



Barbary Macaque *Macaca sylvanus* (Linnaeus, 1758)

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Common Names

English	Barbary macaque (also wrongly called Barbary ape)
German	Berberaffe, Magot
French	Magot, singe magot, macaque Berbère
Spanish	Mona de Berberic, mona/mono de Gibraltar
Italian	Bertuccia, macaco Berbero
Russian	Берберийская макака

Taxonomy and Systematics

The Barbary macaque belongs to the genus *Macaca* comprising approximately 25 species (Li et al. 2009). It is the only nonhuman primate in Europe, the northernmost African nonhuman primate and the only extant species of the genus *Macaca* outside East-Asia. The genus *Macaca* probably originated in North Africa around 5.5 million years ago (Modolo et al. 2005), and then radiated into Europe and Asia (Li et al. 2009). However, extant macaque species all live in East Asia, with the exception of the Barbary macaque, between Afghanistan and Pakistan to the East and Japan to the West, and between China to the North and Indonesia to the South. By the early Pleistocene the Barbary macaque lineage disappeared in most of Europe and in the Middle East and as a result became separated from the other macaque lineages. The reduction in the distribution of the Barbary macaque was probably due to climate change and associated changes in vegetation and availability of resources (Elton and O'Regan 2014). Due to the geographic distance between the Barbary macaque and other macaque species, there is no record of hybridization with related species in the wild.

The Barbary macaque population living in Gibraltar has both Algerian and Moroccan origins (Modolo et al. 2005). The origins of the Gibraltar population are unclear: it may have been originated from a remnant European population or it may have been established through the translocation of some animals from Africa (Modolo et al. 2005). In any case, the current Gibraltar

population might not include any remnants of the original European population, since there are no fossil records of Barbary macaques in Gibraltar after the last glaciation (Shaw and Cortes 2006).

Paleontology

The fossil record and the modeled reconstruction of their geographic distribution suggest that the Barbary macaque inhabited vast parts of Europe, North-Africa, and the Middle East (Syria and the Caucasian region) between the Miocene and Pleistocene (Fig. 1; Elton and O'Regan 2014). Humans have probably affected the geographic range of the Barbary macaques since at least the last 4,000 years (Modolo et al. 2005). In historic times, the Barbary macaque faced a dramatic decline in its distribution. In Europe, this species was restricted to Spain by the end of the nineteenth century and it was only found in Gibraltar by the beginning of the twentieth century (Taub 1984).

Current Distribution

The current distribution of the Barbary macaque is limited to Gibraltar (36°09'N, 05°21'W) and to small relic patches of forest in Morocco and Algeria (Fig. 2). In Gibraltar, around six groups of macaques, for a total of approximately 200 individuals, inhabit the Upper Rock Nature Reserve; some of these groups rely extensively of food provisioning from humans.

Description

The Barbary macaque is often wrongly called the tailless monkey or Barbary ape. The Barbary macaque is not an ape (i.e., anthropoid primate) and it has a vestigial tail, which varies in length from 4 mm to 22 mm (Fooden 2007). Sexual dimorphism can be observed in relation to body length (males: 550–600 mm, females: 450 mm)

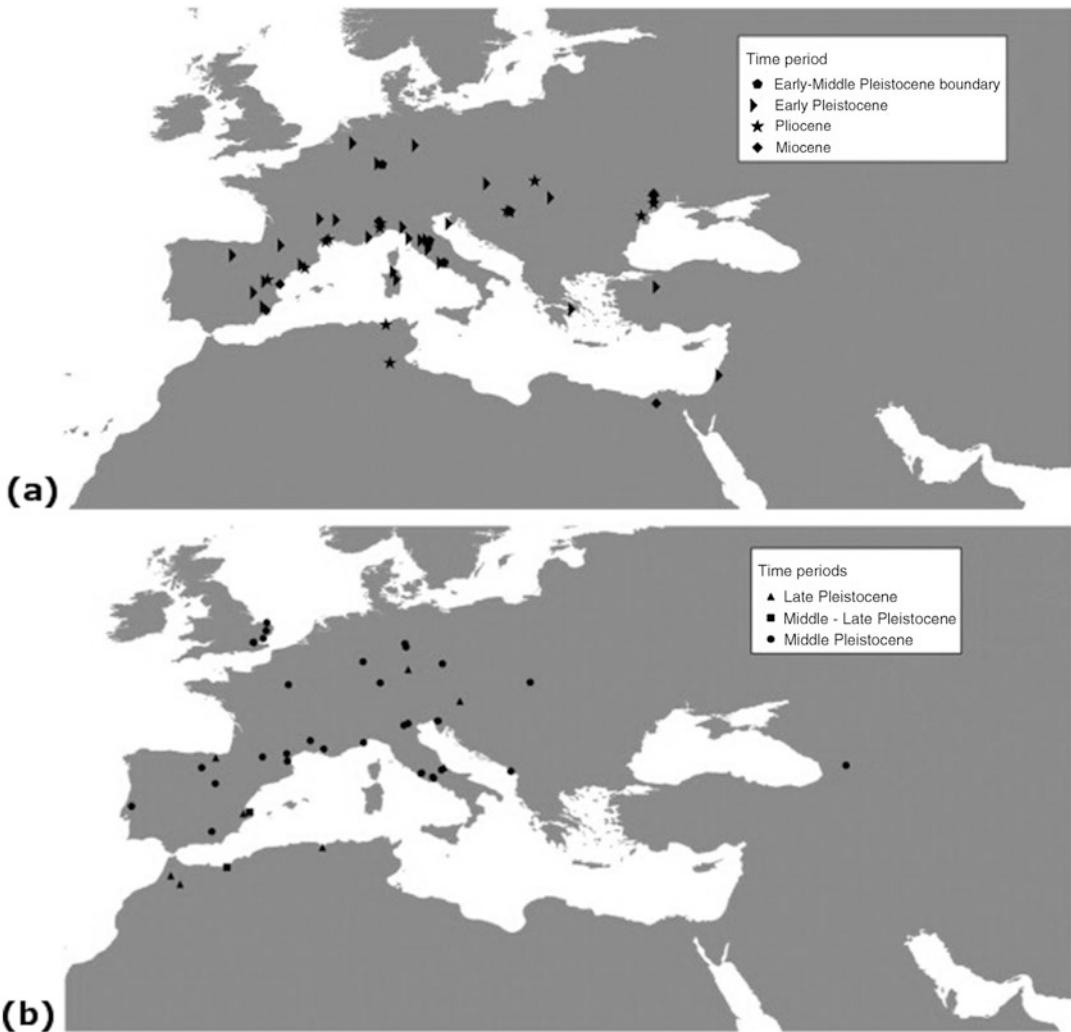


Fig. 1 Location of *Macaca* fossils in Europe, North Africa and Caucasus from (a) the Miocene to the Early-Middle Pleistocene boundary and (b) in the Middle and

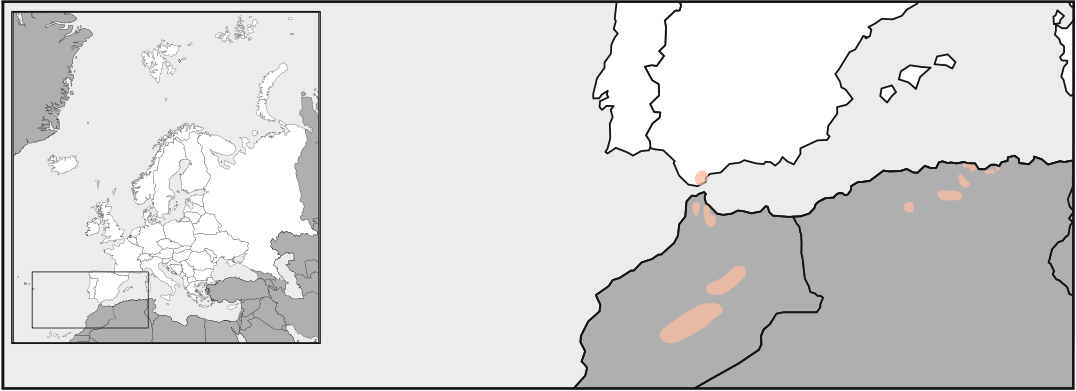
Late Pleistocene. Note that not all Miocene *Macaca* sites in North Africa are shown in the figure. (Redrawn from Elton and O'Regan (2014) with permission from Elsevier)

and weight (males: 15–17 kg, females: 10–11 kg; Fa 1989). The body size and morphology of Barbary macaques varies depending on age and on whether measurements are taken from provisioned or non-provisioned individuals (Fa 1984; Fooden 2007; Borg et al. 2014; Table 1 and Fig. 3). Provisioned macaques have a significantly larger body size than non-provisioned animals (Borg et al. 2014; Maréchal et al. 2016a).

The dental formula of a Barbary macaque is $I2/2, C1/1, P2/2, M3/3$. Sub-adult and adult males

have long canine teeth, surpassing their incisors, which play an important role in dominance-related behaviors, while females do not display long canine teeth.

During the mating period (see section “Genetics” below), female sexual displays are characterized by a sexual swelling (Fig. 4). This swelling varies during the reproductive cycle of a female (Brauch et al. 2007; Young et al. 2013a) but, in provisioned conditions, a swelling might be still visible outside of the mating season despite the



Map template: © Getty Images/iStockphoto

Fig. 2 Current geographic distribution of the Barbary macaque. The distribution is based on the IUCN Red List of Threatened Species. Version 2020-2 (Wallis et al. 2020; redrawn with permission from IUCN)

Table 1 Body measurements of Barbary macaque by age/sex class

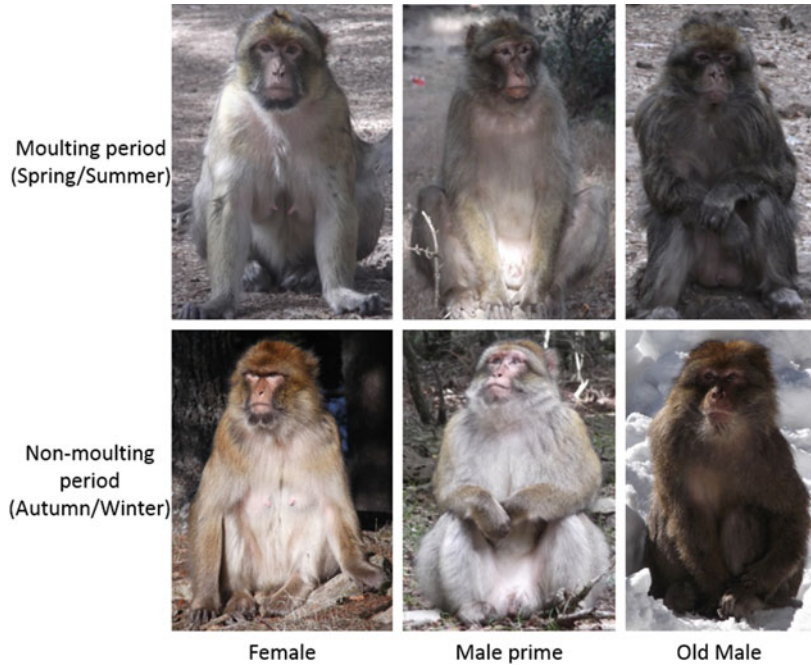
Age/sex class	Weight (kg)		Sitting height (cm)	Head and body length (cm)
Infants <1 year	/	0.9–1.0	/	24.6–28.7
Infants 1 year	1.9–2.1		/	
Juveniles 1–2 years	4.1–4.4	/	/	/
Juveniles 2–3 years	5.7–6.2	6.2–8.6	30–33	50.0–55.3
Juveniles 3–4 years	7.5–8.1		35–38	
Sub-adults 4–5 years	8.6–10.4	/	40–43	/
Sub-adult males 5–6 years	12.2	/	49	/
Sub-adult males 6–7 years	14.3	/	53	/
Adult males	15.3–17.0	10.0–18.0	55–60	60.5–65.3
Adult females	10.2–11.0	8.0–12.0	45	54.0–56.6
Reference	Fa et al. (1984)	Fooden (2007)	Fa et al. (1984)	Fooden (2007)

female not being fertile at the time. There is no sexual dimorphism in the pelage color in the Barbary macaque. In adult and sub-adult Barbary macaques, the pelage coloration on the dorsal surface from the top of the head to the hindquarter is highly variable from light gray, beige, light brown, golden brown, burnt orange, to dark (Fig. 3; Fooden 2007). The ventral fur is generally lighter than the dorsal fur, and it is also not as thick, leaving ventral body parts often visible. To cope with extreme climatic conditions, with hot and dry summer (up to +40 °C) and cold winter (up to –20 °C), Barbary macaques have a thicker fur during autumn and winter, which molts during spring and summer (Fig. 3).

Age determination is difficult in the Barbary macaques, especially at older age, because the

different traits used to age a macaque (e.g., dentition, pelage, locomotion, social behavior; Table 2) may significantly vary across individuals of the same age due to factors like dominance rank, diet, and feeding efficiency. In captivity or under provisioned conditions, Barbary macaques may live up to around 20–28 years; the maximum recorded lifespan of a Barbary macaque is 28 years, in captivity (Sue Wiper pers. comm.; Fooden 2007). Macaques are unlikely to live beyond 20 years in the wild in non-provisioned conditions. New noninvasive markers for immune function, urinary neopterin levels, have been recently found to significantly increase with age (Müller et al. 2017), which may provide a useful additional tool to assess age in wild individuals in the future.

Fig. 3 Adult pelage of the Barbary macaque during molting and non-molting periods; the pictures depict the same macaque (top/bottom) at the two different periods. Pictures taken from macaques living in Ifrane National park (33° 24'N–005°12'W). (©Pictures with permission from Laëtitia Maréchal)



Provisioned female macaques



(A) Non-mating season (April 2012) (B) Mating season (October 2012)

Non-provisioned female macaques



(C) Non-mating season (May 2012) (D) Mating season (October 2012)

Fig. 4 Sexual swellings in female Barbary macaque. Pictures taken from two females living in Ifrane National park (33°24'N–005°12'W). The female on the left experienced daily provisioning of high caloric food from tourists and local people (A = non-mating season April 2012;

B = mating season October 2012); the female on the right fed only on natural resources available in her habitat (C = non-mating season May 2012; D = mating season October 2012). (©Pictures with permission from Laëtitia Maréchal)

Table 2 Age classes of Barbary macaques based on dentition, pelage, body morphology, dexterity, mobility, and behavior (Fa 1984; Fooden 2007; Bissonnette et al. 2009; Maréchal unpublished data)

Stage of development	Age	Dentition	Pelage/body morphology	Dexterity and mobility	Social and other behavior
Infant 1	Birth-145 days	Deciduous teeth only	At birth, the dorsal pelage is dark and gradually becomes brownish between 45–145 days old	Carried ventrally by adults (mother and males) but also dorsally from around 45–75 days old. Stays within short distance from infant carer	Social interactions mostly with mother, gradually interacting with males and other group members under mother's supervision
Infant 2	145 days–1 yr		Light brown infant	Becoming more independent, developing their dexterity and mobility through play	Weaning is usually completed by year 1 but it may last longer if the mother does not have a new infant in the following year. Initial social play with other infants and juveniles
Juvenile	1–3 yrs	Some permanent teeth erupted	Light brown/beige	Mostly independent, developing their dexterity and mobility through play	Frequent play with other juveniles, becoming more independent from their mother
Sub-adult female	3–5 yrs	Molar 3 incompletely erupted	Small face, no beard, slender body	Reaching peak of their dexterity and mobility with great interindividual differences due to previous injuries, diet, rank, and personality	Still engage in play, initial attempts to mate with males
Sub-adult male	3–5 yrs	Canines incompletely erupted	Body grows from adult female size to large body size, but high inter-individual differences emerging (pelage color, body size)		Initial attempts to mate with females during the mating season, often prevented by adult males and/or rejected by high ranking females
Young adult female	5–6 yrs	All permanent teeth completely erupted	Small face, small dark beard under the chin. Sexual swelling appearing.		Stable social bonds with other group members and dominance rank
Young adult male	5–7 yrs		Larger body and full testicular size		Actively participating in sexual behavior, not tolerated by high ranking males
Prime adult female	6–15 yrs	Variation in dentition condition due to diet, rank, competition	Reaching full body size, beard becoming larger and darker, nipples longer, large sexual swelling.	Peak of their dexterity and mobility with great interindividual differences due to previous injuries, diet, rank, and personality	Peak of their sexual activity
Prime adult male	7–12/15 yrs		Reaching full body size with great interindividual		Peak of sociosexual competition and sexual activity

(continued)

Table 2 (continued)

Stage of development	Age	Dentition	Pelage/body morphology	Dexterity and mobility	Social and other behavior
			differences (pelage, body size)		
Old adult female	15 yrs. +	Deterioration of dentition, missing, worn, or broken teeth	Deterioration of the overall body condition with body size reduction, arched back	Degradation in mobility; limping, and arthritis possible	Less socially active
Old adult male	12/15 yrs. +	Deterioration of dentition, missing, worn, or broken teeth	Deterioration of the overall body condition with body size reduction, arched back		Socially more active than females of same age, progressively becoming more peripheral to the core group

Physiology

The Barbary macaque lives in extremely variable ecosystems in terms of food availability, habitat type, and climate. A large proportion of Barbary macaques live in anthropogenic habitats where interactions with humans are frequent (Waterman et al. 2020). Barbary macaques exert flexible metabolic strategies in response to these environmental and social conditions.

Barbary macaques have demonstrated a clear metabolic flexibility to cope with extreme environmental variations. Cristóbal-Azkarate et al. (2016) found that fecal thyroid hormone levels, an index for basal metabolic rate, were negatively related to temperature and food availability, indicating higher energetic expenditure when temperatures were low, and food scattered. In addition, social factors were found to modulate Barbary macaque metabolism responses to environmental stress. For instance, the degree of sociality has been positively associated with an individual's chance of survival in extremely cold winter in Morocco (McFarland and Majolo 2013b). Huddling behavior was also suggested to be a behavioral strategy to modulate thermoregulation and energy in Barbary macaques (Campbell et al. 2018).

Although living in social groups helps individuals to regulate the impacts of environmental

conditions, Barbary macaques have shown a distinct metabolic flexibility to deal with social demands. For example, social tension due, for example, to within group aggressive conflicts, is marked by an increase in physiological stress levels in Barbary macaques, but such metabolic responses seem to be buffered by strong social bonds in males (Young et al. 2014b), and by taking part in grooming interactions (Shutt et al. 2007). As many mammals, the gestation period in Barbary macaque is associated with higher physiological stress levels compared to non-gestational states (Maréchal et al. 2016a). In addition, sexual hormones have been shown to influence different behaviors and morphological traits during mating season (see section “Genetics”). The size of female sexual swelling and sexual behavior are positively related to estrogen/progesterone ratio (Möhle et al. 2005; Brauch et al. 2007; Young et al. 2013a). Female fertile phase also appears to affect male sexual behavior and metabolism (Heistermann et al. 2008; Young et al. 2013a). Fecal glucocorticoid metabolite levels increase during the mating season for males but not females (Maréchal et al. 2016a). Fecal thyroid hormone levels and androgen levels also show a significant increase before the onset of the mating season and are generally higher throughout the season compared to outside the mating period (Cristóbal-Azkarate et al. 2016;

Rincon et al. 2017). These hormonal changes appear to coincide with males' body size growth (Maréchal et al. 2016a) and suggest that the mating season requires a major energetic expenditure for male Barbary macaques to cope with. Male-infant grooming during highly social stress periods, such as the mating season and periods of rank instability, was associated with lower androgen levels (Rincon et al. 2017).

Barbary macaques are often encountered in, or in proximity of human-modified landscapes, increasing opportunities for human-macaque interactions. However, such close interactions with humans have been shown to bear often negative impacts on the metabolism and body condition of Barbary macaques. Agonistic interactions with humans increase the physiological stress levels of male Barbary macaques with negative consequences on their health and reproduction (Maréchal et al. 2011). Food provisioning, linked to unregulated tourism, has also shown to have a negative impact on the health of Barbary macaques in Gibraltar and Morocco, increasing their body size, parasite load, stress levels and mortality, changing dietary patterns and nutrition, negatively affecting body condition, and potentially lowering reproductive rates in provisioned macaques in comparison to animals not/less exposed to tourists (Fuentes 2006; Schurr et al. 2012; Borg et al. 2014; Maréchal et al. 2016a).

Genetics

The Barbary macaques live in extremely fragmented sub-populations. The Algerian and Moroccan populations diverged around 1.6 million years ago (Modolo et al. 2005). A study on the phylo-geography of the Barbary macaques found that the Algerian population is paraphyletic whereas the Moroccan population is monophyletic (Modolo et al. 2005). Moreover, genetic analyses found evidence of genetic fragmentation across sub-populations and some sub-populations are genetically isolated from the others (Scheffrahn et al. 1993; Von Segesser et al. 1999). Therefore, such a fragmentation is a major concern for the conservation of this species.

However, genetic analyses on the Algerian population estimated the genetic heterozygosity of Algerian Barbary macaques to be comparable to other mammalian species, thus suggesting no restriction to the genetic diversity of the Barbary macaque (Von Segesser et al. 1999).

All of the extant Gibraltarian mtDNA haplotypes have also been found in the Moroccan and Algerian populations (Modolo et al. 2005). Indeed, various introductions of macaques, captured in Morocco or Algeria have taken place in Gibraltar up until at least the eighteenth century; the last reported reintroduction of macaques, probably coming from Morocco, took place during the Second World War (Fa 1984).

Life History

The Barbary macaque is a seasonal breeder (Paul and Kuester 1988). The mating season starts around the beginning of September and lasts



Fig. 5 A sexual mount in the Barbary macaque in the Middle Atlas Mountains of Morocco. (©Picture with permission from Christopher Young)

approximately until January. The birth season in Gibraltar is between May and August (Fa 1984); in Morocco and Algeria the birth season is between March and June (Ménard and Vallet 1993a; Young et al. 2013b).

Barbary macaques form consortships during the mating season that can last from a few minutes to several hours; during these consortships a male and female spend time in proximity, co-feeding, exchanging grooming and mating. Females are most likely to form consortships when in estrus; however, males are not always capable to detect the peak of a female's fertile period (Young et al. 2013a; see section "Description"). Sexual mounts in the Barbary macaques are dorso-ventral (Fig. 5) and composed of a series of single mount-dismount sequence during which usually the male ejaculates after a few pelvic thrusts (Fooden 2007). Toward the end of the mount-dismount sequence and during ejaculation, the female often produces a copulation call, a series of low frequency grunts. These copulation calls may indicate the female's receptive status to males and/or elicit male–male competition for access to estrous females (Semple 1998).

Barbary macaques usually give birth to one infant per birth season; twins are rare. Gestation period ranges from 145 to 177 in captive Barbary macaques (Paul and Kuester 1987); in wild macaques in the Moroccan Middle Atlas Mountains the average gestation length was calculated to be 170 ± 3.8 days (Young et al. 2013a). Gestation period appears to be longer for female infants (165.3 ± 4.6) than for male infants (163.2 ± 5.4 ; Fooden 2007). In Gibraltar, females give birth to their first infant when they are between 4.05 and 6.99 years old (Fa 1984). In non-provisioned Barbary macaques in Algeria, females give birth to their first infant at an average age of 5.4 years (Ménard and Vallet 1993a). Female fecundity reaches a peak at 7–8 years but then declines rapidly as females become older (Paul et al. 1993). The majority of inter-birth intervals fall within a 1-year period, particularly in provisioned macaques (Fa 1984), but it can be longer (2–3 years) in non-provisioned macaques, especially in years of high ecological pressure due, for example, to low food and/or water

availability. Inter-birth intervals become longer the older the female (Paul et al. 1993). In the Moroccan Rif Mountains, the adult female birth rate is 0.58 per year (Mehlman 1989). In Morocco and Algeria males become sexually active between the age of 5–7 years old (Deag 1980; Ménard et al. 1985).

Infants start eating solid food when around 1–2 months old. Weaning is completed when infants are between 1 and 2 years old (Fa 1984). Mortality rate is highest in infants, especially in the first 6 months of their life, in both provisioned and non-provisioned macaques, then it decreases until senescence (Fa 1984; Mehlman 1989; Ménard and Vallet 1993a).

The overall sex ratio (male/female) in Gibraltar is 0.99; the sex ratio for macaques above 5 years of age is 0.66 (Shaw and Cortes 2006). In the Moroccan Rif Mountains the sex ratio was 0.73 (Mehlman 1989); in the southernmost Moroccan population of Barbary macaques in the High Ourika valley, High Atlas Mountains, the adult sex ratio is 1 (Namous et al. 2017). At two sites in Algeria (Tigounatine and Akfadou), the adult sex ratio was 1.05 (Ménard et al. 1990).

Habitat and Diet

The Barbary macaque inhabits evergreen and deciduous forests, scrubs, grasslands, and rocky areas with herbaceous plants. The vegetation of the Upper Rock Reserve in Gibraltar is composed of patches of medium/tall plants (mainly *Olea europaea*, *Rhamnus alaternus*, *Pistacia lentiscus*, *Pistacia terebinthus*, and *Osyris lanceolata*) and areas covered by herbaceous plants (Fa 1984). In Morocco and Algeria the dominant tree species where the Barbary macaque lives are cedar (*Cedrus atlantica*) and oak trees (*Quercus ilex*, *Quercus faginea*, and *Quercus afares*), and the Spanish fir (*Abies pinsapo*; Fooden 2007). The majority of macaques are found in mountainous forests and, in those habitats, macaques are reluctant to move to open areas away from trees. However, it is not clear whether macaques prefer forested habitats or whether the present-day geographic distribution of the species is due to

competition for land with humans and livestock, which forced macaques to move to areas less accessible to humans (Fa 1984).

The elevation distribution of the Barbary macaque lies at an altitude between zero and 2300 meters above sea level. The Barbary macaque mostly lives within the Mediterranean climate. In Gibraltar, and in the Moroccan and Algerian sub-populations living close to the sea, winter is generally mild, but the summer is hot and dry. In the mountainous areas of Morocco and Algeria the Barbary macaque experiences strong seasonal differences, from dry and hot summer months, where temperature can reach up to 40 °C, to wet and snowy winter months with snow and temperatures often going well below 0 °C (Majolo et al. 2013; El Alami et al. 2013).

The Barbary macaque is a diurnal and mostly a terrestrial species, spending between 58% and 100% of the daylight hours on the ground (Fooden 2007). The Barbary macaque is a non-territorial species; the size of its home range varies greatly depending on geographic location, group size, season, and presence of neighbor groups. The “Middle Hill” group in Gibraltar had a home range of 0.25km² (Brauch et al. 2007); in Morocco and Algeria the home range varies from 1.8km² to a maximum of 12km² (Ménard and Vallet 1993b; Ménard et al. 2014a; Fooden 2007). There may be limited to extensive home range overlap between neighboring groups. In the Middle Atlas Mountains of Morocco, the average percentage of home range overlap of four groups was 35% (Majolo et al. 2013a) whereas in the Rif Mountains 85% of the home range of the study groups overlapped with that of other groups (Mehlman 1989). In the Rif Mountains, the average daily traveled distance of the monkeys was 1.43 km (Mehlman 1986).

As a possible consequence of some strong food availability seasonality, the Barbary macaque is a very eclectic forager (Ménard 2002; Ménard et al. 2014a). Macaques are known to eat more than 150 different plant species (Table 3); their primary food source is plant matter (fruit, leaves, seeds, roots, and flowers), which accounts for approximately 70%–90% of their diet (Ménard 2002). Macaques supplement their diet with insects,

spiders, small vertebrates, mealworms, and bird eggs (Fooden 2007; Young et al. 2012). Macaques also rely on low energetic food (e.g., bark and lichens) in areas where macaques compete intensively with livestock and during periods of low availability of other food sources (Ménard et al. 2014a).

Behavior

The Barbary macaque lives in multimale-multi-female groups (Ménard 2002), composed of individuals of different age classes (Table 1). Group size ranges from 9 to 88 individuals. The provisioned groups of Gibraltar are composed of around 40–80 individuals. In Djebela North Morocco, average group size was calculated to be 9.9 from nine groups (Waters et al. 2007). In the High Atlas Mountains of Morocco the average group size is 21 macaques (range 7–42; El Alami et al. 2013). The percentage of immature individuals in a group is around 50% (range 41%–62%; Ménard 2002). Groups usually fission when they reach the maximum sustainable group size in relation to the local availability of resources (Ménard and Vallet 1993b). In Algeria, adult females played a key role in group fission; maternally related macaques tended to stay in the same group following fission (Ménard and Vallet 1993b). During daylight hours, the Barbary macaques spend a significant proportion of time feeding, foraging, and traveling, and approximately 40% of the time resting or engaged in social behavior (Majolo et al. 2013). Their activity budget varies across the season (Fig. 6) and it is affected by climatic conditions and snow coverage (Majolo et al. 2013).

In the Barbary macaque, females are the philopatric sex and males are the dispersing sex (Thierry et al. 2004). Females stay in their natal group throughout their lives whereas males tend to emigrate to new groups when they reach sexual maturity and can continue to emigrate to new groups during their lives. There is no record of males forming bachelor groups. Barbary macaques experience both scramble and contest food competition (Thierry et al. 2004): scramble

Table 3 List of plant species eaten by the Barbary macaques (a: Deag 1974; b: Drucker 1984; c: Mehlman 1988; d: Ménard et al. 2014a)

Plant species (scientific name)	Food item						Reference
	Stem & bark	Leaf	Flower & strobilus	Fruit	Seed & acorn	Root, bulb & tuber	
<i>Abies pinsapo</i>	x	x	x		x		c
<i>Acer granatense</i>			x	x			b
<i>Acer monspessulanum</i>		x					d
<i>Acer opalus</i>		x	x				c
<i>Agropyron junceum</i>					x		d
<i>Agropyron marginatum</i>		x		x	x		a, c
<i>Agropyron panormitanum</i>		x		x	x		a, c
<i>Allium paniculatum</i>		x				x	c
<i>Alysum sp.</i>						x	d
<i>Ampelodesmos mauritanicus</i>	x	x					d
<i>Anthemis chia</i>			x				c
<i>Anthoxanthum odoratum</i>		x					c
<i>Arabis alpina caucasica</i>		x	x				d
<i>Armeria plantaginea</i>		x					d
<i>Arrhenatherum elatius</i>						x	d
<i>Asperula cynanchica</i>					x		d
<i>Asphodeline lutea</i>					x		d
<i>Asphodelus microcarpus</i>	x	x			x		d
Asteraceae		x	x		x		d
<i>Astragalus armatus</i>			x		x		c, d
<i>Atractylis sp</i>					x		d
<i>Avena macrostachya</i>					x		d
<i>Balansea glaberrima</i>		x				x	d
<i>Bellis perennis</i>	x						d
<i>Bellis sylvestris</i>		x	x			x	a, d
<i>Berberis hispanica</i>		x					c, d
<i>Biscutella laevigata</i>					c		c
<i>Bonium alpinum</i>						x	a
<i>Brassica gravinea</i>		x					d
<i>Brisa maxima</i>					x		d
<i>Bromus rigidus</i>					x	x	d
<i>Bromus squarrosus</i>					x		d
<i>Bromus sterilis</i>		x		x	x		a, c, d
<i>Bromus tectorum</i>		x		x	x		a, c
<i>Bunium alpinum</i>						x	d
<i>Bupleurum atlanticum</i>		x					d
<i>Calicotome spinosa</i>		x					d
<i>Cardamine hirsuta</i>		x				x	d
<i>Cardunculus pinnatus</i>					x		d
<i>Carduus nutans</i>		x			x		d
<i>Carlina atlantica</i>					x		d

(continued)

Table 3 (continued)

Plant species (scientific name)	Food item						Reference
	Stem & bark	Leaf	Flower & strobilus	Fruit	Seed & acorn	Root, bulb & tuber	
<i>Carlina corymbosa</i>					x		c
<i>Carthemis arborescens</i>					x		c
<i>Carum montanum</i>						x	d
<i>Catananche caerulea</i>	x	x			x	x	a, d
<i>Cedrus atlantica</i>	x	x	x	x	x		a, b, c, d
<i>Centaurea incana</i>		x				x	d
<i>Centaurea nana</i>		x				x	a
<i>Centaurea pullata</i>						x	a
<i>Centaurea tougourensis</i>					x		d
<i>Cephalanthera rubra</i>					x		d
<i>Cerastium gibraltarium</i>		x					d
<i>Cerastium glomeratum</i>		x					d
<i>Cerastium vulgatum</i>		x					c
<i>Chamaepeuce casabonae</i>		x				x	a
<i>Chenopodium murale</i>		x			x		c
<i>Chrysanthemum sp.</i>	x						d
<i>Cirsium acarna</i>		x			x	x	c
<i>Cirsium syriacum</i>		x			x		d
<i>Cotoneaster racemiflora</i>				x			d
<i>Crataegus laciniata</i>		x	x	x			a, b, c, d
<i>Crataegus monogyna</i>		x					b
<i>Crocus salzmannii</i>						x	c
<i>Crocus nudiflorus</i>						x	a
<i>Crocus nevadensis</i>						x	a
<i>Cruciata pedemontana</i>		x					d
<i>Cynara hystrix</i>				x	x		a
<i>Cynosurus echinatus</i>		x			x		c
<i>Cynosurus elegans</i>				x	x		a, c
<i>Dactylis glomerata</i>		x			x	x	c, d
<i>Daphne laureola</i>				x			c, d
<i>Dasyphyllum brevistaratum</i>					x		d
<i>Dianthus caryophyllus</i>		x			x		d
<i>Diploxaxis catholica</i>			x				d
<i>Erinacea anthyllis</i>		x					d
<i>Erodium sp.</i>						x	c, d
<i>Eryngium campestre</i>		x			c		c, d
<i>Erysimum bocconeii</i>		x				x	a, d
<i>Euphorbia characias</i>					x		c
<i>Ferula communis</i>		x					d
<i>Festuca geniculata</i>					x		d
<i>Festuca paniculata</i>				x	x		a
<i>Festuca triflora</i>		x		x	x		a, c

(continued)

Table 3 (continued)

Plant species (scientific name)	Food item						Reference
	Stem & bark	Leaf	Flower & strobilus	Fruit	Seed & acorn	Root, bulb & tuber	
<i>Ficaria verna</i>		x					d
<i>Gagea arvensis</i>						x	c
<i>Gagea foliosa</i>						x	d
<i>Galium perralderii</i>		x					d
<i>Genista tricuspidata</i>		x					d
<i>Geranium atlanticum</i>		x					a
<i>Geranium lucidum</i>		x					a
<i>Geranium malvaeflorum</i>		x					d
<i>Geranium molle</i>	x	x	x				a
<i>Geum sylvaticum</i>						x	a
<i>Geum urbanum</i>						x	a
<i>Hedera helix</i>		x		x			a, c, d
<i>Helictotrichon jahandiezii</i>	x						a
<i>Heracleum spondilium</i>	x						d
<i>Holcus lanatus</i>					x		c
<i>Hyoseris radiata</i>		x	x			x	d
<i>Hypochaeris laevigata</i>		x	x				d
<i>Hypochaeris radicata</i>		x	x				d
<i>Iberis sempervirens</i>		x					d
<i>Ilex aquifolium</i>		x	x	x			a, b, c, d
<i>Juniperus communis</i>			x				d
<i>Juniperus phoenicea</i>		x					b, c
<i>Juniperus oxycedrus</i>		x	x	x			a, b, c, d
<i>Juniperus thurifera</i>		x	x	x			b, d
<i>Jurinea humilis</i>		x					d
<i>Knautia arvensis</i>			x				d
<i>Lamiaceae sp.</i>		x					d
<i>Lactuca intricata</i>						x	d
<i>Lamium album</i>		x	x				c
<i>Linaria heterophila</i>		x			x		d
<i>Linaria sp.</i>							d
<i>Lobularia maritima</i>					x		c
<i>Lonicera biflora</i>		x					d
<i>Lonicera implexa</i>				x			d
<i>Lotus corniculatus</i>		x					d
<i>Luzula nodulosa</i>		x					d
<i>Mantisalca salmantica</i>		x			x		c, d
<i>Marrubium ayardii</i>						x	d
<i>Medicago falcata</i>						x	c
<i>Medicago minima</i>						x	c
<i>Medicago suffruticosa</i>	x	x	x			x	d
<i>Melica cupanii</i>					x		d
<i>Microlonchus salmanticus</i>	x						a

(continued)

Table 3 (continued)

Plant species (scientific name)	Food item						Reference
	Stem & bark	Leaf	Flower & strobilus	Fruit	Seed & acorn	Root, bulb & tuber	
<i>Moehringia trinervia</i>		x					d
<i>Muscari comosum</i>			x			x	a, c
<i>Muscari grandiflorum</i>			x				a
<i>Narcissus bulbocodium</i>		x				x	c
<i>Narcissus romieuxii</i>						x	d
<i>Narcissus tazeta</i>		x					d
<i>Onobrychis sp.</i>					x		d
<i>Ononis aragonensis</i>		x		x	x		d
<i>Onopordum acaulis</i>			x			x	d
<i>Ornithogalum tenuifolium</i>						x	c
<i>Ornithogalum umbellatum</i>						x	d
<i>Phagnalon saxatile</i>		x					d
<i>Phlomis bovei</i>		x					d
<i>Picnomon acarna</i>			x	x	x		a
<i>Pinus clusiana</i>	x	x	x		x		d
<i>Pinus pinaster</i>		x		x	x		c, c
<i>Plantago sp.</i>						s	d
<i>Poa bulbosa</i>		x		x	x	x	a, c, d
<i>Populus nigra</i>		x	x				d
<i>Prunus prostrata</i>				x			d
<i>Ptilostemon casabone</i>		x			x	x	c
<i>Quercus ilex</i>	x	x	x	x	x		a, b, c, d
<i>Quercus faginea</i>	x	x	x	x	x		b, c
<i>Raffanaldia primuloides</i>						x	a
<i>Ranunculus calandrinioides</i>						x	a
<i>Ranunculus muricatus</i>			x				c
<i>Ranunculus rupestris</i>						x	a
<i>Ranunculus paludosus</i>			x				a
<i>Rhamnus alaternus</i>				x			d
<i>Ribes grossularis</i>		x		x			d
<i>Romulea bulbocodium</i>						x	a, c
<i>Rosa canina</i>		x		x		x	c
<i>Rosa pouzinii</i>	x	x	x				a, b
<i>Rubus sp.</i>	x	x		x			b, d
<i>Rumex acetosella</i>		x					d
<i>Rumex bucephalophorus</i>					x		d
<i>Ruscus aculeatus</i>		x		x			d
<i>Salvia argentea</i>			x				d
<i>Salvia verbenaca</i>		x					c
<i>Sanguisorba minor</i>		x					c
<i>Saponaria sicula</i>		x					d
<i>Saxifraga granulata</i>	x		x				a, c

(continued)

Table 3 (continued)

Plant species (scientific name)	Food item						Reference
	Stem & bark	Leaf	Flower & strobilus	Fruit	Seed & acorn	Root, bulb & tuber	
<i>Saxifraga globulifera</i>		x					d
<i>Saxifraga numidica</i>		x					d
<i>Scandix australis</i>		x					d
<i>Scilla sp.</i>					x	x	d
<i>Scolymus grandiflorus</i>					x		d
<i>Sedum album</i>		x	x				a, c
<i>Sedum multiceps</i>	x						d
<i>Senecio gallicus</i>		x					d
<i>Senecio perralderianus</i>		x					d
<i>Silene italica</i>			x		x		d
<i>Silene vulgaris</i>		x			x		c, d
<i>Smyrniolum olusatrum</i>						x	d
<i>Smyrniolum perfoliatum</i>		x				x	d
<i>Sorbus torminalis</i>		x		x			b, d
<i>Stellaria media</i>	x	x	x				a, c
<i>Sternbergia colchiciflora</i>						x	c
<i>Taraxacum obovatum</i>		x					d
<i>Taraxacum officinale</i>		x	x				c
<i>Taxus baccata</i>			x	x			b, c, d
<i>Teucrium flavum</i>		x					d
<i>Teucrium polium</i>		x					c
<i>Thapsia villosa</i>	x	x				x	a, c
<i>Thlaspi perfoliatum</i>	x						d
<i>Thymelaea virgata</i>	x					x	d
<i>Torilis arvensis</i>						x	a
<i>Torilis elongata</i>		x					d
<i>Trifolium campestre</i>			x				d
<i>Trifolium hirtum</i>		x					d
<i>Trifolium phleoides</i>			x				d
<i>Triticum sp.</i>					x		d
<i>Tulipa sylvestris</i>	x	x				x	a, d
<i>Umbilicus pendulinus</i>		x					d
<i>Umbilicus rupestris</i>		x					a
<i>Valeriana tuberosa</i>						x	a, d
<i>Veronica hederifolia</i>	x	x	x				a, d
<i>Viburnum lantana</i>		x					d
<i>Vicia onobrychoides</i>	x	x					a
<i>Viola sp.</i>						x	d
<i>Vulpia geniculata</i>				x	x		a

competition occurs when macaques, either belonging to the same group or from different groups, feed on the same food source at different time intervals with no direct interaction between

the competing animals. Contest competition occurs when macaques aggressively compete over access or monopolization of a food source. Contest competition is often observed over rare

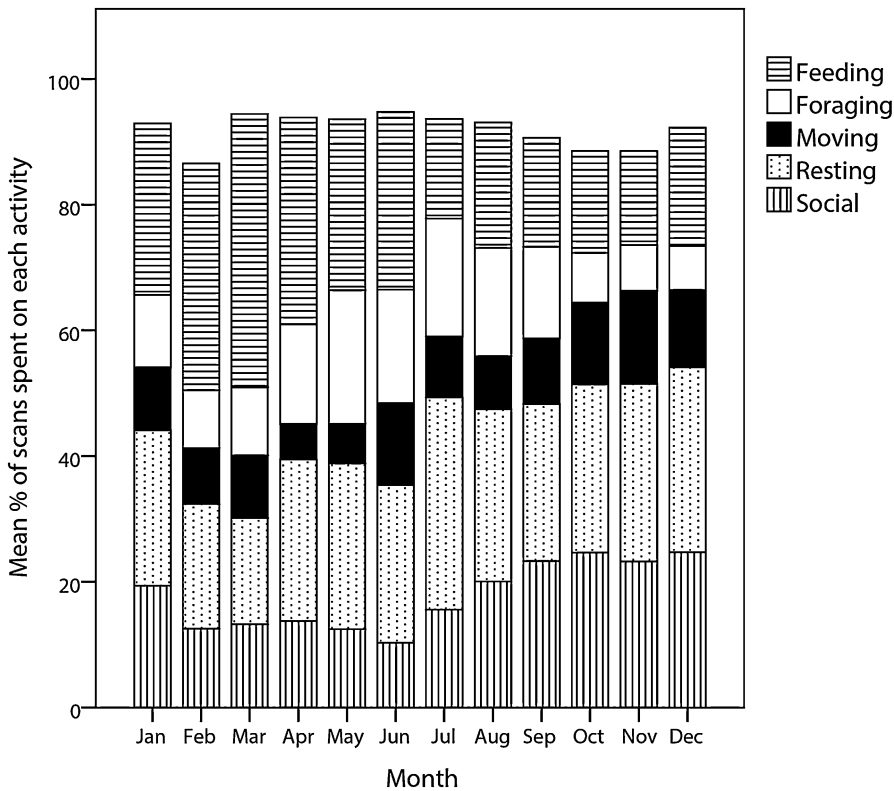


Fig. 6 Activity budget of the Barbary macaque. Mean monthly percentage of times the Barbary macaques spent on each activity during the year in the Middle Atlas Mountains, Morocco, calculated for the period June 2008–

January 2011 from four groups of macaques. (From Majolo et al. (2013) with permission from Springer Nature)

and/or energetically rich food sources. Interactions between neighbor groups are often neutral, but macaques from different groups may exchange aggressive display from a distance or physical aggression involving bites in 20–50% of between-group encounters (Deag 1973; Mehlman 1986).

The personality of Barbary macaques has been studied in the Gibraltar population and in the wild in Morocco (Konečná et al. 2012; Adams et al. 2015). Four dimensions appear to describe personality in this species: Friendliness, Activity/Excitability, Confidence, and Opportunism. Barbary macaques have a complex range of facial and body displays, vocal and gestural communication during feeding and social interactions with other group members and/or other social groups (Hesler and Fischer 2007).

During the mating season, intra- and intersexual competition for mating partners is observed in the Barbary macaque (Small 1990). Females mate promiscuously but also show mate choice, preferentially consorting prime males (Bissonnette et al. 2011). Males compete for estrous females and form male–male coalitions to increase their reproductive success. The interplay of male and female reproductive strategies results in a low reproductive skew in the Barbary macaque (Bissonnette et al. 2011). Indeed, in Gibraltar there is no difference in male and female reproductive success between dominant and subordinate macaques (Kümmerli and Martin 2005). However, in Morocco dominant males have greater mating success than subordinates (Young et al. 2013b).

The Barbary macaque is one of the few primate species where there is extensive infant care from adult males. Males appear to selectively choose

specific infants to interact with (Ménard et al. 2001; Kubenova et al. 2017). Interactions between adult males and infants involve infant carrying, grooming, and protection of the infant from danger (e.g., predators) and aggressive group members (Taub 1980). Infant care from adult males may be a form of parental investment (Trivers 1972), whereby males preferentially care for infant that is likely to be their own offspring. However, Barbary macaque males do not seem to preferentially care for infants that are their own (Paul et al. 1996; Ménard et al. 2001). Alternatively, males may care for infant to increase their mating opportunities in the future, if females preferentially mate with males who provide infant care (Ménard et al. 2001). Triadic male–infant–male interactions, where two males jointly manipulate an infant, are also frequently observed in the Barbary macaques (Taub 1980). Triadic male–infant–male interactions allow males to form social bonds with other group males while reducing the risk of aggression from those males due to the presence of infant, that is, infants function as “social buffers” (Deag and Crook 1971; Paul et al. 1996; Kubenova et al. 2017).

Barbary macaques establish differentiated social relationships with their group companions, varying from overly aggressive and competitive interactions to strong social bonds. The main affiliative/friendly behaviors that Barbary macaques use to establish and maintain social bonds are grooming exchange (the picking through and/or slow brushing aside the fur of another individual with one or both hands), feeding in proximity, huddling, and agonistic support (e.g., McFarland and Majolo 2011a; Young et al. 2014a). Social bonds give a number of benefits to individuals, including increased chances to survive cold winters, improved resilience to stressors, coalition formation against competitors, reconciliation, and increased thermoregulation (McFarland and Majolo 2011c; McFarland and Majolo 2013b; Young et al. 2014b; Campbell et al. 2018). Aggression and competition between group members is relatively common, especially during the mating season or during periods of

food shortage. The majority of aggressive interactions does not involve physical contact but can sometimes result in severe injuries; agonistic support and coalitions are often observed during these aggressive interactions (Bissonnette et al. 2009; Young et al. 2014a). Barbary macaques display a range of post-conflict interactions, from renewed aggression or reconciliation between former opponents (Aureli and de Waal 2000) to third-party affiliation (McFarland and Majolo 2012; McFarland and Majolo 2013a). Grooming, huddling, proximity, lip-smacking, and social play are some of the main behaviors used to analyze reconciliation and third-party affiliation in the Barbary macaque (Patzelt et al. 2009; McFarland and Majolo 2013a).

Species of the genus *Macaca* have been organized into four different categories (grades) depending on their dominance style; such grading system has been proposed to describe differences across macaque species in the type of social interactions females have with other females in their social group (Thierry 2000; Thierry et al. 2004). According to this grading system, species belonging to Grade I (e.g., the Japanese macaque, *Macaca fuscata*) are described as being “despotic”: female macaques in this grade form steep dominance hierarchies where the outcome of a dyadic conflict between two females is predicted by their dominance rank; thus dyadic conflicts should always/often be “decided” (have a clear winner/loser). There should be a low frequency of counter-aggression in despotic species. Moreover, there should be a high degree of kin-bias in grooming, coalition, and aggression whereby females should preferentially bond with their kin females (their matriline) and be aggressive toward group females belonging to other matrilines. As a consequence of this, females from the same matriline should all rank close together in the dominance hierarchy. At the opposing end of the system, in Grade IV, “tolerant” species (e.g., Tonkean macaques, *Macaca tonkeana*), females should have a shallow hierarchy where the outcome of dyadic conflicts is context-dependent and does not only depend on the dominance rank of

the female opponents, counter-aggression should be frequent and there should be a low degree of kin-bias in grooming, coalitions, and aggression. The Barbary macaque is considered relatively tolerant species (i.e., Grade III; Thierry 2000). However, the Barbary macaques also share some social traits that are typically observed in more despotic species. For example, in wild macaques living in the Middle-Atlas Mountains of Morocco only 5% of conflicts were undecided and less than 4% resulted in counter-aggression (McFarland and Majolo 2011b, 2011c). In the same population, females present a steep and linear dominance hierarchy (Kaburu et al. 2012). Indeed, species belonging to Grade III and IV may not be easily categorized into this four grading system (Balasubramaniam et al. 2012) and it is not clear whether the same dominance gradients can be used to describe male–male social interactions across macaque species.

Parasites and Diseases

Barbary macaques are susceptible to similar zoonotic pathogens as other macaque species, including rabies or Tuberculosis (Honest et al. 2006). However, only some pathogens have been reported in the species (Table 4). Limited information on parasites and pathogens is available for wild populations in Morocco and Algeria. This is particularly problematic as primate tourism and associated close interactions between humans and macaques are growing, increasing the risks for potential pathogen transmission between the two species (Carne et al. 2017).

Population Ecology

According the latest CITES report (September 2016), the overall population of Barbary macaque in Morocco and Algeria is estimated between 6,500–13,500 individuals, 7– <10 individuals per km². This estimation varies considerably between geographic regions and surveys. In

Table 4 Summary of recorded parasites and infections in Barbary macaques, in zoos, semi-free ranging conditions, and in the wild

Parasites and infectious diseases			References
Endoparasites	Protozoa	<i>Entamoeba coli</i> , <i>E. histolytica/dispar</i> , <i>E. hartmanni</i> , <i>E. polecki</i> , <i>Iodamoeba butschlii</i>	Borg et al. (2014)
	Helminths	<i>Trichostrongylus</i> spp., <i>Trichuris</i> spp., <i>Physaloptera</i> sp., <i>Dicrocoelium</i> spp., <i>Strongyloides</i> spp., <i>Ascaris</i> spp., <i>Capillaria</i> spp., <i>Oesophagostomum</i> spp., <i>Ancylostoma</i> spp., <i>Necator</i> spp.	Canelli et al. (2010), Borg et al. (2014), Müller et al. (2017)
Ectoparasites	Phthiraptera	Anoplura <i>Pediculus</i> sp.	Cohn et al. (2007)
Infectious diseases	Virus	Distemper virus (<i>Paramyxoviridae</i> , <i>Picornaviridae</i>), hepatitis, simian foamy virus, West Nile virus, Encephalomyocarditis virus, cowpox virus, simian virus 40	Martin (1950), de Turckheim and Merz (1984), Ølberg et al. (2004), Honest et al. (2006), Martina et al. (2006), Engel et al. (2008), Verschoor et al. (2008), Cardeti et al. (2016)
	Bacteria	<i>Salmonella</i> spp., <i>Staphylococcus aureus</i> , <i>Shigella</i> spp., <i>Escherichia coli</i> , <i>Klebsiella pneumoniae</i>	de Turckheim and Merz (1984), Banish et al. (1990) Bachiri et al. (2017)
	Meningitis	Unknown	de Turckheim and Merz (1984)
	Pneumonia	Unknown	
	Peritonitis	Unknown	
	Colitis Cystica superficialis	Unknown	Scott (1978)

Morocco, the population is estimated between 5,000–6,000 individuals, 7 individuals per km² (Lowest estimate provided by van Lavieren and Wich 2010), while other studies suggest that the population is between 8,000–9,000 individuals, <10 individuals per km². This highest estimate in Morocco is for the sub-population of the Middle Atlas Mountains, estimated at 5,000 individuals, 9 individuals per km² (Ménard et al. 2014b), in addition to 1,000 individuals from the High Atlas Mountains, and up to 2,000 individuals from the Northern sub-population of the Rif area (based on recent surveys by Waters et al., unpublished data). In Algeria, the current overall population is unknown (Benrabah 2015). The population in Gibraltar is maintained to around 200 individuals (Shaw, pers. comm.) and it is regularly monitored.

Although the population estimation varies, all experts agree that the wild population of Barbary macaques has dramatically declined since early 1980s from an estimated figure of up to 23,000 individuals (Fa et al. 1984) to fewer than 13,500 individuals in 2016 (CITES 2016). An increase in systematic population surveys across the Barbary macaque range in Morocco and Algeria would give a more accurate estimate of the state of the overall population.

Very little is known about interspecific interactions (e.g., feeding association) with other mammals. Barbary macaques feed on a number of animal species (see section “Life History” above). African wolves, large raptors, golden jackals, and red foxes are all believed to occasionally prey on Barbary macaques: macaques often give alarm calls when spotting these potential predators but direct observations of attacks have never been reported with the exclusion of dogs. In the Middle Atlas Mountains of Morocco several attacks of dogs to macaques have been observed and at least three attacks have resulted in the disappearance or death of the attacked macaque (Majolo & Maréchal unpublished data).

There are not enough detailed records to link climate change and global warming to changes in the population ecology and feeding behavior of the Barbary macaques. However, global warming is expected to prolong the draught period that

macaques experience during the summer and make winter and summer temperatures more extreme. For example, at two sites in Algeria (Tigounatine and Akfadou), the mean annual precipitation decreased from 1205 mm in the period 1914–1938 to 800 mm in the period 1968–1976 (Ménard and Vallet 1993a). In an exceptionally harsh and snowy winter in the Middle Atlas Mountains, in 2008/2009, resulted in the death of approximately half of the adults in two groups of Barbary macaques (McFarland and Majolo 2013b).

Conservation Status

Barbary macaques have been listed in Appendix II of the Convention on International Trade in Endangered Species for the first time in 1975, and listed in Annex B of the European Union Council Regulation in 1997 (CITES, EC 338/97, Annex B). However, the status of the species has recently been upgraded to Appendix I (CITES 2017) due to the steady population decline estimated in recent years. In 2008 the Barbary macaque was classified for the first time as ‘Endangered’ by the International Union for Conservation of Nature (IUCN) (Wallis et al. 2020). The species is also listed on the Wildlife Trade Regulation of the European Union (EU, L27/60, 1 February 2017). Overall, these international legislations aim to increase the protection of the species within its natural habitat as well as limit trade that seriously affects the species recovery.

In Gibraltar, the macaque population is managed by the Gibraltar Ornithological & Natural History Society (GONHS) and the Gibraltar Veterinary Clinic under agreements with the Government of Gibraltar, and is protected by Gibraltarian and EU laws. In Algeria the Barbary macaque is protected under the Executive Decree No. 83-509 (20 August 1983), and the Executive Decree No. 12-235 (24 May 2012), which list all protected non-domesticated animal species. Such conservation status prohibits poaching, capture, poisoning of the species, as well as define the modality for the protection of the species in its natural habitat. However, despite its classification

as endangered species by the IUCN (Wallis et al. 2020), to date the Barbary macaque is not listed as endangered in the Ordinance No. 06-5 (15 July 2006), which would provide the highest protection status of the species in Algeria (Bergin et al. 2018). Therefore, this limits the protection of the species at a national level. An action plan for the conservation of the Barbary macaque in Algeria has recently been published (Alcazar et al. 2019).

In Morocco, the Barbary macaque has been protected under the agricultural minister Decree since 1962, prohibiting capture, hunting, possession, and sale. In addition, the trade of this species is protected under Moroccan Act No. 29-05 (June 2015), which gives legal protection for the species against importation, capture, sale, offer for sale, or killing without a specific license (Van Uhm 2016). Recently the Action Plan for the Conservation of the Barbary in Morocco has been developed by the Haut Commissariat des Eaux et Forêt et à la Lute Contre la Désertification to implement measures to protect the species in Morocco (Moroccan Primate Conservation Foundation 2012).

In Morocco and Algeria habitat destruction due to farming, overgrazing and logging is the main threat for the Barbary macaque. The human–macaque conflict is intense in some parts of Morocco and Algeria and the illegal trade of Barbary macaques is a major concern for the conservation of the species (Van Uhm 2016).

Management

The management of the Barbary macaques is highly related to their relationships with humans (local communities, government, and tourists). These relationships range from very positive to confrontational, and the development of strategies to reduce human–macaque issues and improve positive attitude toward the Barbary macaque are at the core of the management strategy of the species. Throughout their range Barbary macaques often come into contact with humans, particularly with tourists and shepherds, and with shepherds and stray dogs (Waters et al. 2017; Waterman et al. 2020).

The two major threats to the Barbary macaque are habitat loss and degradation, and illegal trade (Wallis et al. 2020). Habitat degradation and over-use by local people lead to an increase in human-primate competition, which are the main factors of the rapid decline of the species. This competition over resources between Barbary macaques and local communities has been reported in Gibraltar, Morocco, and Algeria. Groups of Barbary macaques living at the edge of forests have been reported crop foraging in Morocco (El Alami et al. 2013) or town-foraging in Gibraltar (Perez and Bensusan 2005). Macaques living in oak-cedar forests have been observed bark-stripping creating issues with the forest exploitation industry and forestry authorities in Morocco (Ménard and Qarro 1999; Ciani et al. 2001). In addition, the populations of Barbary macaques live in fragmented forests that are steadily shrinking in size because they are used by shepherds and local communities for their livestock, resulting in overgrazing and fire wood collection (Ciani et al. 2001, Majolo et al. 2013b). The competition over forest between the Barbary macaques and humans explain why this species was considered as pest in some regions in Morocco and Algeria. There, several culls were undertaken to manage the populations of Barbary macaques and reduce their damage before the laws to protect the species were implemented. Recently, translocation plans of macaque groups from farming/living areas to more remote locations or zoos have been considered to reduce conflicts with the local people, but such management solutions have rarely been implemented. One of the few examples of translocation happened in 2015, where a group of macaques were translocated from Gibraltar to a zoo in Scotland (BBC 2014). Translocations to zoos are a debated strategy to save this species in the wild. Moreover, translocations in more remote areas may not be an effective/viable conservation tool for a species those habitats are on the decline.

The illegal trade is another significant factor for the decline of the Barbary macaque in Morocco (van Lavieren 2008; Bergin et al. 2018) and Algeria (Bergin et al. 2018), where young macaques are often sold to national and international tourists in open markets and online.

Sustained efforts are made by governments and NGOs to reduce such trade, but the interest in buying and selling Barbary macaques remain a serious concern for its conservation.

Despite human–macaque coexistence issues reported in all three countries, the Barbary macaque is perceived with pride and a sense of ownership by some local people in Gibraltar (Radford et al. 2018) and with great curiosity and interest by shepherds in Morocco (Waters et al. 2017). In Algeria several places are named after the monkey presence stating the environmental importance of the macaque for the local communities. Barbary macaques can also be perceived by the local community as positive (El Alami and Chait 2015), as they are often related to tourism and the potential benefits in lower-income mountainous regions. For example, with 700,000–1,000,000 visitors per month (GONHS 2018), Gibraltar is the primate tourism hotspot of the endangered and emblematic Barbary macaque. Barbary macaques live freely on the Upper Rock of Gibraltar, which allows visitors to see these animals without any physical barriers. Visitors are commonly observed interacting too closely with the macaques, taking pictures/selfies touching/petting the macaques, or giving food to them, despite these behaviors having negative impacts on macaque welfare, and the latter behavior being prohibited (Perez and Bensusan 2005). To visit the natural reserve in Gibraltar where the macaques are located, a fee is requested (GONHS 2018). After Gibraltar, Morocco is the second most popular destination to encounter wild Barbary macaques, followed by Algeria with a mainly local tourism and occurring at a much lower rate in comparison to Gibraltar and Morocco. Primate tourism in Morocco and Algeria is currently unregulated, and there is no fee to go to see the Barbary macaque in its natural habitat.

Recently, there have been plans to develop regulated primate tourism in Morocco and Algeria as a tool for the conservation of the species. Primate tourism is a growing industry, which has the potential to benefit the local and national economy, and the conservation of endangered species, by increasing positive public awareness and financial support to conservation efforts. However,

serious concerns for animal welfare need to be taken into consideration for primate tourism to be beneficial. Indeed, the negative impacts of unregulated tourism on wildlife and Barbary macaques have been well documented (Moroccan Primate Conservation Foundation 2012, Majolo et al. 2013b; Maréchal et al. 2016a). The presence of tourists and their frequent close interactions with the macaques can affect the behavior of the animals, leading to a reduction in social behavior and an increase in aggressive behavior in the macaques (Majolo et al. 2013b, El Alami et al. 2013; Maréchal et al. 2016b). Some serious negative impacts on the metabolism and body condition of Barbary macaques have also been reported (see details section “[Physiology](#)”).

Future Challenges for Research and Management

In Gibraltar the regulations in place seem to provide an effective means to manage the population of Barbary macaques. Research is challenging on the Gibraltar Rock, due to the steep terrain that makes it difficult to follow the macaques for research purposes. However, with its high competition for space between humans and the Barbary macaque, management strategies and eco-tourism programs, Gibraltar can be at the forefront of research on effective strategies to manage and protect nonhuman primates.

Future challenges for the management of the Barbary macaque populations in Morocco and Algeria will be to fully integrate the species as part of the management and protection of the environment by finding a compromise between habitat usage by humans and the macaques (Waterman et al. 2020). To do so, Morocco and Algeria are each developing a conservation action plan for the conservation of the Barbary macaque. The main actions of these plans will be to increase scientific research on the Barbary macaque behavior and ecology, and conducting systematic population surveys across the Barbary macaque range to have a more accurate estimate of the status of the species. The application of international and national protection laws is currently limited and

has yet to mitigate the threats to the species, which continues to dramatically decline. However, NGOs and other governmental organizations have developed some local projects to improve the conservation of the Barbary macaque in Morocco and Algeria.

These projects can help develop effective tourism management that takes place in areas inhabited by the Barbary macaques. Reducing or removing the feeding of macaques by tourists should mitigate the impacts related to stress and reduce the risks of zoonotic and diet-related diseases.

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