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Behavioral adjustments of endangered Barbary macaques (*Macaca sylvanus*) living at the edge of an agricultural landscape in Morocco

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Abstract

Transition zones between natural and human-altered spaces are eroding in most terrestrial ecosystems. The persistence of animals in shared landscapes depends in part on their behavioral flexibility, which may involve being able to exploit human agricultural production. As a forest-dependent species, the Barbary macaque (*Macaca sylvanus*) is affected by the progressive conversion of forest-adjacent lands into crops. We explore how Barbary macaque behavior differs between groups living in a forest at the edge of agricultural zones (hereafter “disturbed groups”) and groups inhabiting undisturbed forests (hereafter “natural groups”). We compare the diets, activity-budgets, home range sizes, daily path lengths, and sleeping site locations of the groups. We also quantify anthropogenic disturbances (i.e., rates of encounter with humans and dogs) and investigate relationships between such disturbances and the diets and activity budgets of macaques through multiple co-inertia analysis. Disturbed groups included high proportions of cultivated food items in their diet and encountered over 0.5/h anthropogenic disturbances. Activity-budgets differed between disturbed and natural groups and were mostly influenced by diets, not anthropogenic disturbances. Disturbed groups spent more time feeding and less time resting than natural ones. Patterns of space use differed markedly between groups, with disturbed groups displaying smaller home ranges, shorter daily path length, and much higher reutilization of sleeping sites than natural groups. This study highlights the dietary and behavioral flexibility of Barbary macaques living in human-altered environments. Their patterns of space use suggest a reduction in energy expenditure in the disturbed groups due to the inclusion of cultivated food items in their diet possibly leading to increased foraging efficiency. However, the high rates of anthropogenic encounters, including aggressive ones, are likely stressful and may potentially induce extra energy costs and lead to macaque injuries. This could result

Abbreviations: MCOA, multiple co-inertia analysis; PCA, principal component analysis.

Nelly Ménard and Pascaline Le Gouar should be considered joint senior author.

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in demographic costs for crop-foraging groups, threatening the conservation of this endangered species.

KEYWORDS

activity-budgets, anthropogenic pressure, crop-foraging, diets, Macaques, space use

1 | INTRODUCTION

Human activities are affecting most of the world's biodiversity (Boivin et al., 2016), and anthropogenic pressures such as agriculture, logging, and livestock ranching are leading to extensive loss of natural habitats. In response to those high pressures, animals may rely on their behavioral flexibility to survive in modified and degraded habitats, which often translates into modifications in diets, ranging patterns, activity-budgets, and social behaviors (Fehlmann et al., 2020). Agricultural activities represent an important part of those anthropogenic pressures, with croplands and pastures alone occupying about 40% of terrestrial surface and agriculture being responsible for about 80% of deforestation worldwide (Foley et al., 2005; Hosonuma et al., 2012). Such a loss of natural resources is a major threat to biodiversity globally (Newbold et al., 2015). However, the expansion of agricultural lands also brings new food resources to some wildlife species which are able to exploit them. Agricultural food resources are often energetically rich, abundant, clumped and predictable in both space and time, and may thus offer advantages over natural foods and improve foraging efficiency (Saj et al., 1999; Strum, 1994). This results in energetic advantages which have been linked to shorter interbirth intervals, reduced infant mortality, and shorter weaning time (baboons, *Papio* sp.: Higham et al., 2009; Strum, 2010; Tonkean macaques, *Macaca tonkeana*: Riley et al., 2013), as well as better body condition (hedgehogs, *Paraechinus aethiopicus*: Abu Baker et al., 2017), and increased animal densities (coyotes, *Canis latrans*: Fedriani et al., 2001). The consumption of agricultural foods has been shown to influence activity budgets, often resulting in a higher proportion of time spent resting and a lower proportion of time spent foraging or feeding (Buton macaques, *Macaca ochreata brunnescens*: Priston, 2005; vervet monkeys, *Chlorocebus aethiops*: Saj et al., 1999; baboons: Strum, 1994; Warren et al., 2010). The consumption of agricultural foods also influences ranging behaviors: when consuming energy-rich human foods, animals will often be able to reduce the size of their home-range compared to their wild-foraging counterparts (hedgehogs: Abu Baker et al., 2017; Eurasian badgers, *Meles meles*: Davison et al., 2009; vervet monkeys: Saj et al., 1999), as well as their daily path length (hedgehogs: Abu Baker et al., 2017; chacma baboons, *Papio ursinus*: Hoffman & O'Riain, 2012). In nonhuman primates (henceforth, primates), macaques, baboons and vervet monkeys, with their high dietary and behavioral flexibility, are particularly successful at exploiting agricultural food resources (Hill, 2017). Crop-foraging primates may therefore be considered as agricultural pests, which represents a threat to their effective conservation when they are

endangered and protected species. There is thus an urgent need to understand the behavior of crop-foraging primates, and their capacity to adapt and survive in human-modified landscapes.

The Barbary macaque is an endangered (Wallis et al., 2020) forest-dwelling monkey inhabiting temperate mountainous forests. Seventy-five percent of the world's Barbary macaque population inhabits the Middle-Atlas Mountains of Morocco, where forest-adjacent lands are increasingly being converted into agricultural lands (Kouba et al., 2018). Barbary macaques have high behavioral and dietary flexibility and are able to colonize peri-urban areas where they consume human foods, and to forage in crops when these areas are located at the interface with forested habitats (Maibeche et al., 2015). In this study, we examine how including human derived foods in agricultural land influences aspects of the behavior and movement of Barbary macaque groups living in an evergreen cedar-oak forest at the edge of agricultural zones in the Middle-Atlas in Morocco. We hypothesize that agricultural foods are an important part of the groups' diets, which influences their activity-budgets and ranging behaviors. To test this hypothesis, we compare the diets, activity-budgets and patterns of space use of three crop-foraging groups with two wild-foraging groups inhabiting forests without access to agricultural lands in Algeria. Like in other species foraging on agricultural resources, we expect crop-foraging Barbary macaques (i) to spend less time feeding and foraging, and more time resting and socializing than their wild-foraging counterparts (Priston, 2005; Saj et al., 1999; Strum, 1994; Warren et al., 2010), (ii) to display smaller home ranges (Abu Baker et al., 2017; Davison et al., 2009; Saj et al., 1999) and shorter daily path length (Hoffman & O'Riain, 2012), and (iii) to display a more predictable utilization of sleeping sites (Altmann & Muruthi, 1988; Strum, 2010). We also investigate whether the activity-budgets and diets of the groups are influenced by disturbances associated with humans and domestic dogs.

2 | METHODS

2.1 | Sites, study periods, and subjects

One study site was located at the interface of an indigenous evergreen cedar-oak forest (*Quercus rotundifolia* and *Cedrus atlantica*) and agricultural lands near Aïn Leuh (5° 20'W, 33° 18'N; 1400–1700 m altitude; mean annual minimum and maximum temperatures: 9.5°C and 21.1°C, respectively; mean annual rainfall: 830 mm), a rural village in the Middle-Atlas Mountains, in the Ifrane Province of Morocco. Observations at this site took place in the fall

(October–November) of 2021, and in the spring (May–June) and summer (July–August) of 2022. The agricultural areas, located on the edge of the forest, included mainly orchards, with 14.2 ha of cherry and walnut trees, and 0.2 ha of cereal fields. Walnuts in Aïn Leuh had been harvested in September 2021, but some remained on trees in private gardens until early November. In 2022, unripe walnuts were available in the orchards from June, and became ripe in August. Cherries were mature by the end of May 2022, and were harvested in June. A lot of cherries remained in the trees in July, and were left to rot on the ground in August. Orchards were intensely guarded in May, until cherry harvest started in early June. Crops in Aïn Leuh are a recent development, as most of them were planted in the last decade, replacing open areas traditionally used as extensive pastures for domestic livestock. This site was characterized by high human presence, in agricultural areas as well as in the forest where shepherds led sheep to graze. It is hereafter referred to as the “disturbed site.” According to a vegetation map from a consulting agency (Sogreah-Ttoba, 2004), the evergreen cedar-oak forest comprised about 80% of mature forest and 20% of pure oak coppices (<5 m high). The two other study sites were located in Algeria: in a deciduous oak forest (*Quercus faginea* and *Q. afares*, Akfadou, 4°33'E, 36°27'N; 800–1300 m altitude; mean annual minimum and maximum temperatures: 9°C and 21.1°C, respectively; mean annual rainfall: 600 mm) and in an evergreen cedar-oak forest (*C. atlantica* and *Q. ilex*, Tigounatine, Djurdjura National Park; 4°8'E, 36°27'N; 1200–1900 m altitude; mean annual minimum and maximum temperatures: 4.5°C and 16.3°C, respectively; mean annual rainfall: 1000 mm). At the time of observations (1983–1984), they were both well-preserved forests, with very little human and cattle presence, and no cultivated areas nearby. The study site in Akfadou comprised 93% forest, 5% scrub, and 2% grassland (Ménard & Vallet, 1988). The Tigounatine study site comprised 74% forest (including 10% of pure oak coppices), 2% scrub and 24% grassland (Ménard & Vallet, 1988). The Akfadou and Tigounatine sites are hereafter referred to as “natural sites.”

We studied three groups in the disturbed site. Group Depog was the main focal group in which all members were individually identified. We followed this group in the fall of 2021 and in the spring and summer of 2022. It comprised 28 individuals in 2021 and 26 in 2022. The difference was due to the disappearance of three adult females and two immatures, while three infants were born. We followed group Houquette only in the fall of 2021, as we could not find it again in the following spring. It comprised 37 individuals. We followed group Felix, which comprised about 35 individuals, only in 2022. Individuals in groups Houquette and Felix were not individually identified. We followed one focal group in each of the two natural sites in 1983 and 1984. All members were individually identified in both natural sites and, as in the disturbed site, observations covered three seasons: spring (May–June), summer (July–August) and fall (October–November). In Akfadou, the group comprised 38 individuals in 1983 and 41 in 1984. In Tigounatine, the group comprised 46 individuals in 1983 and 47 in 1984.

2.2 | Data collection

During observation sessions, we used “instantaneous scan sampling” (Altmann, 1974) every 15 min to record the activity of five individuals. To avoid bias on activity records, we chose the first individual randomly and observed the others from a right to left direction from the first one. We recorded scans on all individual categories excluding infants (<1-year-old). We divided activities into five mutually exclusive behavioral categories: foraging (i.e., searching for food items, including turning over stones, digging into the ground, searching beneath litter, hunting insects, and cleaning plant items), feeding (i.e., actually ingesting food items), moving (i.e., any type of locomotion that was not associated with another activity), resting (i.e., all inactive postures not associated with another activity), and socializing (i.e., all interindividual affiliative or agonistic interactions). During feeding bouts, we recorded consumed food items. We recorded a total of 7185 scan records in the disturbed site over 887 h of observation, 6703 scan records in the natural Akfadou site over 536 h of observation, and 7272 scan records in the natural Tigounatine site over 558 h of observation. We also recorded all occurrences of macaques being disturbed by humans or domestic animals (dogs and/or cattle).

We recorded the location of the groups every 30 min during observation sessions. In the disturbed site, we recorded locations by global positioning system (GPS) with an uncertainty of about 5 m. In the natural sites, we mapped group locations using a grid system of 50-m quadrats whose intersections were physically marked on the study areas with paint. This grid system allowed us to develop a useful artificial North/South and East/West coordinates system which made it possible to record the position of each group with a maximum uncertainty of about 15 m. We then reported these coordinates on 1/50,000 topographic maps using topographic markers. We later converted the topographic maps and those artificial coordinates into GIS coordinates. In all sites, we conducted observations each month to get activity and location records equally distributed among hours from dawn to dusk.

2.3 | Data analysis

2.3.1 | Diets and activity patterns between sites and months

We estimated diets and activity-budgets of the groups from the scans. We identified consumed food items at the species level. Because species differ between habitats, we grouped food items into broad categories based on their relative importance in the macaques' diets for comparison between sites. In the natural sites, we estimated monthly diets and time budgets as an average over 2 years for certain months (May and June in Akfadou, and May, June and October in Tigounatine). Because the diets and activity-budgets of Barbary macaques differ between age and sex classes (Ménard & Vallet, 1997), we calculated, for each group, mean monthly diets, and activity-budgets as the

weighted mean of three separate age-sex classes: adult females (>4 year-old), adult males (>5 year-old) and immatures (excluding infants <1-year-old), based on a “standard” group composition of this species, which is about 25% adult females, 25% adult males, and 50% immatures (Ménard, 2002). Diet compositions are presented as a percentage of the feeding time spent eating each category of food. To take into account the huge variation in monthly day length (10–15 h), activity-budgets are presented as a number of hours spent in each activity over a 24-h period, assuming that the macaques were not active (i.e., resting) during unobserved nighttime periods. Total resting time thus includes both diurnal and nocturnal rest.

For all statistical analyses, we converted activity-budgets into continuous proportions of time over 24 h. To examine the effects of the type of site (disturbed or natural site) on diets and activity-budgets, we used generalized linear mixed models (GLMM, Baayen et al., 2008) with beta error structure and logit link function. We ran one model for each activity, and for each food category which was consumed in both types of site. In each model, in addition to the type of site, we included the month and type of site * month interaction as fixed effects, and the site and group as random effects. To control for a possible effect of group size on diets and activity-budgets, we included group size (excluding infants) as a control predictor. Whenever a model included a significant interaction of type of site and month, we ran post hoc Tukey's tests to determine in which months the response variable (i.e., food category or activity) differed between types of site. We built the GLMMs using the “glmmTMB” R package (Brooks et al., 2017), and performed the Tukey's tests using the “lsmeans” R package (Lenth, 2016).

2.3.2 | Ranging patterns

We calculated the mean daily path length for each month and site by summing the mean half-hourly distances traveled each day. We computed the home ranges of the groups with the kernel density estimation (KDE) method (Silverman, 1986) using the *Density* tool in ArcGIS 10.8. With this method, the study area is divided into quadrats, and the limits of the home range are determined by analyzing the number of location points found in each quadrat. We used a quadrat size of 100 × 100 m with 100 m search radius to account for the spread of the group which is usually about 100 m (±50 m, NM, *pers. comm.*). In the disturbed site, we estimated the home-range size only for group Depog, which was consistently observed during all three seasons of observation. Because home range size is known to be affected by group size in macaques (Takasaki, 1981), we also estimated home range size *per capita* by dividing total home range size by group size (group size at each site was averaged over the 2 years of observation, excluding infants).

We also analyzed the use of sleeping sites by group Depog in the disturbed site, and by each group in the natural sites. We calculated the percentage of reutilization of sleeping sites two nights in a row, and in the disturbed site, we measured the distance from each sleeping site to the cultivated areas.

2.3.3 | Influence of anthropogenic disturbances and diets on activity-budgets and ranging behavior

We performed a Multiple Co-inertia Analysis (MCOA; Bady et al., 2004) to assess whether the activity-budgets and diets of the groups were influenced by human and domestic dog disturbances. We used three sets of multivariate data for all sites: the monthly activity-budgets of the groups, their monthly diets, and the hourly rates of disturbances by humans or domestic dogs (cattle were not included in this analysis because they were never aggressive towards macaques). The activity-budget data set contains the mean monthly percentages of time spent on the different activities at each site. The diet data set contains the mean monthly percentages of feeding time spent on 10 categories of food items, including 5 types of cultivated items, and 5 types of noncultivated items. Finally, the disturbance data set contains the hourly rates averaged for each month of disturbances by humans and dogs displaying aggression towards the macaques, and by humans and dogs behaving nonaggressively toward the macaques. All the proportional data were arcsine square root transformed. Our analysis was based on three separate Principal Component Analyses (PCA), one on each data set. Because all the tables contain the same rows (18 rows which represent every combination of site and month), but different variables in columns, MCOA allows us to show the relationships between the tables by rotating the axes of each PCA with respect to those of the other PCAs. This rotation leads to new axes which maximize the co-inertia of all the variables of all the tables. We estimated RV coefficients (Robert & Escoufier, 1976) to measure the correlation between each table and the reference structure of the MCOA (i.e., the synthetic plane which maximizes covariance between all data sets), as well as between each pair of tables. We used Mantel permutation tests with 1000 permutations to assess the significance of those correlations. Graphically, the angle between the arrows from the origin to the variables indicates how they are correlated: an acute angle indicates a positive correlation, an obtuse angle a negative correlation, and a 90° angle indicates no correlation. The distance between the origin and the variables represents the strength of the correlation: the longer the distance, the stronger the correlation. All co-inertia analyses were performed using the “ade4” R package (Thioulouse et al., 2018).

2.3.4 | Daily path length

To test the influence of the activity-budgets, diets and anthropogenic disturbances on the distances traveled daily by the studied groups, we first checked, using linear regression, whether group size affected mean monthly daily path length (Majolo et al., 2008). Because mean daily path length is univariate, we could not include it directly in the MCOA. Therefore, we regressed the normed scores of the statistical individuals (i.e., the 18 site-month combinations of each data set) on each axis of the MCOA (i.e., synthetic new variables interpretable as gradients) with daily path length using linear regressions.

3 | RESULTS

3.1 | Diets between sites and months

We grouped food items consumed by the macaques into 10 broad categories. Cultivated food items include 5 broad categories: cherries (divided in 2 categories: found on trees, or found on the ground, because those two categories represent different phenological periods), walnuts, other fruits (almonds, figs, pears, apples, and grapes, grouped together because they each represent a very small proportion of the diet), and cereals (wheat). Noncultivated food items include five broad categories: two categories of herbaceous plants, located either in cultivated areas or in forested areas, products of natural shrubs and trees, insects, and lichens and mushrooms which we grouped together because they were consumed only in the undisturbed sites and represented small proportions of the diets. In the disturbed site, the cultivated foods composed 45% to 79% of the diet from June to August, while they composed less than 17% in May, October and November (Figure 1). By contrast, in May, October and November, the main food (up to 96% of the diet) came from herbaceous plants (30% in forested areas in May; 35% and 68% in cultivated and forested areas in October and November, respectively, Figure 1) and forest tree and shrub products (50%, 48%, and 28% respectively). Regarding cherries, which represented the main cultivated food item in the diet, macaques ate them in trees mostly in June and July (22% and 18%, respectively), while they ate them on the ground mostly in August (25%). In July, wheat composed the main food in the diet (36%), followed by cherries (30%). Walnuts were consumed mainly in August (16%) and October (17%). In both natural sites, natural tree and shrub products were the most consumed items in October and November (50% to 90%, Figure 1), as well as in August in Akfadou (63%). Insects were the main food in May and

June in Akfadou (57% and 32%), and were also an important resource in Tigounatine in June (39%). In all other months, herbaceous items were the main food items in the natural sites (46% to 84%). Natural shrub and tree products were consumed more often by macaques in the natural sites compared to the disturbed site over all (β : coefficient estimate, $\beta = -2.3$, SE: standard error, SE = 0.61; Table 1), and in each month from July to November, but were consumed more often in the disturbed site in May (Supporting Information: Table S1). Time spent feeding on natural shrub and tree products decreased as group size increased ($\beta = -0.04$, SE = 0.02; Table 1). From June to August, herbaceous items found in forested areas were consumed more often on the natural sites than on the disturbed one, while the reverse occurred in October (Supporting Information: Table S1).

3.2 | Activity patterns between sites and months

The type of site had a significant effect on feeding and resting time (Feeding: $\beta = -0.65$, SE = 0.24; Resting: $\beta = 0.26$, SE = 0.13; Table 1), with macaques in the disturbed site spending more time feeding in May (disturbed: 5.3 h per day; natural: 3.6 and 3.9 h per day; Supporting Information: Table S2; Figure 2) and November (disturbed: 3.5 h per day; natural: 2.3 and 2.4 h per day; Supporting Information: Table S2) and less time resting in May (disturbed: 13.7 h per day; natural: 15.4 and 15.6 h per day; Supporting Information: Table S2) and June (disturbed: 14.5 h per day; natural: 16.1 and 16.8 h per day; Supporting Information: Table S2) than macaques on the natural sites. Although foraging time was not affected by type of site over all (Table 1), it was higher in the disturbed site in June (disturbed: 1.2 h per day; natural: 0.2 and 0.5 h per day; Supporting Information: Table S2) and November (disturbed: 1.2 h per day; natural: 0.2 h per day; Supporting Information: Table S2) compared to

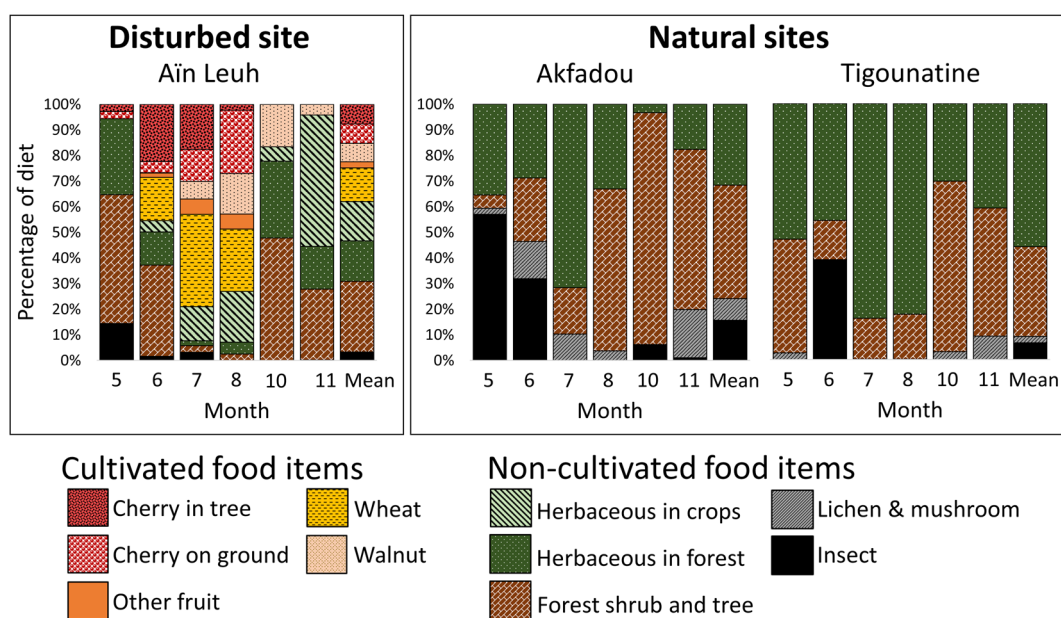


FIGURE 1 Monthly diets, and mean diet over all months at each site.

TABLE 1 GLMM analysis of variance statistics for each food category consumed on both types of site, and for each activity.

Dependant and explanatory variables	LR χ^2	Df	p Value
Food category			
Herbaceous in forest			
Type of site	0.003	1	0.95
Month	43.11	5	<0.001
Group size	2.91	1	0.09
Type of site \times month	86.53	5	<0.001
Natural shrubs and trees			
Type of site	14.25	1	<0.001
Month	98.84	5	<0.001
Group size	5.58	1	0.02
Type of site \times month	73.07	5	<0.001
Insects			
Type of site	0.3	1	0.58
Month	2.68	5	0.75
Group size	1.28	1	0.26
Type of site \times month	1.71	5	0.89
Activity			
Feeding			
Type of site	7.09	1	0.008
Month	16.06	5	0.007
Group size	0.37	1	0.54
Type of site \times month	20.98	5	<0.001
Foraging			
Type of site	0.04	1	0.85
Month	39.17	5	<0.001
Group size	6.62	1	0.01
Type of site \times month	41.16	5	<0.001
Moving			
Type of site	0.55	1	0.46
Month	24.43	5	<0.001
Group size	0.18	1	0.67
Type of site \times month	14.12	5	0.01
Resting			
Type of site	3.88	1	0.04
Month	26.94	5	<0.001
Group size	1.97	1	0.16
Type of site \times month	23.47	5	<0.001
Socializing			
Type of site	0.53	1	0.47
Month	46.8	5	<0.001

TABLE 1 (Continued)

Dependant and explanatory variables	LR χ^2	Df	p Value
Group size	0.02	1	0.89
Type of site \times month	7.77	5	0.17

Note: Likelihood ratio tests compare the full model with a reduced model in which the listed variable is excluded.

Abbreviations: Df, degrees of freedom; LR χ^2 , likelihood ratio χ^2 .

natural sites. Foraging time increased with group size ($\beta = 0.04$, SE = 0.02; Table 1), while other activities were not affected by group size (Table 1). Moving and socializing time did not differ between types of site (Table 1).

3.3 | Influence of anthropogenic disturbances and diets on activity-budgets and ranging behavior

In the disturbed site, the macaques encountered, on average over all observation months, 0.52 anthropogenic disturbances per hour ($N = 485$ disturbance events). Encounters with humans represented 51.4% of those disturbances, while 33.3% were with dogs, 9.7% with cattle (accompanied by dogs in 23% of cases, and by humans in 9%) and 5.6% with vehicles. Fifty percent of encounters with humans were aggressive (i.e., people yelling, or throwing projectiles at the macaques), while 50% were nonagonistic (i.e., people passing by, trying to feed the macaques, calling them, or moving close to take pictures). Seventy-one percent of encounters with dogs were aggressive (i.e., dogs barking or chasing the macaques), while 29% were nonagonistic (i.e., passing by). The macaques in the natural Akfadou site encountered 0.04 anthropogenic disturbances per hour ($N = 17$ disturbance events), including 34.2% with humans, 29% with dogs, and 36.8% with cattle (always accompanied by people, and in 5% of cases by dogs). Forty percent of encounters with humans and 100% of encounters with dogs were aggressive. In the natural Tigounatine site, the macaques encountered 0.06 disturbances per hour ($N = 28$ disturbance events), of which 45.2% were with humans (including 16% with aggression), 40.5% with dogs (including 71% with aggression), and 14.3% with cattle (accompanied by dogs: 5%; by humans: 5%; by both: 2%).

We retained the first two axes of the MCOA which accounted, respectively, for 53% and 18% of the total covariance between the three tables (see Section 2 for details). RV coefficients between the tables and the reference structure were all significant ($p \leq 0.002$), meaning that each of the three data sets was correlated with the reference structure of the MCOA. RV coefficients between each pair of tables showed that activity-budgets were significantly correlated with diets only ($p = 0.04$), while the other two tables (diets and disturbances) were significantly correlated with each other ($p = 0.003$). The composition of the diets and the level of anthropogenic disturbance were most represented on the first axis (Figure 3, $\text{cov}^2_{\text{diets}} = 0.43$; $\text{cov}^2_{\text{disturbances}} = 0.50$), while the activity-budget

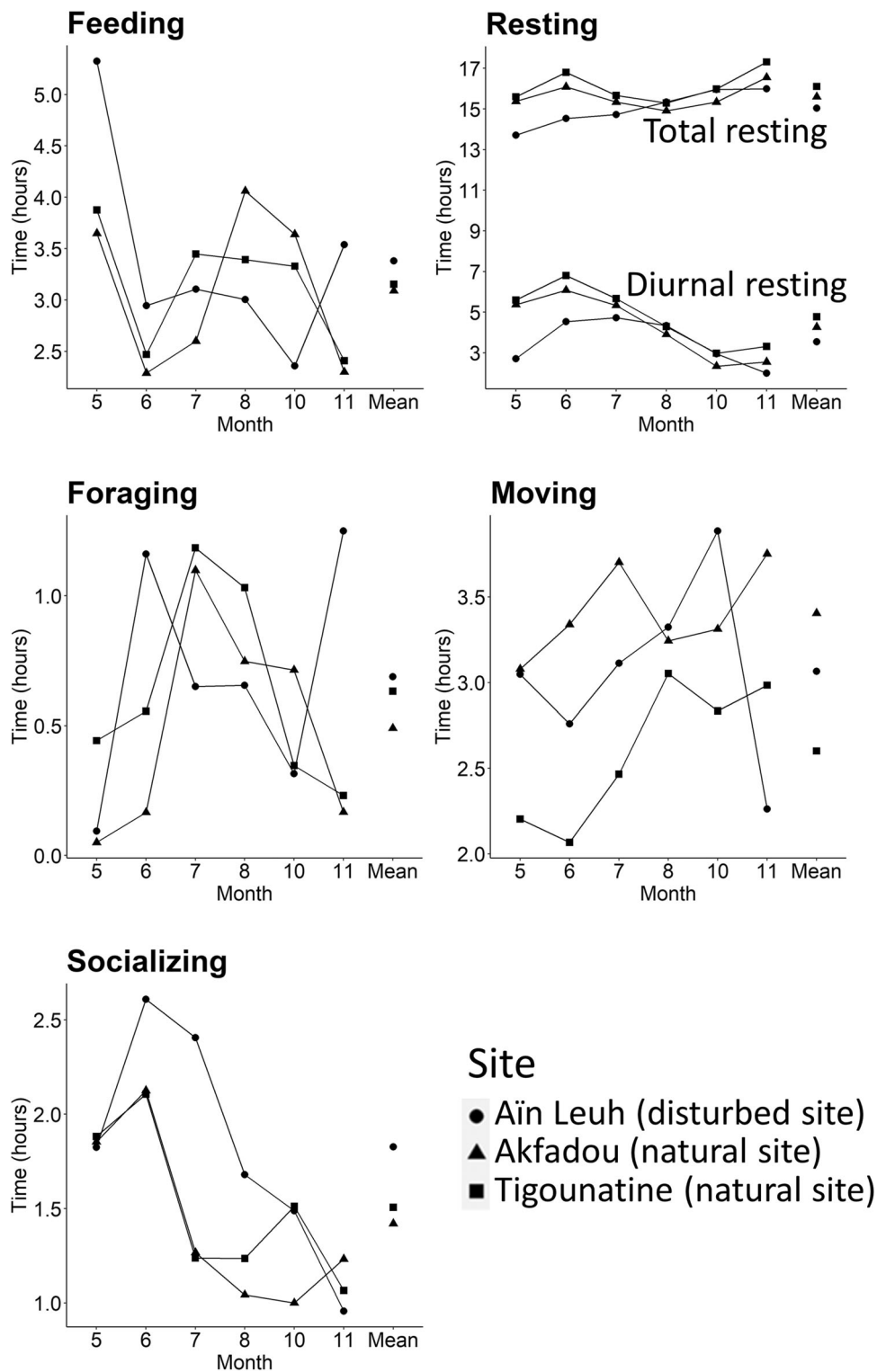


FIGURE 2 Variations in activity-budgets (in hours) depending on the month and the site.

variables were better represented on the second axis ($\text{cov}^2_{\text{activities}} = 0.21$). The first axis of the MCOA opposes the consumption of forest food items to the consumption of agricultural items, associated with anthropogenic disturbances (Figure 3). This axis can thus be interpreted as a gradient of human influence that allows one to

differentiate the disturbed macaques from the natural ones. The lack of correlation between activity-budgets and disturbances shows that global time budgets were not impacted by anthropogenic disturbances. In particular, moving activity was not contributing to the first axis, which suggests that disturbances had little impact on macaque

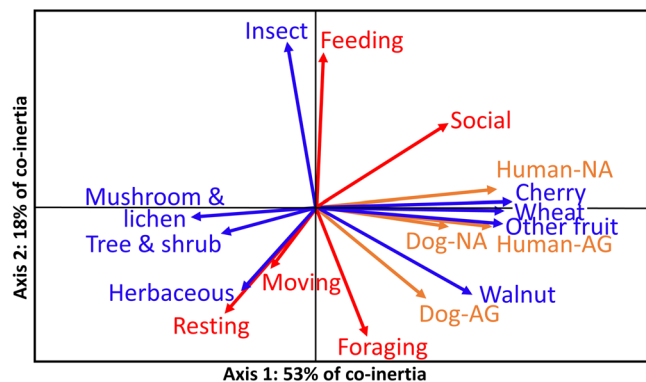


FIGURE 3 Graphical representation of the MCOA analysis. Red: activity-budgets; blue: diets; orange: anthropogenic disturbances. Dog-AG, aggressive dog; dog-NA, nonaggressive dog; Human-AG, aggressive human; human-NA, nonaggressive human.

locomotion. Socializing was represented partially on both axes, and associated with the consumption of cherries, cereals and other fruits on the first axis. This suggests that the consumption of cherries, cereals and other fruits, abundant and easy to access, allowed disturbed macaques to save time for increased social activities compared to natural macaques. The second axis opposes socializing and feeding associated with the consumption of insects to resting associated with herbaceous items, and foraging associated with the consumption of walnuts. By contrast to cherries, cereals and other fruits, when macaques fed on walnuts, they increased their foraging time due to the required processing time before accessing nuts.

3.4 | Daily path length

In the disturbed site, mean daily path length of Barbary macaques ranged from 1291 to 1828 m depending on the month (mean over all months: 1557 m). In the natural sites, they ranged from 1473 to 2904 m in Akfadou (mean over all months: 2028 m) and from 1327 to 2264 m in Tigounatine (mean over all months: 1838 m). We found no significant effect of group size on mean monthly daily path length ($F_{1,16} = 1.79$, $R^2_{\text{adj}} = 0.04$, $p = 0.2$). The regressions of daily path length with the normed scores of the site-month combinations on the MCOA axes showed that distances decreased significantly as human influence increased (i.e., along the positive part of the first axis; $F_{1,16} = 5.41$, $R^2_{\text{adj}} = 0.21$, $p = 0.03$). This means that, as macaques spent more time in human-altered areas, they traveled shorter daily distances.

3.5 | Ranging patterns

In the disturbed site, the home range of group Depog (84 ha, $N = 1610$ GPS locations) was three times smaller than the natural Akfadou group (266 ha, $N = 1069$ GPS locations) and 2.5 times smaller than the natural Tigounatine group (212 ha, $N = 1129$ GPS locations). When accounting for group size, the home range *per capita*

of the disturbed group was 3.8 ha, that is, two times smaller than the natural Akfadou group (8.2 ha) and 1.3 times smaller than the natural Tigounatine group (5.1 ha). Group Depog's home range contained 19% of cultivated areas, with 11 ha of orchards, and 0.2 ha of cereal fields (see details in Supporting Information: Figure S1).

The disturbed group Depog used only three locations for sleeping sites (see details in Supporting information: Figures S1 and S2a). It used the same sleeping site on two consecutive nights in 94% of cases. Its main sleeping site (used 46 times) was only at 130 m from the cultivated areas. Its second sleeping site (used only twice) was at 34 m, and the third (used once) was at 97 m. The sleeping sites of the natural groups ($N > 20$ locations) were more widespread (see Supporting Information: Figure S2b,c), and were used on two consecutive nights in 0% of cases in Akfadou and 8% in Tigounatine.

4 | DISCUSSION

Diet composition is often reported to affect primates' activity-budgets and ranging behaviors. In particular, the inclusion of human foods in primates' diets often results in a decrease in foraging and feeding time, and an increase in resting and/or socializing time (Priston, 2005; Saj et al., 1999; Strum, 1994; Warren et al., 2010). It also leads to smaller home-ranges and shorter daily path lengths (Hoffman & O'Riain, 2012; Saj et al., 1999). In Barbary macaques living in an agricultural site, we showed that cultivated food items were the most consumed foods in three of the six study months (i.e., June–August). In addition, when cultivated foods were scarce, cultivated areas remained attractive because artificial irrigation favored the growth of herbaceous plants that composed almost 50% of macaque's diets at that time. Indeed, although we did not quantify herbaceous resources in forest habitat, we observed that in the evergreen oak forest surrounding the cultivated areas, the dense canopy and closed thickets, in addition to heavy grazing by cattle, limited the growth of the herbaceous layer.

4.1 | Impacts of diets and agricultural resources on activity-budgets

Differences in activity patterns between disturbed and natural sites were not what we expected. Indeed, macaques in the disturbed site spent more time feeding than macaques in the natural sites. Although time spent feeding does not necessarily reflect energy intake, it is known to be affected by habitat quality, and primates living in unfavorable habitats commonly spend more time feeding than counterparts in more favorable habitats (Japanese macaques, *Macaca fuscata*: Nakagawa, 1989; white-headed langurs, *Trachypitecus leucocephalus*: Li & Rogers, 2004), although the reverse has also been observed (lion-tailed macaques, *Macaca silenus*: Menon & Poirier, 1996). Increased feeding time in our disturbed macaques compared to those living in natural habitats were particularly marked in May and November, that is, when disturbed macaques had the

least access to cultivated foods and relied on less nutrient-rich items. In May, when macaques in the disturbed site had little access to cultivated areas due to intense crop-guarding by farmers, they relied on shrub and tree products, which were actually mainly oak leaves. Those resources were rarely consumed on the other sites and are likely a filler fallback food in the disturbed site, that is, a food item used when preferred foods are unavailable, and which can be completely avoided when better foods are available (Marshall & Wrangham, 2007). In November, when cultivated foods were no longer present, macaques fed mostly on herbaceous items. Foraging time also increased in the disturbed site in June and November. In November it was likely due to the high consumption of herbaceous items in orchards. Indeed, at that time, the leaves of cherry and walnut trees had fallen to the ground and were covering the herbaceous layer, making it more time-consuming for macaques to access herbaceous items. In June, however, the increased foraging time in the disturbed site remains difficult to explain. Macaques in the disturbed site spent less time resting than those in the natural sites, especially in May and June, while socializing time was similar. The same pattern was observed by Ménard et al. (2013), with Barbary macaques living in an unfavorable habitat managing to spend the same amounts of socializing time as a group living in a preserved forest by reducing their resting time. Because living in a disturbed habitat with high levels of human disturbances is stressful, maintaining social bonds within the group is likely a priority (Kikusui et al., 2006; Sachser et al., 1998).

Overall, the results suggest that Barbary macaques in the disturbed habitat manage to maintain activity-patterns similar to those living in natural habitats when they have access to cultivated food resources. When those resources are not accessible, changes in activity patterns suggest increased energy costs for the disturbed macaques. Although we did not quantify natural resources in the disturbed site, habitat degradation in forested areas was clearly visible. This was mostly notable at the herbaceous layer which was heavily grazed by sheep and goats, but also at the canopy layer which was regularly pruned by shepherds to feed livestock. It is likely that natural resources in forested areas at the disturbed site are too degraded to sufficiently provide for the macaques, and that cultivated resources are necessary for those disturbed macaques to maintain a viable energy balance. Natural differences in forest characteristics (i.e., evergreen cedar-oak forest and a greater canopy closure in the disturbed site) could be confounding factors in explaining Barbary macaque behavior. However, we are confident that they contribute little as explanatory factors in comparison to overgrazing and the presence of attractive cropland which constitute the major differences between the natural and disturbed sites we studied.

4.2 | Impacts of diets and agricultural resources on ranging behaviors

The reduced daily path length and home range size of crop-foraging macaques suggest a reduction in energy expenditure compared to

macaques living in the natural sites, likely resulting from the consumption of agricultural food items. However, despite the disturbed groups having shorter daily path lengths, their group members did not display less moving time (i.e., energy expenditure) compared to those of natural groups. This could be explained by the high rate of anthropogenic disturbances in the disturbed site, which forced macaques to frequently engage in brief bouts of locomotion to escape aggression, as seen in other species subjected to human presence and anthropogenic noises (Cañadas Santiago et al., 2020; Sheehan & Papworth, 2019). A finer analysis of what motivates individual movements would be required to confirm this hypothesis.

Macaques in disturbed and natural sites displayed contrasting patterns of sleeping site selection. Sleeping site selection in primates depends largely on both proximity to food resources and predation pressure (Albert et al., 2011), resulting in a cost-benefit balance between energetic costs and security. Groups living in the natural sites had numerous sleeping locations covering a large portion of their home range. They avoided using the same sleeping site on consecutive nights, which is a typical behavior in primates, most likely to reduce the probability of predators predicting their location (Albert et al., 2011; Heymann, 1995), and also possibly to limit contact with pathogen load accumulated at sleeping sites from primates' own fecal emissions (Hausfater & Meade, 1982). Macaques in the disturbed site had a very high percentage of reutilization of sleeping sites, and all three sleeping sites were located within 130 m of cultivated areas. This shift in sleeping behavior has been observed in other primates foraging on human resources, using highly regular sleeping sites located near their predictable food source (Altmann & Muruthi, 1988; Strum, 2010). The sleeping site most used by group Depog was located within 50 m of a road, and right above a trail that was regularly used by humans and dogs. This suggests that this group might choose to minimize security while maximizing energetic gains, although this is difficult to ascertain as we do not know how the risks are actually perceived by the group. These areas which appear risky from the observers' point of view could actually feel safer than others to the macaques who know them well and possibly feel that they are able to manage the known dangers regularly encountered there. Decreased risk perception due to habituation to human disturbances is common in many species (Engelhardt & Weladji, 2011; Stillfried et al., 2017), although it is not as well known in primates (but see Mikula et al., 2018). However, opposite patterns have also been observed, with increased risk perception despite long-term exposure to human disturbances, which seems to be related to the lethality of human encounters (Gotanda et al., 2009; Reimers et al., 2009; Stankowich, 2008). Such lethality has not been assessed in our disturbed site, making it more difficult to assess the level of risk perceived by the macaques inhabiting this study site.

Sleeping sites and over all space use patterns at the disturbed site appeared to remain stable during all observation months (i.e., highly centered around the cultivated areas), even when the macaques had little access to cultivated foods. Whether this is due mainly to the attractiveness of cultivated areas, or to other factors such as competition for space with neighboring groups, remains

unknown. The study period, from May to November, encompassed mainly periods of fruit and/or cereal production in the crops. Thus, we do not know if the studied disturbed groups display comparable behaviors in periods when cultivated foods are not available in the winter. We also do not know if rates of anthropogenic disturbances are as high during those periods. Judging by the high consumption of herbaceous items inside the orchards in November (i.e., when fruit was no longer present), we can assume that cultivated areas remain attractive to the macaques during winter, as the herbaceous layer is not grazed by cattle, contrary to forested areas. However, Barbary macaque behavior in those periods remains to be studied.

5 | CONCLUSION

The inclusion of agricultural resources in the diet of Barbary macaques living in a disturbed habitat appears to offset the lack of natural resources resulting from forest degradation, at least in periods of crop production. However, living in highly human-modified landscapes with high rates of anthropogenic encounters, including aggressive ones, is likely stressful and may potentially induce extra energy costs and lead to macaque injuries. This could result in demographic costs for crop-foraging groups, threatening the conservation of this endangered species. Our study adds to previous ones showing that Barbary macaques are behaviorally flexible, allowing them to adapt and persist in a wide range of disturbed habitats such as peri-urban areas (Maibeche et al., 2015), degraded forests (Ménard et al., 2014), tourist sites (El Alami et al., 2012) and agricultural areas (present study). Despite that, their numbers have been substantially declining in the past 40 years (Ménard et al., 2014), and given the intensification of land use change and habitat loss, the long-term viability of their populations remains uncertain. In the global context of expected increase of land-use change and human-macaque conflict, ensuring Barbary macaque conservation will thus require changing current strategies of agricultural lands and wildlife habitat management. New strategies should include favoring more productive natural habitats, decreasing grazing and logging pressure, and keeping buffer zones between natural and human-altered areas.

AUTHOR CONTRIBUTIONS

Elisa Neves: Conceptualization (equal); formal analysis (lead); methodology (equal); writing—original draft (lead); writing—review & editing (equal). **Dominique Vallet:** Investigation (equal); writing—review & editing (equal). **Sidi Imad Cherkaoui:** Funding acquisition (equal); resources (equal); writing—review & editing (equal). **Zouhair Amhaouch:** Project administration (equal); resources (equal); writing—review & editing (equal). **Coline Duperron:** Investigation (equal). **Nelly Ménard:** Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); supervision (equal); writing—original draft (equal); writing—review & editing (equal). **Pascaline Le Gouar:** Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project

administration (equal); supervision (equal); writing—original draft (equal); writing—review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

Our research complied with Moroccan and Algerian laws, adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-human Primates, and followed the American Society of Primatologists Code of Best Practices for Field Primatology. All data collection was noninvasive and was conducted in close partnership with Moroccan Forestry authorities and the managers of the Djurdjura National Park in Algeria.

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SUPPORTING INFORMATION

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