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Demography and ecology of Barbary macaques (*Macaca sylvanus*) in two different habitats

N. MÉNARD AND D. VALLET

Introduction

The distribution of Barbary macaques is limited to Morocco and Algeria and includes populations of various sizes more or less isolated from each other by fragmentation of suitable habitats (Taub, 1977; Fa *et al.*, 1984). The colonisation of different habitat types probably illustrates how very adaptable the species is. However, we can compare the degree of success of the Barbary macaques in their different habitats. At present, monkey density is the only factor available for estimating the state of most Barbary macaque populations. Density varies from 1 to 70 monkeys per km², the lowest values being for thermophilous scrub habitats and the highest values for cedar forests (Deag, 1974; Taub, 1977; Fa, 1984). Large variations in density are also observed between areas of the same habitat type, for example from 8 to 70 monkeys/km² for different populations living in cedar forest. In most cases, the ecological factors that determine these differences are poorly understood without a long-term study. Abundance of resources is generally recognised as one of the principal factors limiting monkey density (Iwamoto, 1978; Southwick, Siddiqi & Oppenheimer, 1983; Altmann, Hausfater & Altmann, 1985). Yet, the carrying capacity of an environment is, in general, difficult to estimate for omnivorous non-human primates. One must consider quantity, quality and availability of resources, and then evaluate their use by the animals over the whole annual cycle (Bourlière, 1979). This type of study is rare but studies have been done in tropical forest (Hladik, 1977; Oates, 1977; Waser, 1977; Gautier-Hion, Gautier & Quris, 1981), in savanna (Norton, Rhine & Wynn, 1987) and in temperate habitats (Ménard, 1985; Ménard & Vallet, 1986, 1988). It is widely supposed that the high eclecticism of the diet of the Barbary macaques is a strategy that allows them to exploit different habitats (Deag, 1974; Drucker, 1984; Fa, 1984).

As shown by Ménard, Vallet & Gautier-Hion (1985), demographic parameters differ according to the habitat colonised by the species. This chapter describes the ecology and demography of Barbary macaque groups living in two different forest habitats and tries to identify environmental factors which might explain the observed differences.

Methods

Two parks were studied: one at Tigounatine in the cedar-oak forest of the Djurdjura National Park (4° 8' E, 36° 27' N) and the other in the deciduous oak forest at Akfadou (4° 33' E, 36° 27' N). The study of demography and group dynamics was carried out between February 1983 and July 1990 in the course of observations organised so as to cover the birth season and part of the mating season. In each group, individuals were identified by coloured ear tags and/or morphological characteristics and their presence recorded during each day of observation. Group composition was established using age/sex classes previously defined on the basis of morphology and degree of sexual maturity (Ménard *et al.*, 1985, see also Tables 6.1 and 6.2). Group size and composition are given for July of each year (i.e. the end of the birth season) and for February 1983.

Dates of birth, sex and affiliations of infants were recorded; birth rate for 1982 was estimated from group composition as determined in February 1983. Data on birth rate and infant mortality rate were uncertain because it was not possible to confirm for 1982 and 1989 whether or not four females at Tigounatine and two at Akfadou had given birth then lost their infants prior to the start of observations. Unweaned infants and juveniles socially dependent on their mothers were presumed not to have survived if they had disappeared. Individuals who left the study groups were only considered to be 'emigrants' if subsequently relocated, otherwise they were recorded as disappearances.

The study of diet and available resources was carried out from February 1983 to July 1987 using methods detailed elsewhere (Ménard, 1985; Ménard & Vallet, 1986, 1988). However, the majority of data quantified was from 1983 and 1984; the collection of these data was structured to be representative of an annual cycle. Observations on animals were conducted six days per month on average. 'Scan samples' (Altmann, 1974) were recorded every 15 min on five animals, and the type of activity and the foods consumed noted.

Study areas were mapped using a grid system of 50 m or 100 m quadrats depending on visibility in the habitat. The study of available resources was

carried out each month. Acorn production was estimated along 10 transects with a total length of 500 m. Transects were also used to estimate shrub cover. For the herbaceous layer, vegetation sampling was carried out in 1 m quadrats placed at the intersections of a 200 m grid covering the group's home ranges. Plant species were recorded along with the degree of ground cover and the height of plants. Leaf volume was calculated for each herbaceous species and used to estimate the relative abundance of their available resources. The phenological state of all plants was also recorded.

Indices of specific diversity (D) of resources and of diet were calculated for each vegetation layer according to Simpson's formula (Levins, 1968): $D = (\sum P_i^2)^{-1}$, where P is the frequency of different species in each vegetation layer, or the frequency of different species eaten over the year. D can vary from 1 to N , where $D = 1$ when a single species is present in the vegetation layer or in the diet, and $D = N$ when N species are of equal importance.

The degree of selectivity exercised by the monkeys was estimated by dividing the rate of consumption for each species by its rate of relative abundance. The species are thus classified: (1) preferred, when their rate of consumption is more than 1.5 times the relative rate of abundance; (2) avoided, when the rate of consumption is less than 0.5 times the relative rate of abundance; (3) neutral, when the rate of consumption is more or less equal to the relative rate of abundance. Certain species that were rare both in the habitat and the diet were not classified.

The spatial use of the habitat was quantified from 1983 to 1990. In the course of observations, the centre of the group was positioned with reference to the grid system every 30 min, 6125 data points at Tigounatine and 4275 at Akfadou.

Results

Demography

Size and structure of groups

Tables 6.1 and 6.2 show size and structure of the groups studied from February 1983 to July 1990. Group size varied from 13 to 88 individuals. The initial Tigounatine group increased from 38 to 88 animals and then split into three new groups (SM, LØ and UL) of 50, 24 and 13 animals, respectively that had together reached a total of 106 individuals by 1990. At the same time, the Akfadou group increased from 33 to 53 animals. The mean annual growth rate of the groups from July 1983 to July 1990 was

18.6% at Tigounatine and 5.1% at Akfadou. In each case, more than 75% of this increase was accounted for by the natality/mortality balance, while the immigration/emigration balance had less effect (Ménard & Vallet, 1993a,b).

At both sites, groups had a multimale structure. The mean overall sex ratio (males:females) and the mean adult sex ratios were relatively balanced, varying from 1:0.7 to 1:1.2 (range 1:0.6 to 1:1.4) and from 1:0.9 to 1:1.2 (range 1:0.8 to 1:1.9), respectively. Group UL was an exception and temporarily had a single-male group structure with one adult male for five adult females in 1989 after the splitting of the initial Tigounatine group. The proportion of immatures did not differ between the groups, varying from 0.41 to 0.59 at Tigounatine and 0.42 to 0.58 at Akfadou according to the year.

Natality

Seasonality

Ménard & Vallet (1993b) have shown that almost all births occurred between 14 April and 8 July in Algeria, with a significant earlier median birth date at Akfadou than at Tigounatine (3 May and 19 May, respectively). At both sites, primiparous females and multiparous females without any previous infant (whether they did not give birth the year before or whether they had lost their previous infant) gave birth significantly earlier than multiparous females accompanied by their previous infant (Fig. 6.1) (ANOVA, $F = 4.07$; $p < 0.05$). This difference did not vary according to the year (ANOVA, $F = 2.00$; $p > 0.05$).

Birth rate and female fertility

The mean birth rate over nine years varied from 0.56–0.58 ($N = 97$ –101 infants) at Tigounatine to 0.63–0.65 ($N = 66$ –68 infants) at Akfadou with considerable inter-annual variations, ranging from 0.14 to 0.80 and from 0.33 to 1.00, respectively. There was no significant difference between the sites (for a more detailed analysis see Ménard & Vallet, 1993b).

Primiparous females averaged 5.5 years old at Tigounatine and 5.3 years old at Akfadou (ranging from 4 to 8 years). Females of 3 years of age never gave birth and 4 year olds only rarely (Table 6.3). Females showed their maximum reproductive rate between 8 and 15 years and, seemingly, declined thereafter.

The mean inter-birth interval was not significantly correlated with the

Table 6.1. Demographic parameters of the Tigounatine groups from February 1983 to July 1990

A. Initial group

Classes	Age (years)	Date (month-year)						
		02-83	07-83	07-84	07-85	07-86	07-87	07-88
Adults	>5	7	9	9	10	16	20	26
♂♂	>5	7	9	9	14	17	19	23
♀♀	4	2	1	5	4	3	4	0
Sub-adults	4	2	0	2	4	2	1	1
♂♂	3	0	2	3	2	3	1	5
♀♀	3	1	5	4	3	4	0	6
Juveniles	2	2	3	2	3	1	5	4
♂♂	1	3	2	3	1	5	4	2
♀♀	2	5	4	3	4	0	6	4
	1	4	3	5	0	7	5	5
Infants	0-1	2	3	1	6	5	3	5
♂♂	0-1	3	5	1	8	6	5	7
♀♀								
Group size		38	46	47	59	69	73	88
Overall sex ratio ♂:♀		1:1.4	1:1.4	1:1.4	1:1.3	1:1.2	1:1.1	1:1
Adult sex ratio ♂:♀		1:1.3	1:1.1	1:1.6	1:1.8	1:1.3	1:1.2	1:0.9
Proportion of immatures		0.58	0.59	0.51	0.53	0.48	0.41	0.44

B. New groups

Classes	Age (years)	SM		LO		UL	
		07-89	07-90	07-89	07-90	07-89	07-90
Adults	>5	14	15	7	9	1	6
♂♂	>5	12	14	7	7	3	5
♀♀	4	2	2	0	1	2	1
Sub-adults	4	3	2	2	2	0	0
♂♂	3	2	2	2	0	0	0
♀♀	3	2	1	1	0	1	3
Juveniles	2	2	0	0	2	0	0
♂♂	1	0	4	2	1	0	1
♀♀	2	1	2	0	0	3	0
	1	2	3	0	3	0	2
Infants	0-1	5	3	1	4	1	3
♂♂	0-1	5	7	3	1	2	0
♀♀							
Group size		50	55	24	30	13	21
Overall sex ratio ♂:♀		1:0.9	1:1.1	1:0.8	1:0.7	1:5.5	1:1.1
Adult sex ratio ♂:♀		1:1	1:1.1	1:1	1:0.9	1:5	1:1
Proportion of immatures		0.44	0.44	0.42	0.43	0.54	0.43

Table 6.2. Demographic parameters of the Akfadou group from February 1983 to July 1990

Classes	Age (years)	Date (month-year)												
		02-83	07-83	07-84	07-85	07-86	07-87	07-88	07-89	07-90				
Adults														
♂♂	>5	8	9	10	7	7	9	12	11	13				
♀♀	>5	6	6	8	11	11	12	9	11	15				
	4	0	2	2	2	2	0	4	4	0				
Sub-adults														
♂♂	>4	1	1	3	0	3	1	2	2	2				
♀♀	3	1	3	3	3	1	2	2	2	5				
	3	2	2	1	2	0	4	4	0	1				
Juveniles														
♂♂	2	3	3	3	1	2	2	2	5	3				
♀♀	1	3	1	2	2	4	4	0	3	4				
	2	2	1	0	4	4	1	1	1	2				
xx	1	1	0	4	4	1	1	1	2	0				
	1	1	1	1	1	1	1	1	1	1				
Infants														
♂♂	0-1	3	3	2	2	3	8	3	4	4				
♀♀	0-1	2	3	6	4	2	2	2	0	4				
Group size		33	39	41	36	41	47	46	45	53				
Overall sex ratio ♂:♀		1:0.6-1:0.7	1:0.7-1:0.8	1:0.9	1:1.4	1:1.3	1:1	1:0.8	1:0.7	1:0.7				
Adult sex ratio ♂:♀		1:0.8	1:0.9	1:1	1:1.6	1:1.9	1:1.3	1:1.1	1:1.4	1:1.2				
Proportion of immatures		0.58	0.56	0.51	0.50	0.51	0.55	0.46	0.42	0.47				

xx, represents sex unknown.

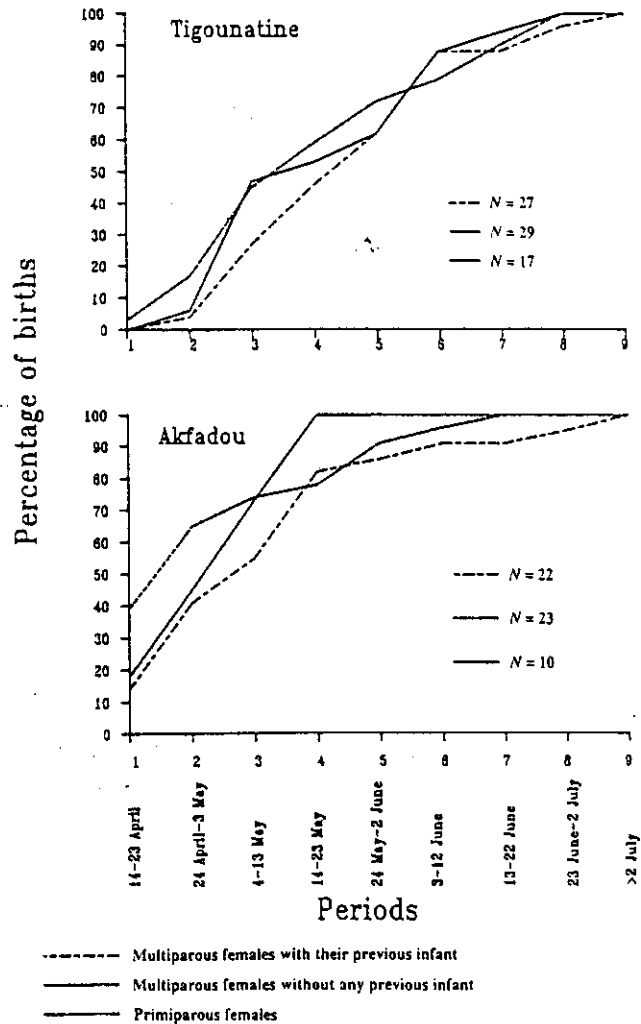


Fig. 6.1. Distribution of births over time depending on the reproductive status of the mothers. The birth season is divided into nine 10-day periods: Period 1: 14–23 April; period 2: 24 April–3 May; period 3: 4–13 May; period 4: 14–23 May; period 5: 24 May–2 June; period 6: 3–12 June; period 7: 13–22 June; period 8: 23 June–2 July; period 9: > 2 July.

sites (1.4 years, $N = 85$, at Tigounatine and 1.3 years, $N = 52$, at Akfadou), the reproductive status of the mother or the sex of the previous surviving infant (ANOVA, $p > 0.3$, NS). A one-year interval was found in the majority of cases (57% and 79%, respectively, at Tigounatine and at

Table 6.3. Age-specific birth rates of wild Barbary macaques in Algeria

Age (years)	Reproductive females × years	Birth rate
3	43	0.00
4	37	0.03
5	32	0.56
6	23	0.57
7	18	0.67
8	14	0.71
9	8	0.75
10-15	56	0.71
> 15	17	0.65

Reproductive females × years is the cumulative number of females observed over the years.

Akfadou) and females rarely failed to give birth for more than two years (Table 6.4).

At both sites, the interval between births was shorter after the death of an infant (1.2 years) than when the previous infant survived (1.5 and 1.4 years at Tigounatine and at Akfadou, respectively) but the difference was not significant (ANOVA, $F = 3.39$, $p = 0.06$).

Sex ratio at birth

Females tended to give birth to more infant females at Tigounatine than at Akfadou between 1982 and 1990 (55%, $N = 96$ and 46%, $N = 63$, respectively, Table 6.5), but the difference was not significant (Wilcoxon, $p > 0.2$). Higher inter-annual variations occurred at Akfadou (0-75%) than at Tigounatine (44-63%).

Mortality

Infant mortality rate was 0.23-0.27 ($N = 78-82$) at Tigounatine and 0.38-0.40 ($N = 58-60$) at Akfadou, with great inter-annual variations (0-0.67 and 0-0.83, respectively). The differences were not significant (for a more detailed analysis see Ménard & Vallet, 1993b).

Mortality rate was 0.26 for infant males and 0.24 for infant females at Tigounatine and 0.30 and 0.48, respectively, at Akfadou (Table 6.6), but did not differ significantly according to the sex of the infant (Wilcoxon, $p > 0.05$). Mortality of the infant females tended to be higher at Akfadou. Mortality did not differ significantly between infants of primiparous mothers and those of multiparous mothers at either site (Wilcoxon, $p > 0.05$).

At both sites, the majority of infant deaths occurred between June and

Table 6.4. Percentage of different lengths of inter-birth intervals and mean length of inter-birth interval (years)

	Tigounatine								Akfadou							
	Interval (years)				Mean	N	Interval (years)				Mean	N				
	1	2	3	4			1	2	3	4						
Overall intervals	57	42	1	0	1.4	85	79	17	0	4	1.3	52				
After first birth	38	62	0	0	1.6	21	78	22	0	0	1.2	9				
After subsequent births	63	35	2	0	1.4	64	79	16	0	5	1.3	43				
With previous infant surviving	47	52	1	0	1.5	64	71	26	0	3	1.4	34				
Male	31	65	4	0	1.7	26	62	33	0	5	1.4	21				
Female	58	42	0	0	1.4	38	85	15	0	0	1.2	13				
After infant loss	86	14	0	0	1.2	21	94	0	0	6	1.2	18				

Table 6.5. *Percentage of females at birth from 1982 to 1990. Four infants with unknown sex were excluded. Number of infants is given in parentheses*

Year	Tigounatine	Akfadou
1982	60 (5)	40 (5)
1983	63 (8)	50 (6)
1984	50 (2)	75 (8)
1985	57 (14)	67 (6)
1986	55 (11)	63 (8)
1987	56 (9)	25 (12)
1988	58 (12)	33 (6)
1989	59 (17)	0 (4)
1990	44 (18)	50 (8)
Overall	55 (96)	46 (63)

Table 6.6. *Infant mortality rate. Number of infants is given in parenthesis*

	Tigounatine	Akfadou
All infants	0.23-0.27 (78-82)	0.38-0.40 (58-60)
Males	0.26 (31)	0.30 (27)
Females	0.24 (42)	0.48 (23)
Born from primiparous	0.24 (17)	0.50 (10)
Born from multiparous	0.25 (56)	0.40 (43)

November (78% at Tigounatine and 77% at Akfadou), whereas infant mortality was relatively low during the winter months. Springtime mortality was higher at Akfadou than at Tigounatine (39% vs 6%) with the greatest disparity in June, when 24% vs 0% of annual deaths occurred (Ménard & Vallet, 1993b).

Transfers and disappearances

Migration rates

At Tigounatine 55 transfers or disappearances were noted, including 29 immigrants, 14 emigrants, 3 transfers between the new groups SM, LO and UL, and 9 disappearances. At Akfadou, 20 transfers or disappearances were noted, including 7 immigrants, 3 emigrants and 10 disappearances (Fig. 6.2).

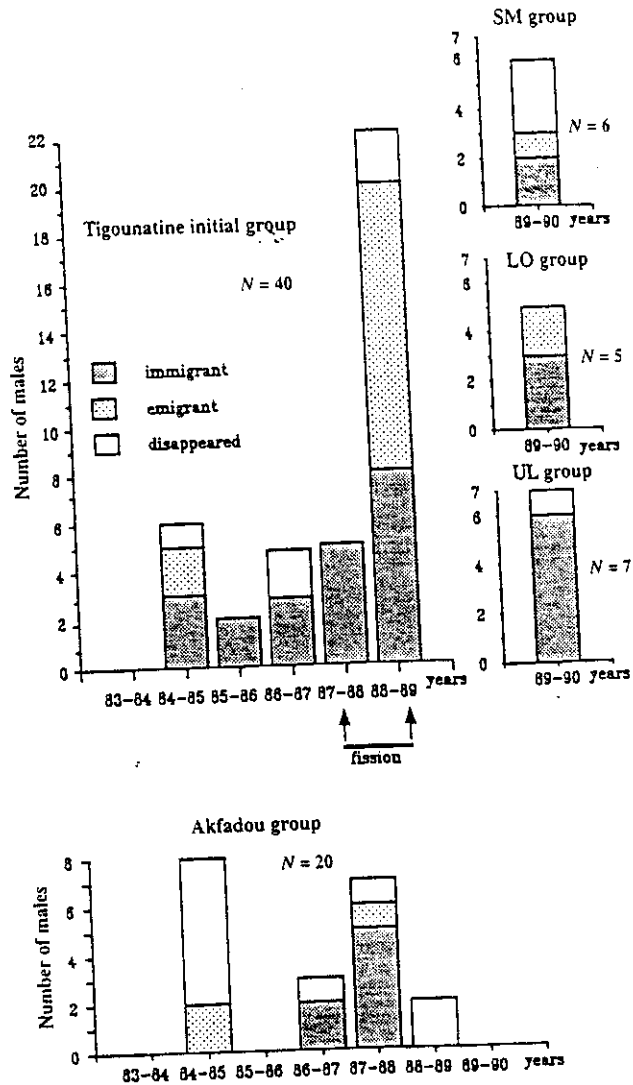


Fig. 6.2. Distribution of transfers of adult and sub-adult males in the two habitats.

Ménard & Vallet (1993b) found that the rate of emigration for males over 3 years old neither differed between groups nor showed a relationship with the increase in group size. Nevertheless, the overall proportion of immigrants was significantly higher in the Tigounatine group than in the Akfadou group. The proportion of immigrants to the Akfadou group did not vary according to group size, whereas the Tigounatine group received the greatest proportion of immigrants as it grew in size in the period leading up

to fission. Indeed, 45% ($N = 29$) of all immigration occurred during the fission process, between 1987 and 1989. As a result of transfers, only three of the nine resident adult males observed in 1983 at Tigounatine still belonged to one or other of the three new groups in 1990, while at Akfadou two of the nine resident males still belonged to the group in 1990.

Age of migrants

At Tigounatine 78% ($N = 46$; excluding animals which had disappeared) of migrants were adult males (> 5 years old), 54% being more than 8 years old, whereas 22% were sub-adult males (3–5 years old) (Table 6.7). Nevertheless, the rate of immigration did not differ significantly with the age of animals (Kolmogorov–Smirnov $D_{\max} = 0.20$, $N = 17$, $p > 0.05$). At Akfadou all migrants ($N = 10$) were adult males, most of them over 8 years old. Even if ten other animals that had disappeared were considered as emigrants, 75% of the migrants were adult males. Given uncertainties regarding the status of animals that had disappeared, the relationship between age and the rate of emigration could not be tested.

At Tigounatine five of the 16 males born between 1980 and 1985 emigrated before adulthood, three disappeared, while eight others (5–9 years old) still belonged to one or other of the three groups in July 1990. At Akfadou seven out of the 14 males born between 1980 and 1985 disappeared before adulthood, whereas seven others (from 5–10 years old) belonged to the group in 1990. Therefore, at both sites, 50% of males reached adulthood in their natal group and some were still in the same group when 9 years old.

Pattern of transfers

At Tigounatine, at least 11 of the 23 males that left the group joined neighbouring groups, one in one group and ten in a second group; three others were only temporary emigrants. At Akfadou, only two out of 13 males that disappeared could be located, each in a different neighbouring group; one was a temporary emigrant.

At both sites, immigrants stayed in the studied groups for periods ranging from less than one month to more than five years; twenty-six (72%) stayed at least a year. Out of a total of 40 observed migrants of different identity, five were seen to transfer twice and all of the emigrants that left their original group for more than a month (17) were never again seen with that group. Therefore, males that transfer several times during their life probably visit several different groups.

Table 6.7. Age-specific male migrations. Rate of emigration: number of emigrants/group's number of males \times years

Age of migrants (years)	No. of migrants	No. of immigrants	No. of emigrants	No. of males \times years	Emigration rate
Tigounatine					
3-4	2	1	1	20	0.05
4-5	8	6	2	14	0.14
5-8	11	8	3	46	0.07
>8	25	14	11	66	0.17
Total	46	29	17	146	0.12
Akfadou					
3-4	0	0	0	16	0.0
4-5	0	0	0	12	0.0
5-8	3	3	0	24	0.0
>8	7	4	3	41	0.07
Total	10	7	3	93	0.03

No. of males \times years is the cumulative number of males observed over the years.

Periods of transfers

Almost all transfers occurred outside the birth season, except in the cases of two migrants that temporarily visited the studied groups during June in Akfadou. At least 40% and 62.5% of transfers (at Tigounatine and at Akfadou, respectively) took place between October and February, during the mating season.

Habitat characteristics and use by monkeys

Availability of resources

Ménard & Vallet (1988) have described several differences between the two habitats studied (see also Table 6.8).

1. The Akfadou forest, at a lower altitude than that at Tigounatine, has a lower rainfall, a drier summer and less winter snow.
2. The ranges of the two groups are both forested but the forest of Tigounatine has 74% tree cover dominated by two evergreen species (*Cedrus atlantica* and *Quercus ilex*), while Akfadou has 93% tree cover composed mostly of two deciduous species (*Quercus faginea* and *Quercus afares*).

Table 6.8. Ecological characteristics of the two sites

Habitat type	Tigounatine-Djurdjura (cedar-oak forest)	Akfadou (deciduous oak forest)
Altitude (m)	1200-1900	800-1300
Annual temperatures, 1914-38		
Mean minima (°C)	+4.5	+9.0
Mean maxima (°C)	+16.3	+21.1
Mean annual precipitations (mm)		
1914-38	1410	1010
1968-76	1000	600
Snowy period	December-March	January-February
Composition of the habitat		
Forest	74%: <i>Cedrus atlantica</i> , 50% <i>Quercus ilex</i> , 24%	93%: <i>Quercus afares</i> , 54% <i>Quercus faginea</i> , 36%
Scrub areas	2%	5%
Grassland areas	24%	2%
Specific diversity		
Trees	1.80 ($D = 0-5$)	1.08 ($D = 0-4$)
Shrubs	3.10 ($D = 0-26$)	1.61 ($D = 0-8$)
Ground vegetation	9.68 ($D = 0-240$)	9.26 ($D = 0-152$)
Monthly percentage herb cover <20%	0-49 August-October February-March	0-33 April-March

Data on temperatures and precipitations are provided by Seltzer (1946) and the Division d'études de recherche hydraulique of Algeria.

- Lists of 271 and 164 plant species have been recorded for Tigounatine and Akfadou, respectively. There were 65 species of herbaceous plants common to the two habitats, representing 27% ($N = 240$) of species at Tigounatine and 43% ($N = 152$) at Akfadou. Moreover, species diversity is greater at Tigounatine than at Akfadou for all vegetation types. Consequently, the Tigounatine forest represents a habitat buffered against a drastic fall in the production of any single food species, a wider choice of other species being available to make up the temporary deficit.
- Marked seasonal variations are found in both habitats, but the production of plant resources is more evenly spread over the course of the year at Tigounatine due to phenological asynchrony among the various species (particularly shrubs).

Spring re-growth at Akfadou begins about three weeks earlier than at Tigounatine. Spring production is abundant but concentrated in two months (April–May) when oak and *Cytisus triflorus* flower and proliferation of caterpillars takes place. At Tigounatine, production extends until July owing to new leaf growth and flowering of shrubs (April–June), oak flowering and the proliferation of caterpillars (June). Herbaceous plant cover is greatest in May in both habitats but is higher at Tigounatine than at Akfadou (49% vs 33%). It is greatly reduced (<20%), or negligible by the end of spring, but the dry summer begins earlier and lasts longer at Akfadou as the autumn rains are much less than at Tigounatine. Moreover, when the lower strata of vegetation (herbaceous cover and shrubs) are covered with snow the two evergreen tree species at Tigounatine provide an important food source absent from the deciduous oak forest of Akfadou.

For both habitats, most inter-annual variation in resources was related to the occasional springtime proliferation of caterpillars that feed on oak leaves, resulting in little or no acorn production in the autumn of the same year, when generally less than 32% of oaks fruit and then yield only 3–4 acorns per tree. Invasions of caterpillars occurred in 1983, 1986 and 1987 in Tigounatine, and in 1983, 1984 and 1985 in Akfadou.

At first sight, the Akfadou oak forest with its denser structure looks as if it could provide more food for a population of monkeys than the more open cedar–oak forest of Tigounatine. Yet, the results show that, overall, the deciduous oak forest is a habitat with poorer and less reliable nutritional resources than the mixed cedar–oak forest, and where the dry summer, particularly the month of June, is always a critical period even in years of good acorn production.

Diet

The Barbary macaques that we studied modified their diet to suit different habitats (Ménard, 1985; Ménard & Vallet, 1986). At Akfadou 63% of food taken came from trees and shrubs, compared with 41% at Tigounatine (Ménard & Vallet, 1988). This probably reflected the difference in extent of tree and shrub cover between the two habitats. Similarly, the proportion of herbaceous plants in their diet was higher at Tigounatine, where there was more herbaceous cover, than at Akfadou (59% vs 37%). The macaques of both study groups were essentially seed and leaf eaters (see Table 6.9); seeds and leaves together represented an annual average of 75% and 59% of time spent feeding at Tigounatine and Akfadou, respectively. At both sites, acorns and leaves of herbaceous plants made up the largest part of seed and leaf consumption. However, at Tigounatine the proportion of tree leaves

Table 6.9. Diet and food selectivity

Habitat type	Tigounatine-Djurdjura (cedar-oak forest)	Akladou (deciduous oak forest)
Dietary composition (%)		
Seeds	26.7	32.1
Acorns	14.2	26.2
Herbs	11.3	5.9
Leaves	48.1	27.3
Trees	12.1	0.1
Shrubs	0.9	8.7
Herbs	35.1	18.5
Animal prey	5.6	10.5
Caterpillars	5.5	9.5
Lichens	1.9	14.2
Roots	7.7	6.9
Others	5.9	10
Specific diversity (<i>D</i>)		
Trees	2.06 (<i>D</i> = 0-4)	2.02 (<i>D</i> = 0-3)
Shrubs	3.40 (<i>D</i> = 0-19)	2.12 (<i>D</i> = 0-6)
Ground vegetation	7.78 (<i>D</i> = 0-101)	2.33 (<i>D</i> = 0-63)
Selectivity (%)		
Preferred species		
Proportion (<i>N</i>) ^a	9 (24)	6 (10)
Abundance on home range	20.3	3.1
Avoided species		
Proportion (<i>N</i>)	8 (21)	11 (17)
Abundance on home range	46.6	33.0
Neutral species		
Proportion (<i>N</i>)	2 (5)	1 (2)
Abundance on home range	25.8	59.8
Non-classified		
Proportion (<i>N</i>)	82 (221)	82 (132)
Abundance on home range	7.3	4.1

D. is diversity of species according to Simpson's formula (Levins, 1968).

^aNumber of species in parentheses.

was more important because of the winter consumption of cedar leaves, with lichens being the comparable winter food at Akfadou. Animal prey consisted mainly of caterpillars. In parallel with annual variations of available foods, the amount of caterpillars eaten by the macaques varied according to the year and when the former were absent the monkeys supplemented their diet with flowers of oak and *Cytisus triflorus* at Akfadou and herbaceous leaves at Tigounatine.

Seasonal variations in diet are marked in both habitats with two folivorous phases, one in spring and one in winter, and one granivorous phase in summer and autumn. According to the month, the monkeys use 8 to 27 plant species of which only 2 to 3 were important staples that made up 51–93% of the diet at Akfadou and 43–85% of the diet at Tigounatine.

In connection with the higher species diversity of food resources at Tigounatine than at Akfadou we noted that species diversity in all three categories of food plants at Tigounatine was higher than at Akfadou (Table 6.9).

Selectivity

Ménard & Vallet (1988) have shown that out of 271 species of plants listed at Tigounatine and 161 at Akfadou 47% of the former and 48% of the latter are found in the monkeys' diet over the course of a year. Overall the Tigounatine monkeys avoided a smaller proportion of available species than those at Akfadou (8% vs 11%) whereas a larger proportion of species were selected (9% vs 6%). Species avoided at Tigounatine represent a larger proportion of resources than do those avoided at Akfadou (47% vs 33%), whereas the species selected at Tigounatine represent a resource seven times as abundant as those selected at Akfadou (20% vs 3%). It, therefore, appears that the degree of selectivity exercised on plant foods by the macaques is much greater at Tigounatine.

Home range use

As Fig. 6.3 indicates, the curve representing the area of home range flattens out at the end of 1984 for both sites after 1600 and 1800 observations, evenly distributed over a year, at Tigounatine and Akfadou, respectively. In 1984, 74.2% (2.79 km²) and 77.1% (3.27 km²) of the 1990 home range size was then known at Tigounatine and Akfadou, respectively.

The initial Tigounatine group, which had varied from 46 to 73 individuals between 1983 and 1988 used an area of 3.76 km² (Fig. 6.3). The three groups that emerged from the fission of the initial group, a total of 106 animals, continued to use the same area but as three overlapping home

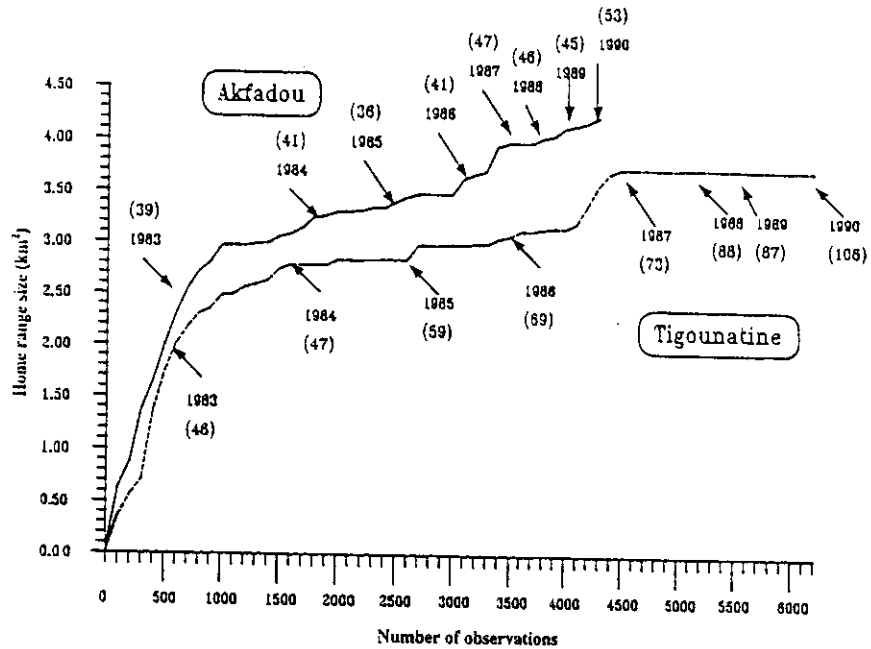


Fig. 6.3. Cumulative curves of the home range size over the years for the groups studied at Tigounatine and at Akfadou. Corresponding number of troop members is indicated in parentheses. For 1989 and 1990, home range corresponds to the total area used by the three new groups at Tigounatine.

ranges. The degree of overlap of the three ranges was still large in 1989–90 with between 48% and 80% of any range being shared. However, the three home ranges still lay within the limits of the home range of the initial group.

The Akfadou group, with 39 to 45 animals between 1983 and 1990, used an area of 4.24 km² as their home range. This range expanded progressively as they explored new areas.

Even though the total number of animals for the Tigounatine groups had more than doubled between July 1984 and July 1990, the area taken up by their home ranges had expanded relatively little (46%). An abrupt expansion was noted in 1987 when the acorn production was negligible and the monkeys moved into new areas of grassland to look for food. At Akfadou, however, the home range expanded by 40% between July 1984 and July 1990, even though the size of the group stayed relatively stable. Thus, the density of monkeys at Tigounatine was twice as high as that at Akfadou (28.2 individuals/km² vs 12.5 individuals/km²). At both sites this is probably an underestimate because of the degree of overlap with

neighbouring groups, but as this differs little between the two sites the comparison is still valid.

Discussion

Resource availability and macaque use

The two groups of Barbary macaques studied live in habitats with totally different ecological characteristics; there are large seasonal variations in food availability, linked with the temperate climate, as well as large inter-annual variations. In response to habitat type, the Barbary macaque adjusts its diet according to the nutritional resources available.

In the cedar-oak forest of Tigounatine, there is less tree cover and there are more extensive areas of open grassland than in the deciduous oak forest of Akfadou. However, Tigounatine shows a higher number and diversity of plant species than Akfadou. At the same time, the Barbary macaques at Tigounatine have a higher diet diversity and eat more leaves and seeds of herbaceous plants and fewer acorns than those living in the oak forest. In both habitats, monkeys are able to shift from one month to the next between a carnivorous diet based on caterpillars, to a folivorous diet composed of herbaceous leaves, or to a granivorous diet based on acorns. Moreover, there are almost no caterpillars in the diet in some years, and the contribution of acorns can be spread over 4-10 months depending on their production.

Although the Barbary macaque is considered to be an eclectic feeder, the animals are selective in the two habitats studied, as only 48% (Tigounatine) and 47% (Akkfadou) of available plant species are actually included in the diet. The degree of food selectivity by the animals, higher overall at Tigounatine than at Akfadou, seems to be a response to the conditions of a less limiting habitat. Moreover, the resources preferred by the monkeys at Tigounatine are three times more abundant in their home range than at Akfadou. In addition to these differences in overall food availability, resource availability is more evenly distributed throughout the year at Tigounatine than at Akfadou, owing mainly to the shorter and less intense summer at the former site.

Demography

In the two habitats studied, the groups showed the multimale-multifemale structure typical of the species, with a relatively balanced sex ratio, the

exception being the temporary formation of a one-male group. The proportion of immature animals, which varies from 0.41 to 0.54 according to the group and the year, is comparable to that found by Mehiman (1989) in Morocco (0.47).

Inter-habitat variation of seasonal resource distribution affects the birth season (which is earlier by about 15 days at Akfadou than at Tigounatine) and the critical period for infant survival. The latter, which is during the dry season at both sites, when more than 77% of infant deaths occurred, is a month shorter at Tigounatine than at Akfadou. In addition, infant mortality is particularly high in June at Akfadou, the beginning of the dry season when resources are severely reduced. However, infant mortality is low during the winter.

The demographic parameters are subject to large inter-annual variation and inter-group differences were not statistically significant. Nevertheless, the proportion of females at birth tended to be higher and infant mortality lower (especially for females) at Tigounatine than at Akfadou (18.6% vs 5.1%) and is essentially the result of differences in the natality:mortality ratio. The high rate of increase of the Tigounatine group is similar to that of provisioned macaque groups (13 to 21%, Koford, 1965; Drickamer, 1974; Sugiyama & Ohsawa, 1982; Malik, Seth & Southwick, 1984; Paul & Kuester, 1988), whereas at Akfadou it is comparable with that of wild macaque groups (0–4.9%, Dittus, 1977; Teas *et al.*, 1981; Sugiyama & Ohsawa, 1982; Southwick & Siddiqi, 1988). This last point, as well as the aforementioned ecological differences, suggest that the cedar-oak forest is a more favourable habitat for the development of monkey groups than the oak forest of Akfadou. The fact that the Tigounatine group uses a smaller home range, and has a population density more than double (28 vs 13 individuals/km²) that at Akfadou, supports this hypothesis. Moreover, the carrying capacity of the habitat does not seem to have been reached at Tigounatine, since the number of monkeys continues to increase without a noticeable change in the size of the area used.

Nevertheless, it is difficult to show that the ecological factors particular to each habitat are responsible for the observed demographic differences because of the large inter-annual variations in resource availability. As highlighted by Dittus (1977) and Altmann, Hausfater & Altmann (1988), infant mortality is the parameter most sensitive to environmental change. Ménard & Vallet (1993b) have indicated that in both these habitats, mortality was positively correlated with the frequency of caterpillar plagues and subsequent reduction of the acorn crop. The conclusion that can be drawn from this is that the more frequent the caterpillar invasions of a

habitat, the worse the habitat becomes for the Barbary macaque population. These results illustrate the importance of long-term studies, especially in the case of species inhabiting temperate habitats with strong seasonality and strong inter-annual variations in resource production.

The comparison of demographic parameters between wild and captive groups clearly shows the effect of food availability on female fertility (age of first breeding, birth rate, inter-birth interval) and on infant mortality. The birth rate is lower for the studied groups (0.56–0.65) than for captive groups (0.75; Paul & Kuester, 1988) and is also lower whatever the age of the females; age at first breeding is later (5.2 and 5.3 years, this study, vs 4.5–4.9 in captivity; Fa, 1984; Paul & Kuester, 1988). The fertility pattern as a function of age differs little between the wild (this study) and captivity (Paul & Kuester, 1988), showing highest fertility between 8 and 15 years. However, the decline in fertility appears less obvious in the studied groups than in captive groups, probably because of lower female life expectancy in the wild.

The most frequent inter-birth interval in the study groups is one year (57% and 79% of cases at Tigounatine and Akfadou, respectively). Intervals of two years are, however, more frequent than in captivity (17–42%, this study, vs 12%, Burton & Sawchuk, 1982; Paul & Thommen, 1984). As Paul & Thommen (1984) observed, the reproductive status of the mother or the sex of the infant did not appear to affect the interval between births. Nevertheless, the loss of an infant tended to reduce the ensuing interval. As Altmann, Altmann & Hausfater (1978) emphasised, the effect of such an occurrence should be less marked in a seasonally breeding species, whereas the interval is cut shorter in the case of a species that breeds nearly all year round, such as *Papio cynocephalus* (Altmann *et al.*, 1977). However, the loss of an infant has the effect of bringing forward the time of birth within the season, as was noted by Paul & Thommen (1984).

Dispersal

The different rates of increase of the two groups are expressed in different patterns of dispersion. The large increase of the Tigounatine group led to its division into three new groups. This division facilitates the introduction of males from outside the old group and explains the higher immigration rate at Tigounatine than at Akfadou. Contrary to the suggestion made by Paul & Kuester (1988), rate of emigration is not influenced by group size.

In both study groups, the male Barbary macaques do not migrate before they are 3.5 years old and, unlike other macaque species, they migrate late.

Fifty per cent reach sexual maturity in their natal group and some are still breeding there at the age of 9; most of the observed migrants are over 5 years old. However, the emigration rate does not vary significantly according to age. In the study groups, the migration rate of sub-adult males (0.05 at age 3–4 years) is lower than in captivity (0.136; Paul & Kuester, 1988), whereas the migration rate of adults over 8 is higher (0.17, this study, vs <0.07; Paul & Kuester, 1988). Contrary to the hypothesis of Paul & Kuester (1985, 1988) according to which 'if Barbary macaques avoid mating with close relatives, migration rate in the wild should be higher than in Salem [captive colony]', the average annual migration rate observed (0.12–0.16, Ménard & Vallet, 1993b) differs little from that of captive groups (0.07). In fact, as Melnick & Kidd (1983) suggested, because of a longer inter-birth interval and a shorter female life expectancy in the wild, the length of lineages is relatively shorter and the number larger for captive groups of comparable size. Therefore, group composition, more than group size, has a determining role to play in the male migration rate, insofar as this avoids matings with close kin. Nearly all migrations took place during the mating season and males joined neighbouring groups, as has already been observed in other species (Pusey & Packer, 1987).

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