent group and SM is negligeable. Surprisingly, the fixation index of the group LO 1989 additionally shows a deficit of heterozygotes in many genetic markers whereas the group SM 1989 exhibits values mainly indicating an excess of heterozygotes (Table 6). A very similar result can be obtained from the cluster analysis where the findings exhibit similarity figures for the parent group 1987 and for the new group SM, which are comparatively high yielding no large genetic difference due to this fission event. In contrast to this statement the group LO has a lower similarity value (or a higher figure of genetic distance). One explanation for the observed post-fission differences between the groups SM and LO might be sought in the pre-fission process of genetic differentiation of the matrilines. Table 8 summarizes the evidence of the informative parameters, which lead to the conclusion that the corresponding matrilines were genetically differentiated before the group fission and conserved this degree of differentiation after the split into the groups of SM and LO. Non-random mating might contribute to such a genetic differentiation of matrilines, but this phenomenon might not be so relevant to the genetic differentiation of a promiscuous primate society such as that of *Macaca sylvanus* (MÉNARD et al., 1992).

The overall evidence convincingly illustrates how demographic events such as group fission can determine the gene pool composition of groups from the very first generation on. In addition to this conclusion it is worth mentioning that the individuals mainly separated not randomly but according to their genealogical relatedness (matrilineage, kin-structured migration) so that the population genetic consequences of this linkage between founder effect (genetic drift) and kin-structured filial groups (genetic relatedness) are responsible for this *a priori* genetic distinction between groups after fission. It is note-

worthy that genetic consequences of group fission are not readily predictable but, apparently, represent the result of a combination of different demographic and evolutionary factors. Genetic heterogeneity between matrilines before a split plays a major role and can be enhanced by non-random division of a parent group. Furthermore, it depends on the conventional microevolutionary events and in particular on the degree of isolation and/or migration as to what final effects such a group fission might produce after several generations. In this respect, speculation continues with regard to the hypothesis that these processes have also played a role in the evolution of man.

REFERENCES

Altmann, J., G. Hausfater, & S. A. Altmann, 1985. Demography of Amboseli baboons, 1963 – 1983. *Amer. J. Primatol.*, 8: 113 – 125.

Biedermann, V., 1979. *Untersuchungen über die Serumproteinsysteme Albumin, Transferrin, C3 (betaIC-Globulin) und Bf (GBG) bei einigen Spezies der Cercopithecinae (Primates).* Diplomarbeit, Zürich.

Camperio Ciani, A., R. Stanyon, W. Scheffrahn, & B. Sampurno, 1989. Evidence of gene flow between Sulawesi macaques. *Amer. J. Primatol.*, 17: 257 – 270.

Chapman, C. A., 1990. Ecological constraints on group size in three species of Neotropical primates. *Folia Primatol.*, 55: 1 – 9.

Cheney, D. L., 1983. Proximate and ultimate factors related to the distribution of male migration. In: *Primate Social Relationships: An Integrated Approach*, R. A. Hinde (ed.), Blackwell, Oxford, pp. 241 – 372.

————— & R. Seyfarth, 1983. Nonrandom dispersal in free ranging vervet monkeys: social and genetic consequences. *Amer. Naturalist*, 122: 392 – 412.

Crockett, C. M. & J. F. Eisenberg, 1987. Howlers: variations in group size and demography. In : *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, & T. Struhsaker (eds.), Univ. of Chicago Press, Chicago, pp. 54 – 68.

Dittus, W. P. J., 1988. Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Anim. Behav.*, 36: 1626 – 1645.

Dugoujon, J. M., M. Blanc, & J. Ducos, 1981. New antigens on primate immunoglobulins determined by antiglobulins of normal human sera. *Folia Primatol.*, 36: 144 – 149.

Fa, J. E. (ed.), 1984. *The Barbary Macaque: A Case Study in Conservation.* Plenum Press, New York/London.

Fooden, J. & S. M. Lanyon, 1989. Blood-protein allele frequencies and phylogenetic relationships in *Macaca*: a review. *Amer. J. Primatol.*, 17: 209 – 241.

Fukuda, F., 1988. Influence of artificial food supply on population parameters and dispersal in the Hakone T troop of Japanese macaques. *Primates*, 29: 477 – 492.

KAWAMOTO, Y., K. NOZAWA, & T. M. ISCHAK, 1981. Genetic variability and differentiation of local populations in the Indonesian crab-eating macaque (*Macaca fascicularis*). *Kyoto Univ. Overseas Report of Studies on Indonesian Macaque*, 1: 15–39.

————, O. TAKENAKA, & E. BROTOISWORO, 1982. Preliminary report on genetic variations within and between species of Sulawesi macaques. *Kyoto Univ. Overseas Research Report of Studies on Asian Non-human Primates*, 2: 23–37.

MELNICK, D. J., 1987. The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. *Genetica*, 73: 117–135.

————, 1988. The genetic structure of a primate species: Rhesus macaques and other cercopithecine monkeys. *Int. J. Primatol.*, 9: 195–231.

————, J. J. CLIFFORD, & K. K. KIDD, 1984. The genetics of a wild population of rhesus monkeys (*Macaca mulatta*): I. genetic variability within and between social groups. *Amer. J. Phys. Anthropol.*, 63: 341–360.

———— & G. A. HOELZER, 1992. Differences in male and female macaque dispersal lead to contrasting distributions of nuclear and mitochondrial DNA variation. *Int. J. Primatol.*, 13: 379–393.

———— & K. K. KIDD, 1983. The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). *Behav. Ecol. Sociobiol.*, 12: 229–236.

MÉNARD, N., R. HECHAM, D. VALLET, H. CHIKHI, & A. GAUTIER-HION, 1990. Grouping patterns of a mountain population of *Macaca sylvanus* in Algeria: a fission-fusion system? *Folia Primatol.*, 55: 166–175.

————, W. SCHEFFRAHN, ————, C. ZIDANE, & C. REBER, 1992. Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics for wild Barbary macaques. In: *Paternity in Primates: Tests and Theories*, R. D. MARTIN, A. DIXSON, & E. J. WICKINGS (eds.), Karger, Basel, pp. 155–174.

———— & D. VALLET, 1988. Disponibilités et utilisation des ressources par le magot (*Macaca sylvanus*) dans différents milieux en Algérie. *Rev. Ecol. (Terre Vie)*, 43: 201–250.

———— & ————, 1993. Population dynamics of *Macaca sylvanus* in Algeria: an 8-year study. *Amer. J. Primatol.*, 30: 101–118.

———— & ————, in press. Dynamics of fission in a wild Barbary macaques group (*Macaca sylvanus*) in Algeria. *Int. J. Primatol.*

NOZAWA, K., T. SHOTAKE, Y. KAWAMOTO, & Y. TANABE, 1982. Population genetics of Japanese monkeys. II. Blood protein polymorphism and population structure. *Primates*, 23: 252–271.

————, ————, Y. OHKURA, & ————, 1977. Genetic variations within and between species of Asian macaques. *Jap. J. Genet.*, 52: 15–30.

OBER, C. L., J. BUETTNER-JANUSCH, & T. J. OLIVIER, 1979. Genetic differentiation between matrilines in the Cayo Santiago macaque groups. *Amer. J. Phys. Anthropol.*, 50: 468.

OLIVIER, T. J., C. L. OBER, & J. BUETTNER-JANUSCH, 1978. Genetics of group fissions on Cayo Santiago. *Amer. J. Phys. Anthropol.*, 48: 424.

————, ————, ————, & D. S. SADE, 1981. Genetic differentiation among matrilines in social groups of rhesus monkeys. *Behav. Ecol. Sociobiol.*, 8: 279–285.

PAUL, A. & J. KUESTER, 1988. Life-history patterns of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. In: *Ecology and Behavior of Food-enhanced Primate Groups*, J. E. FA & C. H. SOUTHWICK (eds.), pp. 199–228.

PHILLIPS-CONROY, J. E., C. J. JOLLY, P. NYSTROM, & H. A. HEMMALIN, 1992. Migration of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. *Int. J. Primatol.*, 13: 455–476.

POPE, T. R., 1990. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single male troops using genetic markers. *Behav. Ecol. Sociobiol.*, 27: 439–446.

————, 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the Red Howler monkey (*Alouatta seniculus*). *Evolution*, 46: 1112–1128.

PRUD'HOMME, J., 1991. Group fission in a semifree-ranging population of Barbary macaques (*Macaca sylvanus*). *Primates*, 32: 9–22.

DE RUITER, J. R., W. SCHEFFRAHN, G. J. J. M. TROMMELEN, A. G. UITTERLINDEN, R. D. MARTIN, & J. A. R. A. M. VAN HOOFF, 1992. Male social rank and reproductive success in wild long-tailed macaques. In: *Paternity in Primates: Tests and Theories*, R. D. MARTIN, A. DIXSON, & E. J. WICKINGS (eds.), Karger, Basel, pp. 175−191.

SCHEFFRAHN, W., 1992. Elektrophoretische Methoden. In: *Anthropologie. Handbuch der vergleichenden Biologie des Menschen*, R. KNUßMANN, H. W. JURGENS, I. SCHWIDETZKY, & G. ZIEGELMAYER (eds.), G. Fischer, Stuttgart, pp. 371−421.

———— & J. R. DE RUITER, in press. Genetic relatedness between populations of *Macaca fascicularis* on Sumatra. In: *Evolution and Ecology in Macaque Societies*, J. E. FA & D. G. LINDBURG (eds.), Cambridge Univ. Press, Cambridge.

SCHMITT, J., H. RITTER, C. SCHMIDT, & R. WITT, 1981. Genetic markers in primates: pedigree patterns of a breeding group of Barbary macaques (*Macaca sylvana* LINNAEUS, 1758). *Folia Primatol.*, 36: 191−200.

SHOTAKE, T., 1981. Population genetical study of natural hybridization between *Papio anubis* and *P. hamadryas*. *Primates*, 22: 285−308.

———— & C. SANTIAPILLAI, 1982. Blood protein polymorphisms in the troops of the toque macaque, *Macaca sinica*, in Sri Lanka. *Kyoto Univ. Overseas Research Report of Studies on Asian Non-Human Primates*, 2: 79−95.

SMITH, D. G., 1980. Paternity exclusion in six captive groups of rhesus monkeys (*Macaca mulatta*). *Amer. J. Phys. Anthropol.*, 53: 243−249.

SOCHA, W. W., E. MERZ, & J. MOOR-JANKOWSKI, 1981. Blood groups of Barbary apes (*Macaca sylvanus*). *Folia Primatol.*, 36: 212−225.

———— & J. RUFFIÉ, 1983. *Blood Groups of Primates: Theory, Practice, Evolutionary Meaning.* Alan R. Liss, New York.

SOUTHWICK, C. H. & M. F. SIDDIQI, 1988. Partial recovery and a new population estimate of rhesus monkey population in India. *Amer. J. Primatol.*, 16: 187−197.

STRUHSAKER, T. T., 1976. Further decline in numbers of Amboseli vervet monkeys. *Biotropica*, 8: 211−214.

SWOFFORD, D. L. & R. B. SELANDER, 1989. *Biosys-1.* Natural History Survey, Illinois.

SYMINGTON, M. M., 1987. *Ecological and Social Correlates of Party Size in the Black Spider Monkey* (Ateles paniscus chamek). Princeton Univ. Press, Princeton.

TAUB, J. E., 1977. Geographic distribution and habitat diversity of the Barbary macaque *Macaca sylvanus* L. *Folia Primatol.*, 27: 108−133.

TURNER, T. R., C. S. MOTTAND, & J. E. MAIERS, 1984. *Genetic and morphological studies on two species of Kenyan monkeys*, Cercopithecus aethiops *and* Cercopithecus mitis: *Proceedings of International Primatological Society, Nairobi 1984, Nairobi.*

Authors' Names and Addresses: WOLFGANG SCHEFFRAHN, *Anthropologische Institut der Universitat Zurich, Switzerland*; NELLY MÉNARD, DOMINIQUE VALLET, *CNRS, UA 373, Station Biologique de Paimpont, Plelan-le-Grand, France*; BELKACEM GACI, *Djurdjura National Park, Tikjda-Bouira, Algeria.*