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Comparative Density, Demography, and Ranging Behavior of Barbary Macaques (*Macaca sylvanus*) in Marginal and Prime Conifer Habitats

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A semiisolated study population of 162 Barbary macaques (six groups) inhabiting the Ghomaran fir forests of the Moroccan Rif mountains has a density of 6.73 individuals/km². The adult sex ratio is 0.725, and immatures comprise 46.9% of the population. Births are seasonal, occurring from April to June, and the adult female birth rate is 0.58 per annum. Mortality appears relatively low in all age classes until old age. Group size ranges from 12 to 59 individuals, with a median value of 24. Home-range sizes vary between 3 and 9 km², with a mean of 7.2 km². Home-range overlap is approximately 80%. On the basis of macaque density, conifer density, and herding competition from domestic animals, the Ghomaran environment can be considered "marginal" compared to the Moyen Atlas. Despite the marginal habitat of the Ghomaran population, it is surprisingly similar in demographic characteristics to a Barbary macaque population in the Moyen Atlas. Two characteristics of the population dynamics in the Ghomara differentiate it from the former. (1) The mean home range is five times larger in the Ghomara, roughly inversely proportional to the sixfold decrease in macaque density, confirming Caldecott's (1986) principle that, in macaque species, range size adjustments are a primary proximate response to poor-quality habitat. (2) Smaller groups in the marginal habitat of the Ghomara appear to have better rates of growth than small groups in prime habitat. This may result from an overall decreased home-range defensibility in marginal habitat (larger home ranges), resulting in an ecological and demographic

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release of small groups from the levels of intergroup competition they would normally experience in prime habitat.

KEY WORDS: Barbary macaque; demography; population ecology; population density; ranging behavior.

INTRODUCTION

Many interpopulational studies of cercopithecine species indicate that regional differences in habitat quality are positively correlated with regional population densities (Gartlan and Brain, 1968; Yoshiba, 1968; Altmann and Altmann, 1970; Clutton-Brock, 1972; Struhsaker, 1975; Taub, 1977; Iwamoto, 1978; Freeland, 1979; Ménard *et al.*, 1985; Caldecott, 1986) and negatively correlated with regional differences in mean home-range size (Hall, 1963; Altmann and Altmann, 1970; Neville, 1968; Caldecott, 1986; Yoshiba, 1968; Gartlan and Brain, 1968; Cords, 1987; Clutton-Brock, 1972). In a review of several species of macaques, Caldecott (1986) proposed a general principle that relates habitat quality to group size, group composition, and home-range size. He suggests that "both within and between species, alteration of ranging behavior rather than group size or composition appears to be by far the most important proximate response for the macaque group to changes in its resource base" (1986, p. 208).

The present study presents populational and ecological data collected on a wild Barbary macaque (*Macaca sylvanus*) population in the Ghomaran region of the Moroccan Rif mountains (Mehlman, 1984, 1986a; Taub 1977; Fa *et al.*, 1984) and compares them with data collected on Barbary macaque populations from the Moyen Atlas mountains of Morocco (Deag, 1974; Taub, 1978; Drucker, 1984; Fa *et al.*, 1984). Interpopulational differences in habitat quality, mean group size, mean home-range size, population density, and demographic parameters are analyzed in order (i) to identify the ecological and populational factors that operate to bring about density reductions in regional populations of Barbary macaques; (ii) to derive a simple equation that quantitatively relates differences in regional macaque densities to shifts in mean group size, home-range size, and home-range overlap; and (iii) to determine whether Barbary macaque populations confirm or deny Caldecott's (1986) suggested principle and whether their population dynamics resemble those of other cercopithecines.

METHODS

Results for the Ghomaran population are derived from a 2-year study (August 1981 to August 1983) conducted by the author in the Moroccan Rif

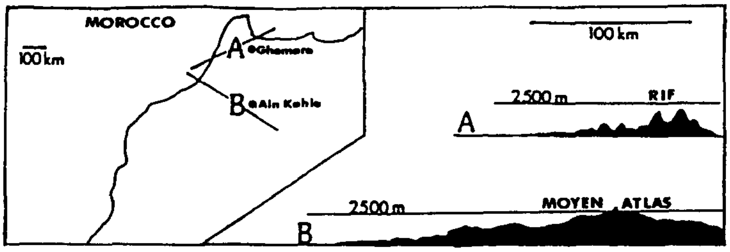


Fig. 1. Comparative topographic transects of the Rif and Moyen Atlas mountains (adapted from Metro, 1958).

mountains (Fig. 1). Further methodological details are given by Mehlman (1986a, b, 1988) and Mehlman and Parkhill (1988). The data from Moyen Atlas populations, used for comparison in the present study, derive from long-term studies at Ain Kahla (Deag, 1974; Taub, 1974) and at Bou Jirrir (Drucker, 1984), about 40 km northeast of Ain Kahla (Fig. 1). Qualitative ecological observations were also made at the Ain Kahla site during a 2-week survey of the Moyen Atlas in July 1982, made in conjunction with Dr. David Taub.

In the Ghomara, a focal group was observed for 746 hr, and another 187 observation hr was divided nearly equally among five nonfocal groups. Locating nonfocal groups for census-taking required many days of searching. When they were located, complete censuses took between 3 hr and a full day, since groups had to be followed in difficult terrain until they passed through open areas. Censusing was also made difficult by topographical complexity, high intragroup dispersion, and general difficulties in habituating all groups. Accurate censuses of all nonfocal groups were made only for the period of September to December 1982, and since it is only during this time frame that all group compositions were simultaneously known, the present study considers the cross-sectional composition of the entire Ghomaran population as it is displayed in Table I.

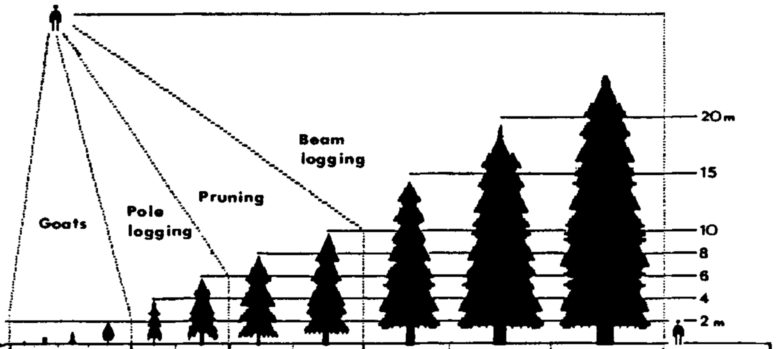
Birth rates were estimated from ratios of newborn infants (pooled for males and females) observed during two birth seasons. All age-sex classes are estimates based on descriptions given by Fa (1984b, Appendix 1), with the exception of male adulthood, which, for the present study, was defined as beginning at 6 years of age (Mehlman, 1986a, b; Taub, 1978).

The focal group's ranging behavior was determined by plotting all movements and sightings, relative to key topographic features spaced at irregular intervals of less than 200 m, onto a topographic map (1:10,000) of the area. Similar methods were used to determine the home ranges for the five nonfocal groups, with additional evidence from habitat use (characteristic digging, spoor, snow tracks), and local vegetational zones known to delimit the ranging behavior of the macaques (Mehlman, 1986b). All surface area calculations

Table I. Group Compositions of the Ghomaran Study Population Between September and December 1982[a]

Group	C/S	AF	(%)	sF	(%)	AM	(%)	sM	(%)	juv	(%)	i2	(%)	% Immatures	Total size
g1	4/5	3	(25.0)	1	(8.3)	2	(16.7)	1	(8.3)	3	(25.0)	2	(16.7)	(50.0)	12
g2	2/3	3	(25.0)	0	(0.0)	1	(8.3)	1	(8.3)	5	(41.7)	2	(16.7)	(58.3)	12
g3	1/4	4	(22.2)	1	(5.5)	3	(16.7)	1	(5.5)	6	(33.3)	3	(16.7)	(50.0)	18
g4	1/3	8	(26.7)	2	(6.7)	6	(20.0)	2	(6.7)	7	(23.3)	5	(16.7)	(43.3)	30
g5	2/4	7	(22.5)	2	(6.5)	6	(19.4)	3	(9.7)	8	(25.8)	5	(16.1)	(41.9)	31
Focal		15	(25.4)	5	(8.5)	12	(18.6)	4	(6.8)	18	(30.5)	6	(10.2)	(47.5)	59
Total		40	(24.7)	11	(6.8)	29	(17.9)	12	(7.4)	47	(29.0)	23	(14.2)	(46.9)	162

[a] C = censuses; S = sightings (counts of most adults and identification of key individuals). AF = adult females (5+ years); sF = subadult females (3–4 years); AM = adult males (6+ years); sM = subadult males (4–5 years); juv = juveniles (males, 1–3 years; females, 1–2 years); i2 = infant twos (0.3–1.0 years); immatures = all individuals ≤3 years.



	A B C D	E	F	G	H	I	J	K	transects
OPEN	258	36	24	29	8	11	10	22	740 × 5m
	175	9	0	2	3	2	1	0	500 × 5m
DENSE	12	4	0	3	2	4	10	14	300 × 5m
				cone production (maturity)					

Fig. 2. *Abies pinsapo* age classes and transect data. The number of firs in age classes A–K (visual estimations of height) in three transects are displayed below. The 740-m transect was made across slope; the 500-m transect was made with the slope (see text). Primary human disturbances to the fir forest are displayed above the figure (also see Mehlman, 1984, 1986b). Goat cropping affects the youngest age classes, pole logging and pruning for fodder occur in tandem with goat herding, and some illegal beam logging occurs on mature firs. Age class A = seedlings; B = <0.5 m; C = 0.5–1 m; D = 1–2 m.

were made with the above map and a Bruning Areagraph Set (4850 No. 1) and were not corrected for slope. Groups were identified by their relative size and the recognition of several adult females and males.

Vegetation cover in the study area was classified into three main habitat types by updating a recent vegetation map of the area (Gerardin and Lecompte, 1975): (i) conifer forest, (ii) Meditteranean oak maquis (oak forests to scrub vegetation), and (iii) meadows (Table III). Conifer forest was further divided into closed canopy stands (75% horizontal canopy cover) and "open" stands (50–75% horizontal canopy cover).

Ghomaran conifer forest is dominated by the Moroccan fir (*Abies pinsapo*). Although cedar (*Cedrus atlantica*), the dominant conifer at Ain Kahla and Bou Jirrir, is present in the Ghomara, it accounts for only 12% of the coniferous biomass (SCET-International, 1973). To determine conifer density, two linear transects (5-m swaths) were made through open canopy forest (one with and one against the slope), and a third transect was made through closed canopy forest (Fig. 2); firs and cedars were placed into one of 11 age categories by a visual estimation of height and were included in a transect if one-half of their diameter rested within the swath. The ratio of closed to open transect lengths (Fig. 2) approximate the ratio of closed

Table II. Proportion of Habitat Types in Home Range of Focal Group[a]

	km²	% of home range
Conifer forest		
Fir forest (closed canopy)	1.05	11.6
Fir forest (open canopy)	4.06	45.1
Pine forest (open canopy)	0.42	4.7
Cedar forest (open canopy)	0.36	4.0
Total conifer forest	5.89	65.4
Oak maquis (low and high maquis)	1.49	16.5
Open meadows	1.23	13.6
Total range of focal group	9.01	

[a] Conifer forest—major tree species; *Abies pinsapo, Quercus ilex, Cedrus atlantica, Ilex aquifolium, Pinus pinaster, Acer opalus, Pinus nigra, Viburnum tinus, Taxus bacatta, Crataegus laciniata,* and *Juniperus oxycedrus.* Oak maquis—major tree and shrub species: *Quercus ilex, Quercus faginea, Astragalus armatus, Ulex africanus, Cistus* spp., and *Bupleurum spinosum.* Open meadows dominated by the following families: Gramineae, Labiatae, Iridaceae, Cruciferae, Compositae, and Umbelliferae (Mehlman, 1988).

to open stand surface areas in the study area (Table II.). In comparing differential conifer density between the Ghomaran and Moyen Atlas forests, it is assumed that density estimates of both fir and cedar approximate their respective biomasses, since another fir (*Abies cilicica*), similar in structure and growth characteristics to *A. pinsapo* (Mitchell, 1972), has a biomass production nearly equivalent to that of *Cedrus atlantica* at 20 years of age (Khalil and Robertson, 1984). No data on biomass production are presently available for *A. pinsapo.*

All statistical tests are two-tailed and use an alpha level of 0.05; methods follow those described by Sokal and Rohlf (1981) and Siegel (1956). Some

Table III. Relative Conifer Density Between Ghomaran Fir Forests and Moyen Atlas Cedar Forests[a]

	Ratio dense:open canopy stands	Trees/ha		
		Closed stands	Open stands	All stands
Ghomara	1:2.10	277	283	280
Bou Jirrir	1:0.36	1300	600	1116
Ain Khala	1:1.00	?		750

[a] Bou Jirrir estimates (quantitative) from Drucker (1984); Ain Kahla estimates (qualitative) by author. At Bou Jirrir, Drucker's data do not appear to include seedlings or the youngest age classes (1984, p. 141); for the Ghomara, the best approximation to Drucker's data is to calculate density from age classes E–K (Fig. 2).

comparisons of data sets necessitated making adjustments for differing methodologies; where appropriate, these are described under Results.

RESULTS

Comparison of the Ghomaran and Moyen Atlas Conifer Forest Habitats

The Ghomaran and Moyen Atlas conifer forest zones are similar in altitude, climate, vegetation physiognomy, and plant genera (Mehlman, 1988). Both regions also suffer ecological degradation from domestic animals that are herded into forested areas to graze (Ghomara, goats; Moyen Atlas, sheep). Although one ecological difference between the two regions is the species of dominant conifer for each forest zone (Ghomara, fir; Moyen, Atlas cedar), this difference is negligible with respect to Barbary macaques: fir and cedar are utilized as a food resource in virtually identical ways by the macaques of each region (Mehlman, 1988). The most important ecological difference between these two regions is slope profile (Fig. 1): the Ghomara is more topographically complex and has much steeper slopes (Mehlman, 1984; Drucker, 1984; Fa *et al.,* 1984).

Ghomaran data on conifer density and herding pressure are compared to similar data collected by Drucker (1984) from a Moyen Atlas cedar forest at Bou Jirrir in Table III and Fig. 3. Conifer density at Bou Jirrir is approximately four times greater than in the Ghomara. The Ghomara is also characterized by (i) a substantial reduction in the ratio of closed: open canopy stands and (ii) a reduction in the mean density of mature conifers. Overall conifer density at another Moyen Atlas site, Ain Kahla, is estimated to be approximately 50–75% less than that of Bou Jirrir, which indicates the former to be about three times denser than in the Ghomara.

There are also substantial differences in herding pressure between these two regions. At Bou Jirrir, sheep are the dominant herd animal and have the highest impact on forest ecology (Drucker, 1984). Drucker has estimated the average monthly energy intake for the total number of sheep using a 532-ha forest sector at Bou Jirrir (Fig. 3). In the Ghomara, goats are the dominant herd animal; equivalent values for average monthly energy intake of goats in the Ghomara were obtained by multiplying a per-day energy intake value for goats [11,155 kJ (Drucker, 1984)] times the number of goats sighted per day in a 375-ha sector of the Ghomaran study area [an adjustment was made for the differences in sector sizes (Mehlman, 1986b)]. These comparisons indicate that the Ghomara is experiencing a herding pressure from the dominant herd animal estimated to be from 5 to 18 times greater

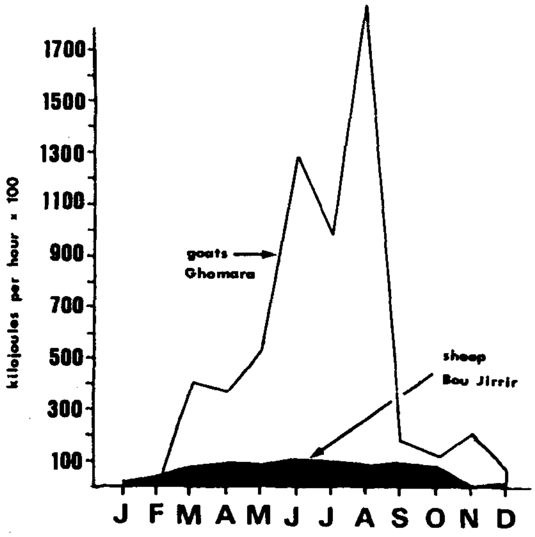


Fig. 3. Average monthly energy intake for dominant herd animals in the study area (Mehlman, 1986b) and at Bou Jirrir in the Moyen Atlas (Drucker, 1984).

than in Bou Jirrir forest. Two other qualitative factors make the grazing pressure in the Ghomara even more severe: herding on steep slopes accelerates erosional processes (Mehlman, 1984), and goats do more serious damage than sheep, since they are better climbers and preferentially browse woody vegetation (Thirgood, 1984).

Comparative Demography of Ghomaran and Moyen Atlas Populations

Birth Rates. The birth season for the six groups in this study occurred within a 2-month period in the spring of each year between April 7 and June 1 (Mehlman, 1986b). Separate birth rates are given for adult females (between the estimated ages of 5 and approximately 22 years) and for females 4 years of age (Table IV), since the latter matured during the study and their exact age could be assessed. Four-year-old females had an overall average birth rate of between 0.444 and 0.555 infant per year, while adult females had an average birth rate of between 0.585 and 0.600. Records for individual females indicated an average birth interval of 1.8 years (Mehlman, 1986b). These data are quite similar to the available data from the Moyen Atlas. Deag (1974) and Taub (1978) recorded birth rates for their focal groups of 0.500

Table IV. Estimated Birth Rates (in Parentheses) for All Groups Based on Ratios of Mothers to Breeding Females of Different Ages[a]

Group	Ratio (rate)		
	A	B	C
g1 (1980–1983)	8:12 (0.667)	1:1 (1.000)	9:13 (0.692)
g2 (1982–1983)	3:6 (0.500)	–	3:6 (0.500)
g3 (1982)	2:4 (0.500)	1:1 (1.000)	3:5 (0.600)
g4 (1982)	5:8 (0.625)	0:1 (0.000)	5:9 (0.556)
g5 (1982)	4:7 (0.571)	1:2 (0.500)	5:9 (0.556)
	or 5:7 (0.714)	0:2 (0.000)	5:9 (0.556)
Focal (1982–1983)	16:28 (0.571)	2:4 (0.500)	18:32 (0.563)
Average for all groups (1982)	21:40 (0.525)	1:5 (0.200)	23:45 (0.511)
	or 22:40 (0.555)	2:5 (0.400)	
Average for all groups	38:65 (0.585)	4:9 (0.444)	43:74 (0.581)
	or 39:65 (0.600)	5:9 (0.555)	

[a] Ratio A: mothers +5 years; all females +5 years. Ratio B: mothers 4 years; all females 4 years; Ratio C: all mothers; all females +4 years. Note that for group 5, it was not clear whether one female was 4 or 5 years of age.

and 0.556, respectively (although Taub, in a subsequent survey in 1977, recorded eight newborns for the nine females of breeding age). Deag (1984) also reported an average birth interval of 2 years. Although 4-year-old Ghomaran females appear to have a high birth rate compared to provisioned, semi-free-ranging groups (Paul and Thommen, 1984), no comparative data are available from wild groups of the Moyen Atlas.

Demographic Characteristics. The only long-term comparative census data, from another wild Barbary macaque population, are Deag's (1974, 1984) censuses of 10 groups (227 individuals) at Ain Kahla in the Moyen Atlas. Since Taub (1978) also censused one contiguous group in this region, and it was not one of the groups censused by Deag (Taub, personal communication), it was also added to the Ain Kahla population (Table V).

Group sizes in these two populations were not significantly different in central tendency or variability (Wald–Wolfowitz two-sample runs tests; Table V). In each population, the proportions of adult males, adult females, subadult males, and "immatures + 4-year-old females" (referred to as "IM + 4": the category of "IM + 4" is used, since Deag's censuses often did not distinguish between subadult and juvenile females) were not significantly different (Kolomogorov–Smirnov two-sample test: D value + 0.009, $p < 0.05$). Moreover, intergroup central tendency and variation in proportions of age–sex classes and adult sex ratio were not significantly different between the two populations (Wald–Wolfowitz two-sample runs tests; Table V).

Table V. Intergroup Variation in Group Size and Demographic Compositions at Ain Kahla (Deag, 1974, 1984; Taub, 1978) and in the Ghomara[a]

Group	Group size	% AM in group	% sM in group	% AF in group	% IM + 4 in group	AM/AF	IM + 4:AF	% IM + 4 (adjusted)
			Ain Kahla (mean group size = 25.3; (SD = 8.8)					
8 (Deag)	12	3 (25.0)	1 (8.3)	4 (33.3)	4 (33.3)	0.75	1.00:1	36.4
Pty. (Deag)	14	2 (14.3)	0 (0.0)	5 (35.7)	7 (50.0)	0.40	1.40	48.3
7 (Deag)	15	2 (13.3)	2 (13.3)	5 (33.3)	6 (40.0)	0.40	1.20	38.7
10 (Deag)	21	2 (9.5)	3 (14.3)	5 (23.8)	11 (52.4)	0.40	2.20	51.2
3 (Deag)	23	4 (17.4)	3 (13.0)	6 (26.1)	10 (43.5)	0.67	1.67	45.4
*FG (Deag)	25	3 (12.0)	2 (8.0)	6 (24.0)	14 (56.0)	0.50	2.33	56.0
4 (Deag)	29	3 (10.3)	2 (6.9)	8 (27.6)	16 (55.2)	0.38	2.00	53.3
11 (Deag)	29	5 (17.2)	2 (6.9)	8 (27.6)	14 (48.3)	0.63	1.75	50.0
2 (Deag)	35	9 (25.7)	3 (8.6)	7 (20.0)	16 (45.7)	1.29	2.29	54.2
5 (Deag)	36	9 (25.0)	2 (5.5)	5 (13.9)	20 (55.6)	1.80	4.00	67.8
*FG (Taub)	39	7 (17.9)	4 (10.2)	9 (23.1)	19 (48.7)	0.78	2.11	52.1
Median	25	17.2	8.6	26.1	48.7	62.5	2.00	50.6
Total	278	49 (17.6)	24 (8.6)	68 (24.5)	137 (49.3)	0.72	2.00	52.1

Ghomara (mean group size = 27.0; SD = 16.2)								
Total	162	29 (17.9)	12 (7.4)	40 (24.7)	81 (50.0)	0.73	2.02	52.9
Median	24	16.7	7.6	25.0	49.6	74.5	2.06	52.4
g1	12	2 (16.7)	1 (8.3)	3 (25.0)	6 (50.0)	0.66	2.00	52.2
g2	12	1 (8.3)	1 (8.3)	3 (25.0)	7 (58.3)	0.33	2.33	56.0
g3	18	3 (16.7)	1 (5.5)	4 22.2)	10 (55.6)	0.75	2.50	58.8
g4	30	6 (20.0)	2 (6.7)	8 (26.7)	14 (46.7)	0.75	1.75	50.0
g5	31	6 (19.4)	3 (9.7)	7 (22.5)	15 (48.4)	0.86	2.14	52.6
Focal	59	11 (18.6)	4 (6.8)	15 (25.4)	29 (49.2)	0.73	1.93	52.2
Wald-Wolfowitz *r* value	8	6	6	7	8	10	6	7

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[a]*FG = focal group of Deag (1974) and Taub (1978); all other data for Ain Kahla from Deag (1984). IM + 4 (immatures) = infants + juveniles + ratio of 0.50 obtained (see text). Wald-Wolfowitz two-sample runs test (two-tailed): $r > 4 = p > 0.05$ ($n1 = 6$, $n2 = 11$).

Population Growth Rate: Ghomara. Southwick *et al.*, (1980) have proposed that, in the absence of long-term demographic data, estimates of population growth rate can be made by examining cross-sectional data on age–sex class composition. On the basis of extensive, long-term censusing of rhesus groups, they maintain that a population must contain about 50% immatures (juveniles and infants, less than 4 years old) to maintain a stable size through time. Although the Ghomaran population had only 46.9% immatures (Table I: juv + i2 + sF's aged 3 years), the value of 50% used by Southwick *et al.* (1980) cannot be considered applicable to the Barbary macaque. The adult sex ratio in wild rhesus groups averages only 0.50; in Ghomara this value is 0.73 (Table V). The higher proportion of adult males in the Ghomara, which has no effect on population growth, biases the comparison by decreasing the relative proportion of immatures. If an adjustment for this is made by "removing" nine adult males from the total population (to give an adult sex ratio of 0.50), the "adjusted" proportion of immatures rises to 49.7%, suggesting that the Ghomaran population may have been close to a stable growth equilibrium when it was censused in 1982 (a similar argument can be made for the data on the Ain Kahla population, Table V).

Although the indicator of Southwick *et al.* suggests that the overall Ghomaran population may have been near growth equilibrium when censused, using the indicator on each group suggests that individual group growth rates varied substantially. If each group's percentage of immatures is adjusted by "removing" adult males to produce a 0.50 adult sex ratio, the three smallest groups were in growth phases, the focal group was in equilibrium, ant the two median-sized groups had negative rates of growth (Table I: % immatures of each group with "adjusted" sex ratios, e.g., for g4, "remove" 2 AM's to produce 46.4% immatures). Thus, using the indicator of Southwick *et al.* (1980), the smallest groups of the Ghomara had the highest estimated rates of growth.

However, an opposite trend occurs with the Ain Kahla population. There is a significant negative correlation between group size and the adjusted percentage of IM + 4's per group (Spearman's $r = 0.75$, $t = 3.01$, $p < 0.01$, df = 9). Thus, at Ain Kahla, the smallest groups have the lowest percentages of immatures per group and the lowest estimated rates of growth (i.e., by the indicator of Southwick *et al.*, the smallest groups had negative rates of growth).

Comparison of Ranging Behavior in the Ghomara and the Moyen Atlas

In general, Ghomaran groups ranged within fir forest with short excursions (<500 m) into surrounding oak maquis, the latter occurring primar-

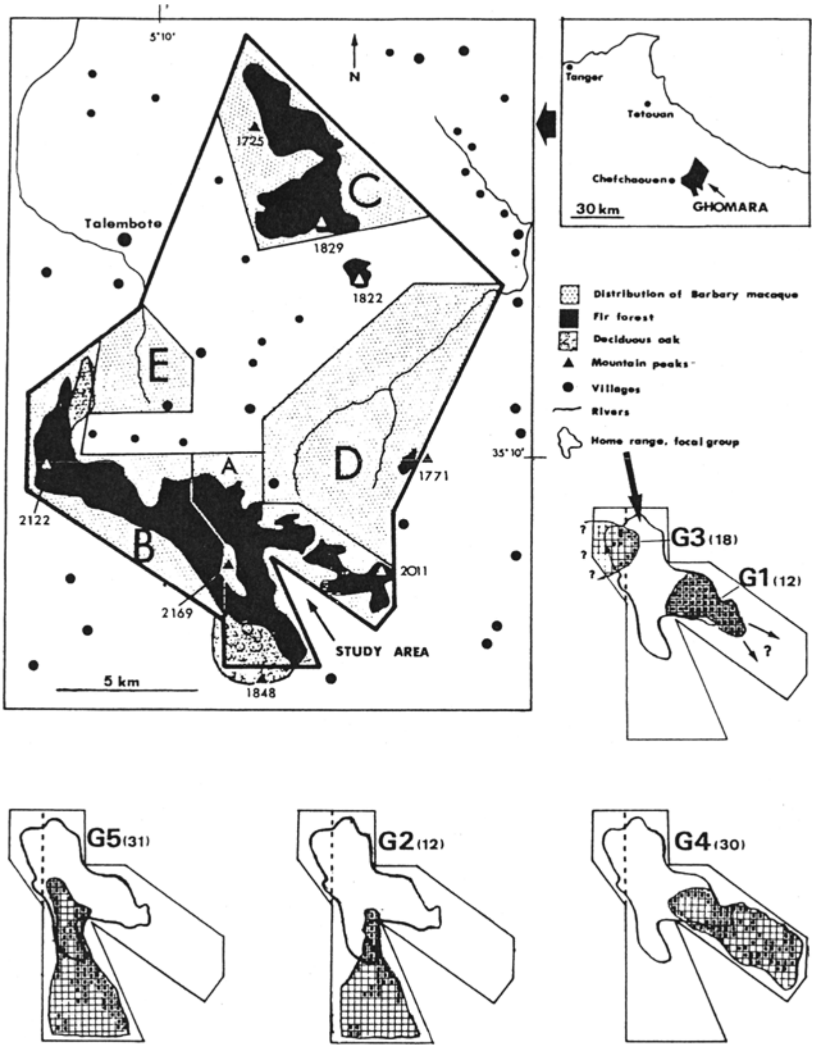

Fig. 4. The Ghomara. Inset at top right displays the location of the Ghomara in northwestern Morocco. Large figure at center displays the location of the study area (A) within the discontinuous areas of macaque distribution in the Ghomara (areas B and C are high-altitude fir forest; areas D and E are low-altitude scrub vegetation gorges). The four figures below display the home range of the focal group as it was overlapped by five other groups (dashed line is artificial division of the study are to calculate macaque density; see text). The grid system of the four lower figures is divided into 6-ha grids, with shaded grids indicating visual sightings of specific groups and open grids indicating home ranges estimated from features of topography and vegetation (see text). The two small areas of midaltitude deciduous oak forest are composed of *Quercus faginea, Q. pyrenaica,* and *Q. ilex.*

Table VI. Estimated Home-Range Sizes of Groups Using the Study Area[a]

	Group size	Home-range size (ha)	Size overlap with focal group (ha)	% overlap by all other groups	*DHR* (ind./km^2)	*HRGC*
g1	12	307	244 (27.1%)	100	3.91	1.62
g2	12	756	51 (5.7%)	100	1.59	1.77
g3	18	?	133 (14.8%)	?	?	?
g4	30	779	225 (25.0%)	39	3.85	2.21
g5	31	884	179 (19.9%)	85	3.51	2.08
Focal	59	901	-	78	6.55	1.92
Mean		725		80	3.88	1.92

[a] *DHR* = macaque density per home-range size (excluding other groups). *HRGC* = mean group carrying capacity per home range: average number of groups each home-range supports. *HRGC* for FG = 0.271 (g1) + 0.057 (g2) + 0.148 (g3) + 0.250 (g4) + 0.199 (g5) + 1 (FG) = 1.92.

ily in autumn (Fig. 4). One exception to this pattern was that groups 2 and 5 often entered a small area of mixed oak forest from September through January (Fig. 4). Estimated home-range sizes and overlaps of each of the groups are displayed in Table VI. Home-range size varied between 307 and 901 ha, with a mean of 725 ha. These are minimum estimates, however, since group 5 may have ranged farther west, and group 1 may have ranged farther east (Fig. 4). Home-range overlap (total overlap by all other groups) varied between 100 and 39%, with a mean of 80%. Although group 4 may have had exclusive use of as much as 61% of its range, this value may be an underestimate, since group 1 probably used more range area than indicated in Fig. 4.

To obtain average home-range size in the Moyen Atlas, data from Ain Kahla (Deag, 1974: Taub, 1978) were combined with Drucker's data for Bou

Table VII. Comparison of Moyen Atlas and Ghomaran Populations of Barbary Macaques (All Study Sites in Morocco)[a]

	Drucker (1984)	Deag (1974)	Taub (1978)	This study
Site	Bou Jirrir	Ain Kahla		Ghomara
Habitat	Cedar–evergreen oak			Fir–evergreen oak
Altitude (m)	1800	2000	2000	1800
Size of study group	40	25	39	59
Mean group size		[25.3]		27.0
Home-range size (ha)	127	117	185	901
Mean home-range size (ha)	[143 (n = 3)]			725 (n = 5)
DHR study group (ind./km^2)	31.5	21.4	21.2	6.5
DHR for all groups	[24.7 (n = 3)]			3.9 (n = 5)
Density estimate (ind./km^2)	?	60–70	44	6.7
Average home-range overlap	?	+100%	?	+80%

[a] Cedar = *Cedrus atlantica;* fir = *Abies pinsapo;* evergreen oak = *Quercus ilex.*

Table VIII. A Comparison of Preferential Home-Range Use by the Focal Group in the Ghomara (Mehlman, 1986b) and an Ain Kahla Study Group (Deag, 1974)[a]

	% of home range (size)	
	Ain Kahla	Ghomara
50% occupancy time	16.2 (15.0 ha)	6.5 (67.4 ha)
75% occupancy time	32.5 (38.0 ha)	16.9 (175.8 ha)
90% occupancy time	49.6 (58.0 ha)	36.4 (378.6 ha)
100% occupancy time, total home range	117.0 ha	1041.0 ha

[a] In each study an identical methodology was employed: the home range was divided into quadrats, and ranging behavior was scored as to the amount of time spent in particular quadrats. Thus, 50% occupancy time indicates that a group spent 50% of its observed time in the same quadrats, which by their surface area accounted for a given percentage of the observed home range.

Jirrir (Table VII). This produces a mean home-range size in prime cedar forest habitat in the Moyen Atlas of 143 ha, approximately five times smaller than in the Ghomara. The preferential use of home ranges also appears to differ between the Ghomara and the Moyen Atlas. The author employed a methodology (Mehlman, 1986b) similar to that of Deag (1974) in determining preferential range use, and the results of both studies are compared in Table VIII. These data suggest that differential range use in the Ghomara is more "uneven" than in the Moyen Atlas; the preferred areas of Deag's group accounted for a much larger proportion of the total home range than was the case in the Ghomaran study group.

Comparison of Population Density Between the Ghomara and the Moyen Atlas

To derive an overall estimate of macaque density in the Ghomara, the study area (Fig. 4, area "A") was reduced to the area lying within the dashed northwestern boundary indicated in the smaller figures in Fig. 4. This excluded group 3, since its range was primarily within area B [Fig. 4, group 3's ranging to the east of the dashed boundary was approximately balanced by the focal group's ranging to the west of this boundary (Mehlman, 1986b)]. Thus, all groups, excluding group 5, ranged in an area of approximately 21.4 km^2; of which 12.4 km^2 was fir forest, producing a macaque density of 6.73 individuals/km^2.

Density at Ain Kahla has been estimated to be 60–70 individuals/km^2 (Deag, 1972) or 44 individuals/km^2 (Taub, 1978). Taub's estimate was derived by dividing the number of animals in this focal group by their total home-range size (Table VII), a value that can be designated as "density per home range" (DHR). Taub then multiplied the DHR of this study group by a factor of two to account for how the home-range overlap of neighboring groups elevated total population density above the DHR of his study group (see Discussion). Deag's estimate was derived by dividing a total population of 350 macaques thought to use an area of 5 km^2 (Deag, 1974). However, Deag included sightings of three groups, totaling 114 individuals (1974, p. 43), but gave no data on how many times these groups were sighted in his 5-km^2 study area. If, for example, these groups made only one or two excursions into the area (e.g., Deag's study area included a Berber well that attracted thirsty macaque groups during the summer dry season) and are excluded from his total population, his estimate would decrease to 47.2/km^2 (350–114/5 km^2), a value similar to Taub's estimate. Also, given Deag's data on mean group and home-range size, it is not clear how 350 macaques were distributed in a 5-km^2 surface area. For example, Deag's study area would contain 4.27 average home ranges (1.17 km^2 for his study group), each containing 25 macaques (mean group size); this would total 107 macaques. To account for the remaining 243 macaques (350–107), each of the 4.27 home ranges would have to support an additional 2.3 groups of average size. This degree of range overlap (3.3 groups with 100% overlap per average home range) appears to exceed that indicated by Deag (1974) in the home-range maps of several groups contiguous to his study group.

Given the above, it appears that Taub's estimate for population density at Ain Kahla (44 individuals/km^2) is more accurate. This indicates that the Ain Kahla cedar forest environment supports 6.5 times more macaques per surface area than the Ghomara.

DISCUSSION

Ecological Determinants of Low Population Density in the Ghomara

Theoretically, a regional reduction in population density can be attributed ultimately to any combination of three ecological factors: (i) increased predation, (ii) increased interspecific competition, and (iii) decreased abundance of harvestable resources (e.g., Caughley, 1977; Ricklefs, 1972).

Predation. Potential natural predators in the Ghomara are the jackal (*Canis aureus*) and the booted eagle (*Hieraetus penattus*). The macaques had well-developed group avoidance behaviors to avian predators (Mehlman, 1984) and were never attacked by jackals, even in terrestrial settings (Mehlman, 1986b). The only potential predators for the Ghomaran macaques were the domestic dogs that accompanied the local goat herders. The macaques had frequent contacts with dogs and/or herders, and they were often forced to seek refuge in trees or on the larger cliff systems. Despite this, only three cases of mortality in all groups were suspected of being the result of human and/or dog predation (Mehlman, 1986b).

Mortality in the Ghomaran population that could be reliably attributed to predation was quite low; mortality in the older adults appeared to result from old age and severe weather conditions (Mehlman, 1986a, b). Juvenile mortality (the majority of intergroup demographic differences was among juveniles; Table V) may have been the result of emigration by young males (Mehlman, 1986a; Paul and Keuster 1986, 1988). Infant mortality in the Ghomara was quite low. Comparative data on mortality rates are not available for the Moyen Atlas, but in three wild study groups in Algeria, the mortality rate for infants (0-1 year of age) was 0.190 per annum (Ménard *et al.*, 1985). As in the Ghomara (FG = 0.222 per annum; mean for size groups = 0.083), this is lower than in other wild populations of macaques [e.g., *M. fuscata*, 0.328 (Ikeda, 1982); *M. sinica*, 0.540 (Dittus, 1975)] and may be linked to the unique system of male-infant care in Barbary macaques (Deag, 1974; Taub, 1978; Mehlman, 1986b).

Based on short-term studies of Ghomaran groups, Whiten and Rumsey (1973) and Fa (1982); who censused some of the groups in the present study, reported group compositions that differ substantially from the results of this study. They speculated that this was the result of high levels of human predation (Fa, 1982; Whiten, cited by Deag, 1977, p. 272). However, the unusual compositions they reported are likely the result if inaccurate censusing and undercounting, due to the complicated terrain and the unhabituated state of groups. In short-term studies of forest-dwelling macaques, inaccurate censusing is a persistant problem. For example, in observing a Barbary group in Algeria, Ménard first believed that it contained 15 members. But after 6 months of study, it was found to contain 37 members (Fa *et al.*, 1984; Ménard *et al.*, 1985). During the first year of the present study, the focal group was consistently undercounted by about 30% (Mehlman and Parkhill, 1988; Mehlman, 1984).

Nonfood Resources. In the Ghomara, sleep sites (stands of mature firs) are abundant, and this particular resource has little effect on population density, on ranging behavior, or on the spatial distribution of groups (Mehlman, 1986b). In the Moyen Atlas habitat, with its much higher conifer density, sleeping sites presumably also exert little influence on population density. Further, water resources can be eliminated as a factor in density reduction because the Ghomara contains more permanent water sources per surface area than in Moyen Atlas habitats (Deag, 1984; Drucker, 1984 Mehlman, 1988, 1986b).

Food Resources. Since predation and nonfood resources do not appear to play any major role in density reduction in the Ghomara, it can be deduced that a reduction in the available food resources must be the major ecological factor responsible for the low macaque density. Conifer foliage is one essential food resource of Barbary macaques in cedar and fir forest during the cold, snowy winters (Deag, 1974; Taub, 1978; Drucker, 1974; Mehlman, 1988). Since foliage biomass and many aspects of forest ecology (e.g., ground layer productivity, areas of secondary succession, logging, etc.) are highly correlated with conifer density (Taub, 1978), one might assume that throughout high-altitude conifer forests, macaque density and conifer density would be linearly related. Employing the conifer density data from Table III and the macaque density data from Table VIII, a ratio of 750 conifers:0.440 macaque per ha can be derived for Ain Kahla. A linear prediction of macaque density from conifer density for the Ghomara (280 conifers per ha) would result in 0.164 macaque per ha. The Ghomaran density is 0.067 macaque per ha, suggesting that density is depressed approximately 59% below a density prediction from a ratio of conifer:macaque density in the Moyen Atlas.

There are several ecological factors specific to the Ghomara that operate to depress its macaque density below a value predicted from conifer:macaque density in the Moyen Atlas. First is the effect of high slope and low forest density on ground layer productivity. The extremely steep slope profile and heavy seasonal rains of the Ghomara (Mehlman, 1986b, p. 40, 1988) produce severe natural erosion, as well as poor soils (Mehlman, 1984). This creates a more open, sclerophyllous ground and shrub layer, with a concomitant reduction in food resources. Second is that the much higher rate of competition from domestic herd animals in the Ghomara that lowers food abundance and selects for ground layer plants with chemical defenses, spines, and thorns, at the expense of more easily exploitable macaque plant foods (Mehlman, 1986b).

Herding also operates indirectly to depress macaque density in the Ghomara. Goat herds are accompanied by humans and dogs. Consequently the macaques are limited in their ranging behavior, preferring to follow major cliff systems and using closed or semiopen canopy stands when making long-distance movements (Mehlman, 1986b). As a result, their differential home-range use is much more "uneven" than one studied group in the Moyen Atlas (Table VIII). This renders them incapable of efficiently harvesting the resource productivity that occurs in areas lacking escape routes from the human and canine predators.

The outcome of all these synergistic effects is that macaques in the Ghomara, in comparison to the Moyen Atlas, must exploit a more patchy forest, a less productive ground layer, and a less accessible food resource base. This reduces the macaque density well below that expected from a simple linear relationship between conifer and macaque density. Unfortunately, these results can be viewed as a general model for the future of this species throughout all high-altitude conifer forests in Morocco and Algeria. In short, as human habitat encroachment accelerates (Taub 1984), macaques will disappear significantly faster than the conifers upon which they are dependent.

POPULATION DENSITY, MEAN GROUP SIZE, AND RANGING BEHAVIOR

The results of the present study indicate that the overall compositions of the Ghomaran and Ain Kahlan populations were highly similar when sampled; therefore, for the following comparisons, population density can be substituted for macaque biomass, and the former can be viewed as

$$D = \frac{\overline{GS}}{HR} (\overline{HRGC}), \tag{1}$$

where:

D = population density (individuals/km^2),
GS = mean group size (No. of individuals),
HR = mean home-range size (km^2),
$HRGC$ = mean number of groups supported per mean home range (overlap), and
DHR = mean density per home range = GS/HR.

This relationship [Eq. (1)] was first implicitly proposed by Taub (1978) when he multipled the *DHR* of his study group by a factor of 2.0 to approximate how home range overlap must elevate *D* above *DHR*. In this case, he set $HRGC = 2.0$, indicating that the total degree of overlap for his study group's home range was equivalent to supporting two groups: one, the study group; and two, different proportions of other groups' range overlaps equivalent to the range of one additional group sharing the range of the study group (for a calculation of *HRGC,* see Table VI). Note that (i) group sizes need not enter the calculation of HRGC, since they are subsumed by GS, and (ii) when $HRGC = 1$, there is no group overlap and $D = DHR$.

Equation (1) can be expanded to represent a density ratio between two populations (where subscripts 1 and 2 represent high- and low-density populations, respectively):

$$\frac{D_1}{D_2} = \left[\frac{(HRGC_1)\ (GS_1)}{HR_1}\right] \left[\frac{HR_2}{(HRGC_2)\ (GS_2)}\right]. \tag{2}$$

One way to interpret Eq. (2) is that if mean group size and mean home-range overlap are equivalent in two regional populations, then any decrease in population density in one region must be accompanied by an exactly proportional increase in mean home-range size in the other (number of groups per surface area must also decrease proportionately). This is nearly the case for the differences found between the Ghomaran and the Ain Kahlan populations. The departure from a perfect 1:1 inverse relationship between density ($D_1/D_2 = 6.5$) and home-range size ($HR_2/HR_1 = 5.0$) may be attributed to (i) *HRGC* in the Ghomara (1.92) being somewhat less than at Ain Kahla [2.0 (Taub, 1978) or 2.5, if the data from Table VII are entered into Eq. (2) above]; (ii) *GS* in the Ghomara (28.8, excluding g3) being slightly larger than at Ain Kahla (25.3); and (iii) *HR* in the Ghomara perhaps exceeding the present estimates (Fig. 2).

Thus, the major difference in population structure in the marginal habitat of the Ghomara is that a smaller number of groups (similar in size to Moyen Atlas groups) exist per given surface area and that these groups occupy larger ranges, roughly inversely proportional (78%) to the density differential between the Ghomara and the Moyen Atlas. Ghomaran groups appear to have increased home-range sizes as a response to the reduction in available food resources (Gartlan and Brain, 1968; Clutton-Brock and Harvey, 1977), and this occurs without any substantial shifts in the central tendency and range in group size or mean home-range overlap.

Demographic Composition of Population

Although the overall demographic compositions of the Ghomaran and Ain Kahlan populations were similar, the *intergroup* growth rates for each population were quite different. What factors would favor the higher growth rates of small groups in the marginal habitat of the Ghomara and, conversely, inhibit the growth of small groups in the prime habitat at Ain Kahla?

Barbary macaque populations, like those of other macaques, are structured into female-bonded groups that compete over patchily distributed resource bases (Wrangham, 1980; Mehlman and Parkhill, 1988). In high-density, prime habitat, small groups, through intergroup competition with larger groups, might experience higher ecological and social stresses and, as a consequence, have low birth rates and/or high mortality rates. This phenomenon had been observed in a high-density, contained population of Barbary macaques at Salem, Germany: two small groups, formed by fissioning, experienced high rates of aggression from larger groups, and this factor is cited as being the direct cause of high mortality in one of the groups (Paul and Kuester, 1988). In contrast, small groups in the Ghomara might experience less intergroup displacement, since large home-range sizes would decrease range defensibility for all groups. Comparative data on the rate per observation hour of intergroup interactions support this view: the Ghomaran focal group experienced 0.021 intergroup interaction per hr (Mehlman and Parkhill, 1988), while one study group at Ain Kahla had at least twice this rate [0.047 (Deag, 1974)]. This suggests that, with the large home-range sizes in the Ghomara, groups encountered each other less often (also see Cheney, 1987) and are, consequently, less efficient at defending their ranges. Thus, small groups in the Ghomara might be able to exist within the ranges of larger groups (Fig. 4), experiencing less intergroup competition and subsisting on resources that cannot be defended efficiently by larger groups.

CONCLUSION

For Barbary macaques in conifer habitat, population density is positively correlated with habitat quality. The density of a Barbary macaque population in the Ghomara is approximately 6.5 times lower than that of a population at Ain Kahla in the Moyen Atlas. This results from a lower abundance and more patchy distribution of food resources, brought about primarily by (i) a lower overall conifer density (ii) a higher ratio of nonconifer stands to conifer stands per surface area, and (iii) a substantial increase in direct interspecific competition from goats herded in the region. Goat herding with domestic dogs also forces the Ghomaran macaques into a strategy of uneven range use, further decreasing access to harvestable food resources.

The primary change in the structure of the Ghomaran population is a fivefold expansion in mean home-range size, without any significant shifts in mean group size or mean home-range overlap. This confirms a regularity suggested by many studies of cercopithecines: mean home-range size is negatively correlated with habitat quality and population density.

With respect to Caldecott's (1986) proposed principle, the results of the present study both confirm it in the general sense and contradict it in a specific sense. In the general sense, regional differences in resource bases of Barbary macaque populations do bring about shifts in mean home-range size, while the mean group size and the age–sex class composition of the total population does not change significantly. However, in the specific sense, correlations between group size and certain important aspects of composition appear to shift with changes in habitat quality. In the prime habitat of the Moyen Atlas, the smallest groups have lower proportions of immatures (and presumably lower growth rates) than larger groups; in the "marginal" habitat of the Ghomara this trend is reversed.

Thus, in Barbary macaques, differences in regional habitat quality do not appear to cause shifts in the central tendency and distribution of group sizes or in the overall populational composition and growth rates.

In contrast, poorer quality habitat appears to improve the growth rates of smaller groups at the expense of larger groups. This is hypothesized to result from a decrease in the home-range defensibility of all groups in low-density, marginal habitats, such that small groups may be ecologically and demographically "released" from the intensity of intergroup competition that they would encounter normally in high-density prime habitats.

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