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# Conflicts Between Humans and Endangered Barbary Macaques (*Macaca sylvanus*) at the Edge of an Agricultural Landscape in Morocco

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► **To cite this version:**

Elisa Neves, Sidi Imad Cherkaoui, Zouhair Amhaouch, Coline Duperron, Nelly Ménard, et al.. Conflicts Between Humans and Endangered Barbary Macaques (*Macaca sylvanus*) at the Edge of an Agricultural Landscape in Morocco. *International Journal of Primatology*, inPress, 10.1007/s10764-024-00422-w . hal-04518091

**HAL Id: hal-04518091**

**<https://hal.science/hal-04518091>**

Submitted on 23 Mar 2024

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1 **Conflicts between humans and Endangered Barbary macaques**  
2 **(*Macaca sylvanus*) at the edge of an agricultural landscape in Morocco**

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21

## 22 **Abstract**

23           The expansion of shared spaces between humans and wildlife, particularly  
24 resulting from agricultural encroachment on natural habitats, leads to increasing  
25 interactions between humans and non-human primates (hereafter “primates”). We  
26 explored how crop-foraging Barbary macaques adapt their behavior to anthropogenic  
27 disturbances and identified deterrents implemented by farmers and their effectiveness.  
28 We observed three groups of crop-foraging Barbary macaques in Aïn Leuh, Morocco, in  
29 2021-2022. We estimated their activity-budgets from 7185 scan records and tested  
30 whether they were influenced by habitat (forest, fruit orchard and cereal field).  
31 Additionally, we examined the impact of time of day, month, and age-sex class (adult  
32 female, adult male, immature) on macaque presence in cultivated areas. We also  
33 analyzed macaque responses to encounters with humans and dogs. Macaques primarily  
34 focused on feeding in cultivated areas while allocating more time to resting and  
35 socializing in forested areas. They used cultivated areas extensively during periods of  
36 human activity. Cereal fields, but not orchards, were predominantly visited by adult  
37 females rather than males or immatures. Macaques experienced 0.34 to 0.67  
38 anthropogenic encounters per hour, with variation across months, and high rates of  
39 aggression from humans and dogs. Preemptive deterrence measures, such as using  
40 slingshots before macaques entered the crops, were more effective than confrontations  
41 inside the cultivated areas. While crop-guarding with slingshots was effective, it poses  
42 risks to the macaques. This study highlights the high risk of crop-foraging for  
43 Endangered Barbary macaques and the need to develop safer and more sustainable crop-  
44 guarding strategies to mitigate conflicts and promote human-Barbary macaque  
45 cohabitation.

46

47           **Key-words:** Crop-foraging; Activity-budgets; Deterrents; Behavioral responses;  
48 Anthropogenic disturbances.

## 49 **Résumé**

50           L'expansion d'espaces partagés entre humains et animaux sauvages, due  
51 notamment à l'empiètement des zones agricoles sur les habitats naturels, entraîne une  
52 augmentation des interactions entre humains et primates non-humains (ci-après  
53 « primates »). Nous explorons comment des magots se nourrissant dans des cultures  
54 adaptent leurs comportements face aux perturbations anthropiques. Nous identifions les  
55 moyens de dissuasion utilisés par les agriculteurs et leur efficacité. Nous avons observé  
56 trois groupes de magots se nourrissant dans des cultures à Aïn Leuh au Maroc en 2021-  
57 2022. Nous avons testé l'influence du type d'habitat (forêt, vergers et champs) sur leurs  
58 budgets-temps à partir de 7185 observations scans. Nous avons testé l'influence du  
59 moment de la journée, du mois et de la classe d'âge-sexe (femelle adulte, mâle adulte,  
60 immature) sur la présence des magots dans les cultures. Nous avons aussi analysé les  
61 réponses des magots aux rencontres avec des humains et des chiens. Les magots  
62 passaient plus de temps en alimentation et moins de temps en repos et interactions  
63 sociales dans les zones cultivées que dans les zones forestières. Ils utilisaient les  
64 cultures lors de périodes de forte activité humaine. Les champs, contrairement aux  
65 vergers, étaient majoritairement utilisés par les femelles adultes. Les magots ont subi  
66 chaque mois 0,34 à 0,67 perturbations anthropiques par heure, avec de forts taux  
67 d'agression par les humains et les chiens. Les mesures de dissuasion préventives, telles  
68 que l'utilisation de frondes contre les magots avant qu'ils entrent dans les cultures, se

69 montraient plus efficaces que les confrontations à l'intérieur des cultures. Bien que les  
70 frondes soient efficaces pour protéger les cultures des magots, elles représentent des  
71 risques pour les magots. Cette étude met en évidence la forte tendance des magots à  
72 prendre des risques et la nécessité de développer des stratégies de dissuasion plus sûres  
73 et plus pérennes pour mitiger les conflits et permettre une cohabitation durable entre  
74 humains et magots.

75 *The publisher did not copy edit the abstract translation.*

76

## 77 **Introduction**

78           With the rapid expansion of human populations and anthropogenic areas  
79 encroaching on wildlife habitat, contact zones and subsequent interactions between  
80 humans and wildlife are increasing (Anand & Radhakrishna, 2017; Bloomfield et al.,  
81 2020; Nyhus, 2016). The conversion of natural habitats into agricultural lands leads to a  
82 loss of natural resources for wildlife, but it also brings new resources to species which  
83 are able to exploit them (Fehlmann et al., 2021). However, because the use of  
84 agricultural resources by animals negatively impacts human livelihoods, it can lead to  
85 human-wildlife conflicts which can represent a real threat to the long-term survival of  
86 species (Strum, 2010; Woodroffe et al., 2005).

87           Non-human primates (hereafter “primates”), especially macaques, baboons and  
88 vervets, with their high dietary and behavioral flexibility, are particularly successful at  
89 exploiting agricultural food resources, and are commonly considered as agricultural  
90 pests (Hill, 2017; McLennan et al., 2017). Farmers employ various methods to deter  
91 primates from foraging on crops. The most commonly used deterrents include barriers  
92 and fences, crop-guarding techniques, alarm systems, and chasing (Findlay & Hill,  
93 2020; Hill & Wallace, 2012; Strum, 2010). Some of these methods can be violent, for  
94 instance chasing primates with packs of dogs or with weapons, and can result in lethal  
95 injuries (Strum, 2010). Crop-foraging primates exhibit a range of strategies to avoid  
96 such interactions. These strategies may involve shifting their activity periods to visit  
97 crops at times of low human activity (chimpanzees, *Pan troglodytes*: Krief et al., 2014)  
98 and minimizing risks of detection by reducing resting and social time in cultivated areas  
99 (chimpanzees: Bryson-Morrison et al., 2017; geladas, *Theropithecus gelada*: Caselli et  
100 al., 2021). In several species, adult or subadult males are more likely to forage in crops

101 than other age and sex classes, as they appear to be more willing to engage in risky  
102 activities (chimpanzees: Hockings et al., 2007; Buton macaques, *Macaca ochreata*  
103 *brunnescens*: Priston, 2005; vervets, *Chlorocebus aethiops pygerthus*: Saj et al., 1999;  
104 olive baboons, *Papio anubis*: Strum, 1994).

105         Given the projected increase in human-primate conflicts, it is imperative to  
106 identify effective solutions for managing these conflicts (Campbell-Smith et al., 2010;  
107 Marchal & Hill, 2009). Achieving this goal first requires understanding the behavior of  
108 crop-foraging primates, which may be both species-specific and location-specific and  
109 thus requires case-by-case analyses (Hill, 2017). By gaining insights into crop-foraging  
110 primates' behavioral patterns, one can develop targeted and informed strategies to  
111 mitigate these conflicts successfully (Hill, 2017).

112         The Endangered Barbary macaque (*Macaca sylvanus*; Wallis et al., 2020)  
113 inhabits temperate mountainous forests in Morocco and Algeria. The Middle-Atlas  
114 Mountains of Morocco host about 75% of the global Barbary macaque population (Fa,  
115 1984; Taub, 1977) and are under increasing anthropogenic pressure, with intense  
116 livestock grazing and progressive conversion of forest-adjacent lands into agricultural  
117 lands (Kouba et al., 2018). With their high behavioral and dietary flexibility, Barbary  
118 macaques have colonized anthropogenic habitats such as peri-urban and agricultural  
119 areas where they are able to forage on human food resources (Maibeche et al., 2015).  
120 While macaques are particularly efficient crop-foragers due to their behavioral  
121 flexibility, aptitude for social learning and semiterrestrial locomotion (Hill, 2017), the  
122 specific behaviors exhibited by crop-foraging Barbary macaques have not yet been  
123 studied.

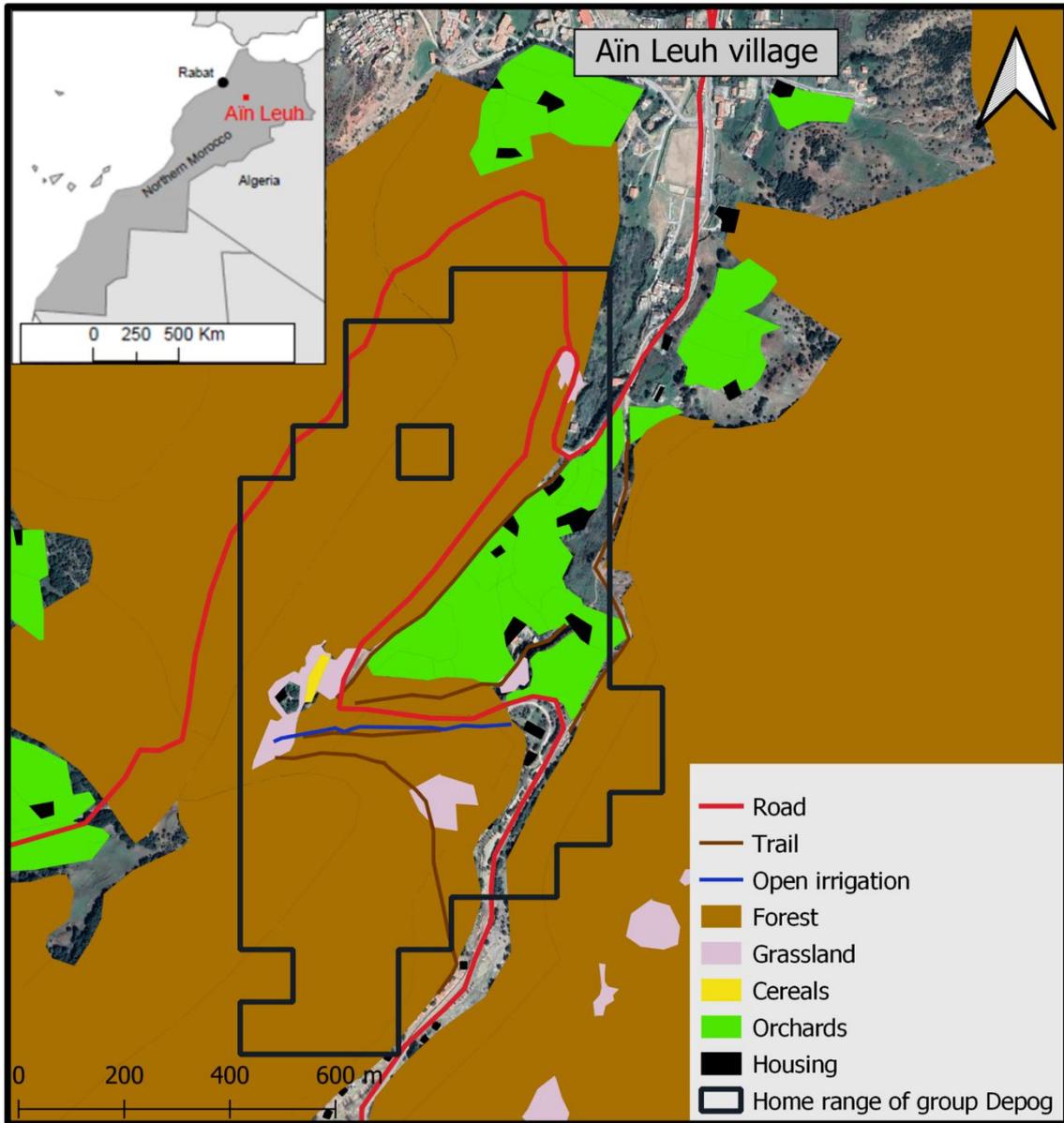
124           In this study, we examined the behavioral adaptations of Barbary macaque  
125 groups to anthropogenic disturbances at the interface between an evergreen cedar-oak  
126 forest and agricultural areas in the Middle-Atlas in Morocco. We also quantified their  
127 agonistic and non-agonistic interactions with local people. Because crop-foraging  
128 primates considered as agricultural pests, like macaques, are typically the targets of  
129 human aggression (Hill, 2017; Strum, 2010), we assumed that humans display  
130 aggressive behaviors towards crop-foraging Barbary macaques, and we hypothesized  
131 that the macaques use strategies to mitigate the resulting risk. Specifically, we predicted  
132 that they minimize the risks of encounters with humans by minimizing the time spent in  
133 the riskiest areas (*i.e.* cultivated areas), which should be devoted mainly to crop-  
134 foraging, while resting and socializing are preferentially performed in safer areas (*i.e.*  
135 forests). To test this prediction, we examined how the groups' activity-budgets vary  
136 between cultivated and forested areas. Because two different types of agrosystems are  
137 present at the study site (fruit orchards and cereal field), we also examined activity-  
138 budget variations between those habitats. We also predicted that the macaques will  
139 predominantly visit risky areas when human activity is low and that adult males will  
140 spend more time in cultivated areas than adult females and immatures. Finally, we  
141 identified the strategies used by the local human population to deter macaques from  
142 crop-foraging, and assessed which, if any, are effective. To that end, we quantified  
143 human behaviors during encounters with the macaques and the macaques' responses to  
144 those different types of behaviors, especially regarding their movements away or  
145 towards the cultivated areas.

146

## 147 **Methods**

148 **Site and subjects**

149 We conducted the study in the Middle-Atlas Mountains in the Ifrane Province of  
150 Morocco, at the interface of an evergreen cedar-oak forest (*Quercus rotundifolia* and  
151 *Cedrus atlantica*) and agricultural lands (Figure 1) near the rural village of Aïn Leuh (5°  
152 20'W, 33° 18'N; 1400-1700 m altitude; mean annual temperatures: minimum 9.5,  
153 maximum 21.1°C; mean annual rainfall: 830 mm). The evergreen cedar-oak forest  
154 encompassed about 80% of mature forest and 20% of pure oak coppices < 5 m high  
155 (Sogreah-Ttoba, 2004). Over the past decade, the area has undergone agricultural  
156 development, with the conversion of open areas traditionally used as extensive pastures  
157 into crops. The study site encompassed 14.2 ha of cherry and walnut orchards, and one  
158 0.2 ha cereal field where wheat was grown (Figure 1). Humans were present daily in the  
159 study area, both in agricultural and forested zones. Humans in agricultural areas were  
160 mainly agricultural workers, mostly present from 9am to 6pm. Humans in the forest  
161 were mainly shepherds leading sheep and goats to graze. We studied three groups of  
162 macaques during three observation seasons, in the fall (October-November) of 2021,  
163 and in the spring (May-June) and summer (July-August) of 2022. We followed the  
164 primary focal group (Depog) during all three seasons. This group consisted of 28  
165 individuals in 2021. Three adult females and two immatures disappeared and three  
166 infants were born, resulting in a total of 26 individuals in 2022. We could identify all  
167 members of Depog group individually. We followed Houquette group (37 individuals)  
168 only in the fall of 2021, as we could not locate it in the following spring. We followed  
169 Felix group (about 35 individuals) only in 2022. We could not identify all members of  
170 Houquette and Felix groups individually.



171

172 **Figure 1.** Map of Aïn Leuh study site, Morocco, in 2021, with land types and home  
 173 range of the focal Barbary macaque group, Depog. We estimated home range size using  
 174 the kernel density estimation method (Supporting Information and Neves et al., 2023a).

175

176 **Data collection**

177           Every 15 minutes, we used instantaneous scan sampling (Altmann, 1974) to  
178 record the activity of five individuals, excluding infants <1-year-old. We chose the first  
179 individual haphazardly among all individuals in sight, then observed the others from  
180 right to left from the first individual. We divided activities into five mutually exclusive  
181 categories: foraging (*i.e.* searching for food items, including turning over stones,  
182 digging into the ground, searching beneath litter, hunting insects, and cleaning plant  
183 items), feeding (*i.e.* actually eating food items), moving (*i.e.* any type of locomotion that  
184 was not associated with another activity), resting (*i.e.* all inactive postures not  
185 associated with another activity), and socializing (*i.e.* all inter-individual affiliative or  
186 agonistic interactions). We recorded 6007 scans for Depog group in 705 hours of  
187 observation, 732 scans for Houquette group in 94 hours of observation, and 446 scans for  
188 Felix group in 88 hours of observation.

189           We recorded all occurrences when Barbary macaques experienced  
190 anthropogenic disturbances, which we define as encounters with humans and domestic  
191 animals, including dogs and livestock (referred to as ‘disturbers’). For each encounter,  
192 we recorded the behavior of the disturber (Table 1), its distance to the closest macaques,  
193 and the duration of the encounter. We also recorded the reaction of the macaques (Table  
194 1), the distance they fled if they fled, and the time it took them to resume their previous  
195 activity or engage in a new activity that was not vigilance, fleeing, or interacting with  
196 the disturber. During observation sessions, we recorded the location of the groups every  
197 30 minutes using a GPS Trimble TERMINAL JUNO 5B, with an uncertainty of about  
198 5m, as estimated by the manufacturer. Additionally, we recorded the macaques’ location  
199 at the time of each anthropogenic encounter and again one hour later.

200 **Table 1.** Ethogram for humans, dogs and livestock ('disturbers') and Barbary macaques  
 201 during encounters in Aïn Leuh, Morocco, in 2021-2022.

<b>Human, dog and livestock</b>	
Neutral	Passing by without interacting with the macaques
<b>Human</b>	
Projectile	Throwing projectiles with slingshots or by hand
Noise	Directing loud noises at the macaques (shouting, hitting objects)
Non-agonistic interaction	Approaching the macaques to take pictures, calling them or trying to feed them
<b>Dog</b>	
Barking	Barking at the macaques
Chasing	Running after the macaques
<b>Macaque</b>	
Defense	Holding its ground and facing the disturber, or chasing the disturber
Fleeing	Moving away on the ground, or climbing up (or higher up) in trees
Alarm call	Specific call signaling potential danger
No visible reaction	No visible change in activity

202

203 **Data analysis**

204 *Activity patterns*

205 We estimated the daily activity-budgets of each group from the scans. The  
 206 activity-budgets of Barbary macaques differ between age and sex classes (Ménard &  
 207 Vallet, 1997). To account for those differences, we calculated mean daily activity-  
 208 budgets for each group as the weighted mean of three age-sex classes, based on group  
 209 compositions observed at several other study sites (Ménard, 2002), which are ¼ adult  
 210 females (>4 years-old), ¼ adult males (>5 years-old), and ½ immatures (excluding  
 211 infants <1 year-old). We present activity-budgets as a percentage of daylight time (*i.e.*  
 212 between sunrise and sunset) spent in each activity. Daylight time varies between 10 and  
 213 14 hours depending on the season. We tested the effects of habitat (forest, orchard or  
 214 cereal field) and group ID (Depog, Houquette and Felix) on the groups' activity-budgets

215 using generalized linear mixed models (GLMM, Baayen et al., 2008). “Forested areas”  
216 encompass high forests and oak coppices and a few grassland formations. Because the  
217 response variables are continuous percentages, we used a beta error structure with logit  
218 link function (Salinas Ruíz et al., 2023). We ran five models, one for each activity (*i.e.*  
219 foraging, feeding, moving, resting and socializing). In each model, we included the  
220 month and observation day as random effects. When a model showed a significant  
221 effect, we ran post-hoc Tukey’s tests to determine between which habitats the activity-  
222 budgets differed. We performed all analyses using the R software (R Core Team, 2020).  
223 We built the GLMMs using the “*glmmTMB*” R package (Brooks et al., 2017) and  
224 performed Tukey’s tests using the “*lsmeans*” R package (Lenth, 2016). We ran residual  
225 diagnostics for all GLMMs using the “*DHARMA*” R package (Hartig, 2021) to ensure  
226 that all model assumptions were met.

227

### 228 *Use of cultivated areas*

229 To assess differences in the presence of the different age-sex classes in  
230 cultivated areas, we calculated the proportion of scans made each day for each of three  
231 age-sex classes (adult females, adult males and immatures) in the three habitats (forest,  
232 orchard and cereal field). We used those proportions as a proxy for relative presence of  
233 the three age-sex classes in the cultivated areas. We used binomial GLMMs (one for  
234 each age-sex class) to test the effect of habitat and group ID on the proportion of scans.  
235 We added the month and observation day as random effects to the models. When a  
236 model showed a significant effect, we ran post-hoc Tukey’s tests to determine between  
237 which habitats the relative presence of an age-sex class differed. To determine whether

238 the macaques visited cultivated areas more frequently at specific times of day, we  
239 divided the day into five periods from sunrise to sunset: 6am-9am; 9am-12pm; 12pm-  
240 3pm; 3pm-6pm; and 6pm-9pm. Using binomial GLMMs, we assessed the effects of the  
241 period of the day, the month and group ID on the macaques' presence in cultivated  
242 areas. Again, we added the observation day as a random effect. We then ran post-hoc  
243 Tukey's tests to determine between which periods of the day and between which  
244 months the percentage of time spent by macaques in cultivated areas differed.

245

#### 246 *Human-macaque interactions*

247 For each month, we calculated hourly rates of anthropogenic encounters as the  
248 number of encounters between macaques and humans or domestic animals divided by  
249 the number of hours of observation. Observation sessions lasted a mean of 9 hours (min:  
250 1h, max: 14h). We defined encounters as any interaction with a human or domestic  
251 animal, regardless of whether it was aggressive or not. We defined aggressive  
252 encounters as those including physical aggression such as chasing or throwing  
253 projectiles, or non-physical aggression such as shouting/barking or directing loud noises  
254 at the macaques. We included instances where humans or domestic animals passed  
255 close enough to be visible by the macaques, but the macaques did not exhibit a visible  
256 reaction to their presence. We assumed that when humans or domestic animals were  
257 visible to the researchers (positioned within 30 m of the macaques), they were also  
258 visible to the macaques, and vice versa.

259 To investigate the effectiveness of the various strategies implemented by the  
260 local human population to keep the macaques out of the cultivated areas, we used a co-

261 inertia analysis (COA). COA identifies relationships between two sets of variables,  
262 based on separate standard multivariate analyses on each of the datasets, which are then  
263 connected (Dolédec & Chessel, 1994). In this case, one of the two datasets contained  
264 data on the nature of the anthropogenic encounters, and the other contained data on the  
265 macaques' reactions. Both tables share the same rows, each representing one encounter  
266 event (N = 485), and gather binary variables with values being either "yes" or "no". The  
267 first table contains three variables regarding the identity of the disturber (either human,  
268 dog, or human accompanied by dog) and six regarding the type of behavior towards the  
269 macaques: neutral, projectile, noise, non-agonistic interaction, barking, or chasing  
270 (Table 1). The second dataset contains four variables regarding the macaques' reactions  
271 to the encounters: defense, fleeing, alarm call or no visible reaction (Table 1). The  
272 standard analyses made on each dataset were multiple correspondence analyses (MCA)  
273 which detect underlying structures in a dataset containing categorical variables, bringing  
274 out a principal axis which is the vector direction maximizing the inertia in each dataset  
275 (Dolédec & Chessel, 1994). COA then identifies dimensions in both MCAs which are  
276 maximally correlated with each other. It thus identifies similar associations present in  
277 both datasets which explain their relationships. We assessed whether there was a  
278 significant correlation between the tables using Monte Carlo random permutation tests  
279 with 1000 permutations. We assessed the correlation between each variable and each  
280 co-inertia axis graphically via the angle between the axis and the arrow from the origin  
281 of the COA factorial plan to the variable: an acute angle indicates a positive correlation,  
282 an obtuse angle a negative correlation, and a 90° angle indicates no correlation.  
283 Variables which display the same type of correlation with the axes are considered as  
284 associated. The normed scores of the statistical individuals (*i.e.* the encounter events)

285 provide insight into how the individuals relate to the variables in each dataset.  
286 Individuals with higher scores on a particular axis are more influenced by the variables  
287 associated with that axis. We tested whether those scores explained variation in three  
288 additional variables: the distances fled by the macaques (in meters), the proportion of  
289 time they spent in cultivated areas that day, and the time before resuming a normal  
290 activity (in seconds). To do this, we regressed, on each axis of the COA, the normed  
291 scores of the statistical individuals with the three variables using linear regression. We  
292 performed the COA analysis using the “*ade4*” R package (Thioulouse et al., 2018).

293 To evaluate the impact of aggression by humans or dogs on the presence of  
294 macaques in cultivated areas, we estimated the distance of the groups from the  
295 cultivated areas at the time of each aggression by humans or dogs, and one hour later,  
296 using GPS locations of the groups. We considered that a group had moved closer to the  
297 cultivated areas if its distance to these areas had decreased by at least 20 m one hour  
298 later. Conversely, we considered a group as having moved away if its distance from the  
299 cultivated areas had increased by more than 20 m. This minimum distance of 20 m  
300 accounts for the uncertainty in GPS accuracy. We tested whether the location of the  
301 aggression (in cultivated or forested areas) influenced the closeness of the groups to the  
302 cultivated areas in the next hour using a Chi-square test with Monte Carlo simulation.

303

#### 304 **Ethical statement**

305 Our research complied with Moroccan laws, followed the IPS Code of Best Practices  
306 for Field Primatology, and was conducted in close partnership with Moroccan Forestry

307 authorities, under DLCDPN permits n°385 and 1367. All data collection was non-  
308 invasive. The authors declare no conflict of interest.

309

### 310 **Data availability statement**

311 The datasets generated and analyzed during the current study are available in an online  
312 OSF repository accessible at <https://osf.io/v2j7c/>.

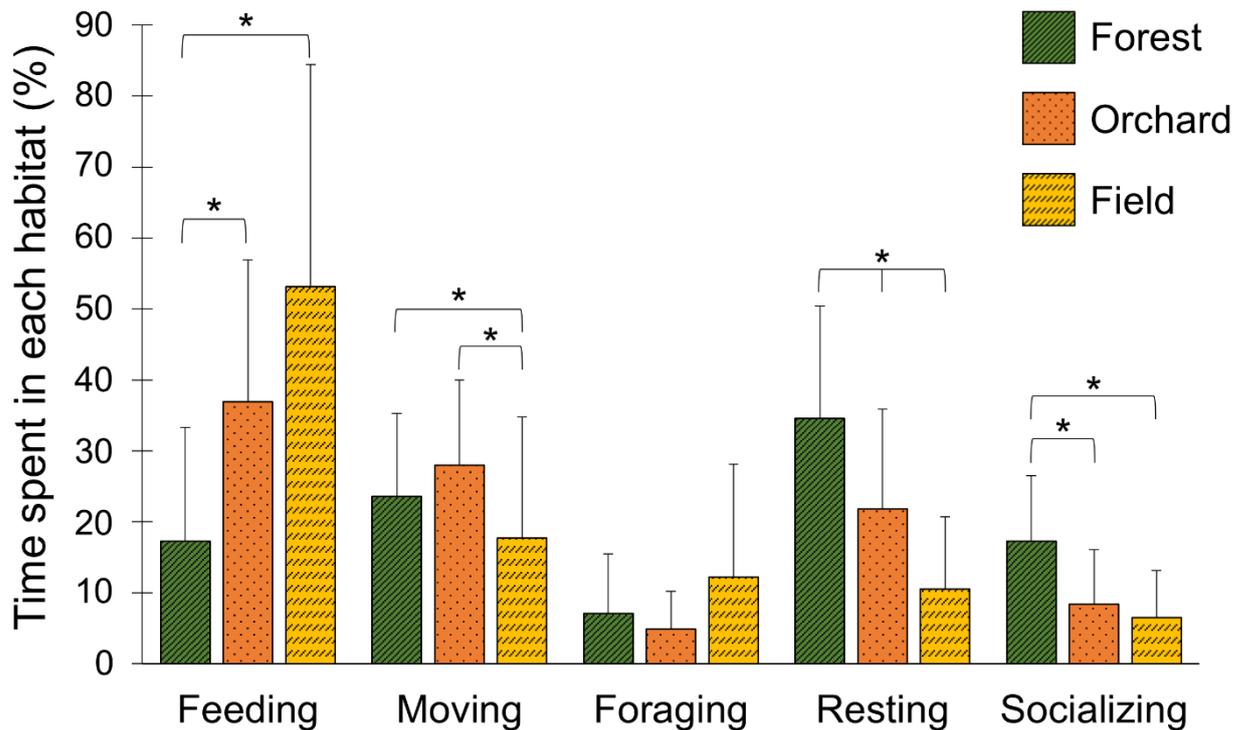
313

## 314 **Results**

### 315 *Activity patterns*

316 Activity-budgets varied between habitats with macaques spending two to three  
317 times more time feeding in cultivated areas than in forested areas (Figure 2, Table 2).  
318 The macaques moved less when they were in the field than in the orchards or the forest  
319 (Figure 2, Table 2). Resting time was highest in the forest and was twice as high in the  
320 orchards compared to the field (Figure 2, Table 2). Socializing time was higher in the  
321 forest than in both types of cultivated areas (Figure 2, Table 2). Group ID had no effect  
322 on time spent on any activity (Table 2).

323



324 **Figure 2.** Mean and standard deviation time spent in different activities in different  
 325 habitats by Barbary macaques in Ain Leuh, Morocco, in the fall of 2021 and spring-  
 326 summer of 2022. Asterisks indicate significant differences based on post-hoc Tukey  
 327 tests following generalized linear mixed models (Table 2).  
 328

329

330 **Table 2.** Results of generalized linear mixed models comparing the time spent in  
 331 different activities in different habitats by Barbary macaques in Ain Leuh, Morocco, in  
 332 the fall of 2021 and spring-summer of 2022, and effect of group ID on each activity.  
 333 Numbers in bold indicate significant p-values.

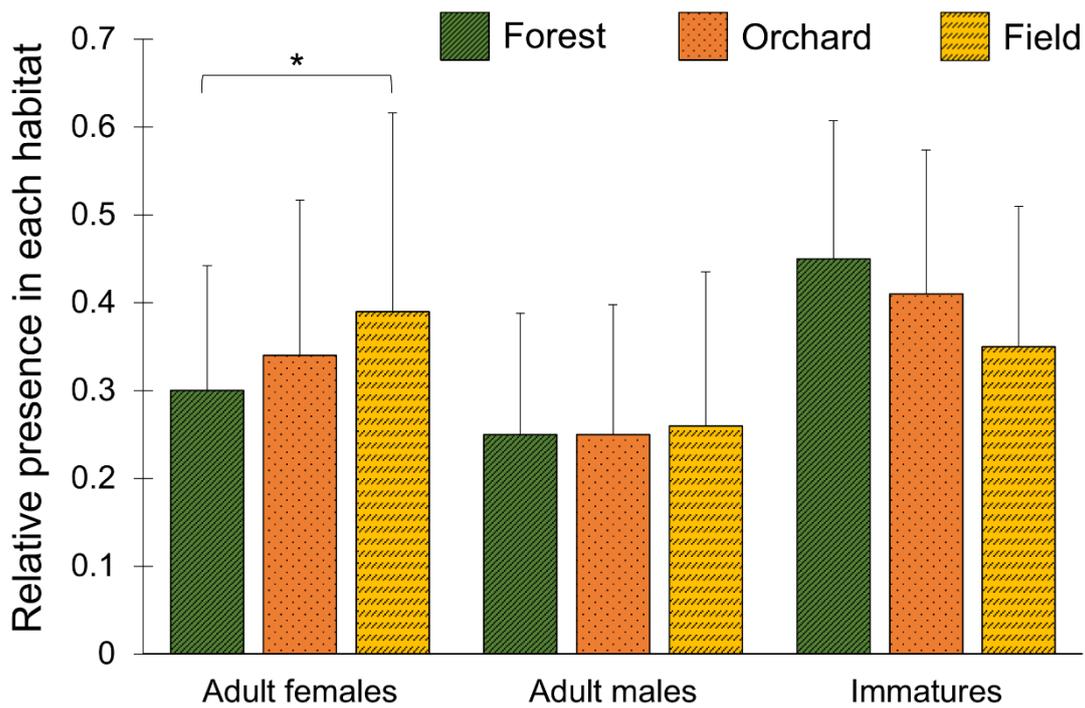
Activity	Likelihood ratio chi <sup>2</sup> , df = 2	p	Time (%) in each habitat		
			Forest	Orchard	Field
Feeding	60.89	<b>&lt;0.001</b>	17.3	36.9	53.1
		0.12			

Group ID	4.20				
Moving	29.69	< <b>0.001</b>	23.6	28	17.7
Group ID	0.34	0.84			
Foraging	3.51	0.17	7.1	4.9	12.2
Group ID	0.32	0.85			
Resting	72.92	< <b>0.001</b>	34.6	21.8	10.5
Group ID	4.14	0.13			
Socializing	90.85	< <b>0.001</b>	17.3	8.4	6.5
Group ID	0.37	0.83			

334

335 *Use of cultivated areas*

336 The macaques visited cultivated areas on 89 of 98 observation days (91%). They  
337 spent 35.9% of observation time (N = 887 hours) in cultivated areas, with 279.9 hours  
338 in the orchards and 38.9 hours in the cereal field. The mean duration of visits was 128 ±  
339 SD 151 minutes in orchards, and 68 ± SD 44 minutes in the cereal field, with high  
340 variability across visits and months. Minimum mean visit durations were 28 ± SD 22  
341 minutes (June) in orchards, and 9 minutes in the field (May, only one visit). Maximum  
342 mean durations were 321 ± SD 208 minutes in orchards (August) and 102 ± SD 73  
343 minutes in the field (November). The relative presence of adult males and immatures  
344 was similar in the three habitats (Figure 3, Table 3). Adult females represented a greater  
345 proportion of the group in the cereal field than the forest (Figure 3, Table 3). Group ID  
346 had no effect on the relative presence of either age-sex class in the three habitats (Table  
347 3).



348

349 **Figure 3.** Mean (and standard deviation) for the relative presence of three Barbary  
 350 macaque age-sex classes in each habitat in Aïn Leuh, Morocco, in the fall of 2021 and  
 351 spring-summer of 2022. Asterisks indicate significant differences based on post-hoc  
 352 Tukey tests following generalized linear mixed models (Table 3).

353

354 **Table 3.** Results of generalized linear mixed models comparing the relative presence of  
 355 three Barbary macaque age-sex classes in three habitats in Aïn Leuh, Morocco, in the  
 356 fall of 2021 and spring-summer of 2022, and effect of group ID. Numbers in bold show  
 357 significant p-values.

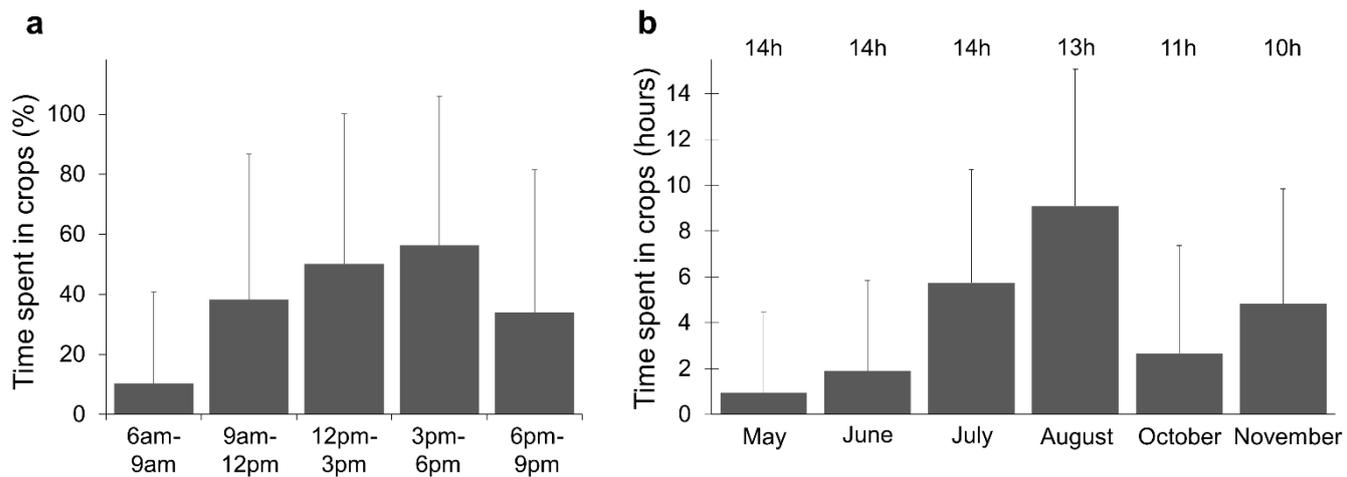
Age-sex class	Likelihood ratio chi <sup>2</sup> , df = 2	p	Relative presence in each habitat		
			Forest	Orchard	Field
Adult females	7.07	<b>0.03</b>	0.30	0.34	0.39

Group ID	2.08	0.35			
Adult males	2.87	0.24	0.25	0.25	0.26
Group ID	0.40	0.82			
Immatures	1.51	0.47	0.45	0.41	0.35
Group ID	0.14	0.93			

358

359           The period of the day and the month both had significant effects on the presence  
360 of macaques in cultivated areas (period of the day: GLMM,  $\text{Chi}^2 = 147.95$ ,  $\text{df} = 4$ ,  $p <$   
361  $0.001$ ; month: GLMM,  $\text{Chi}^2 = 81.2$ ,  $\text{df} = 5$ ,  $p < 0.001$ ). Group ID had no effect on  
362 macaque presence in cultivated areas between periods of the day (GLMM,  $\text{Chi}^2 = 0.03$ ,  
363  $\text{df} = 2$ ,  $p = 0.98$ ) or between months (GLMM,  $\text{Chi}^2 = 1.05$ ,  $\text{df} = 2$ ,  $p = 0.59$ ). The  
364 macaques spent little time inside the cultivated areas before 9am (Figure 4a), less than  
365 in any other period (post-hoc Tukey tests  $p < 0.001$ , Table S1). The percentage of time  
366 spent in cultivated areas then increased until it reached 50-60% between 12pm and 6pm  
367 (Figure 4a), higher than in any other period (post-hoc Tukey tests  $p < 0.001$ , Table S1).  
368 The macaques moved from the cultivated areas to their sleeping sites in the forest quite  
369 late in the day, as they still spent 25% of the time inside cultivated areas between 6pm  
370 and 9pm. They spent most of the daytime in cultivated areas in July, August and  
371 November ( $\geq 5$  hours per day, *i.e.*  $\geq 50\%$  of their time, Figure 4b). They spent  
372 significantly less time in cultivated areas in May, June and October ( $< 3$  hours per day,  
373 *i.e.*  $< 25\%$  of their time, Figure 4b, post-hoc Tukey tests  $p \leq 0.01$ , Table S2).

374



375

376

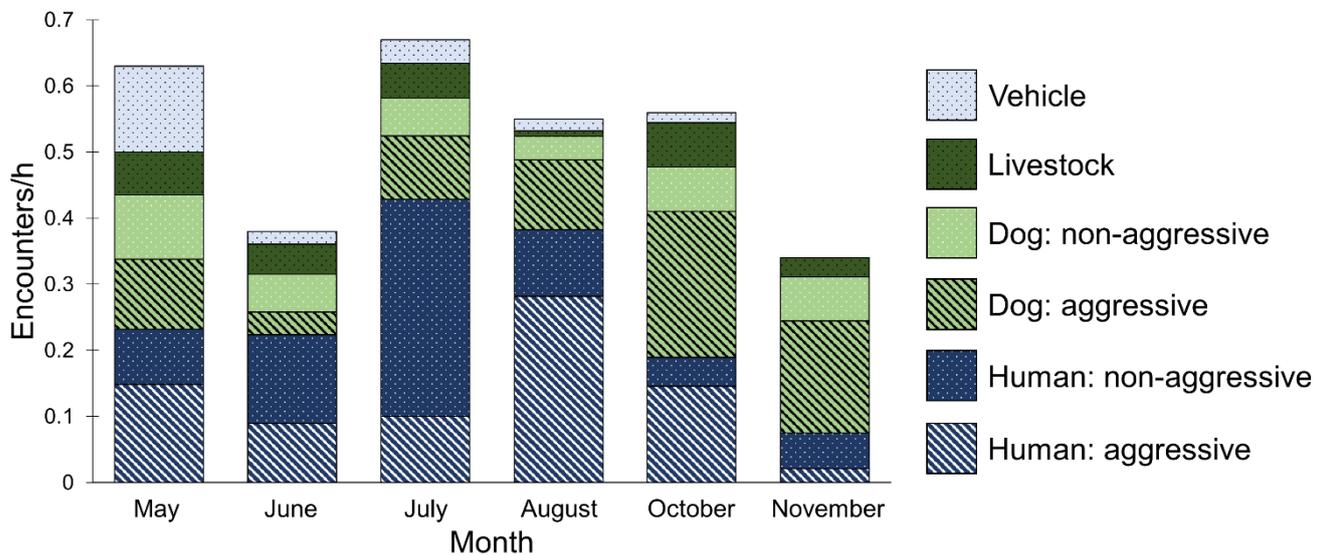
377 **Figure 4.** a) Mean percentage (and standard deviations) of daytime that Barbary  
 378 macaques spent in cultivated areas for each period of the day in Aïn Leuh, Morocco, in  
 379 the fall of 2021 and spring-summer of 2022; b) Mean daily time spent by the macaques  
 380 in cultivated areas each month. Mean day length (in hours) for each month is shown  
 381 above each bar.

382

### 383 *Human-macaque interactions*

384 Mean hourly rates of anthropogenic encounters varied between 0.34/h in  
 385 November and 0.67/h in July (Figure 5). The encounters were with four types of  
 386 disturbers: humans and dogs, who often displayed aggression towards the macaques,  
 387 livestock, who never displayed aggression towards the macaques, and passing vehicles  
 388 (Figure 5). Patterns of human aggression towards the macaques varied over the six  
 389 months of observation. Systematic guarding of cultivated areas occurred solely in May  
 390 and early June, after which the guards were no longer present at the site. The guards  
 391 employed various methods to deter macaques from crops, including throwing rocks

392 using slingshots, shouting, and creating loud noises by hitting the metal guardrails along  
 393 the road that separated the orchards from the forest (Figure 1). In July, August, October  
 394 and November, human aggression primarily came from people living or working near  
 395 the orchards, throwing projectiles (rocks and sticks), shouting at the macaques, and  
 396 encouraging domestic dogs to chase them. We never observed macaque aggression  
 397 towards humans. We observed macaque aggression towards dogs only once, when two  
 398 adult males lunged towards a dog after it had chased a juvenile.



399

400 **Figure 5.** Mean monthly rates of encounters between Barbary macaques and humans,  
 401 dogs, livestock and vehicles each month, and behaviors of humans and dogs in Aïn  
 402 Leuh, Morocco, in the fall of 2021 and spring-summer of 2022.

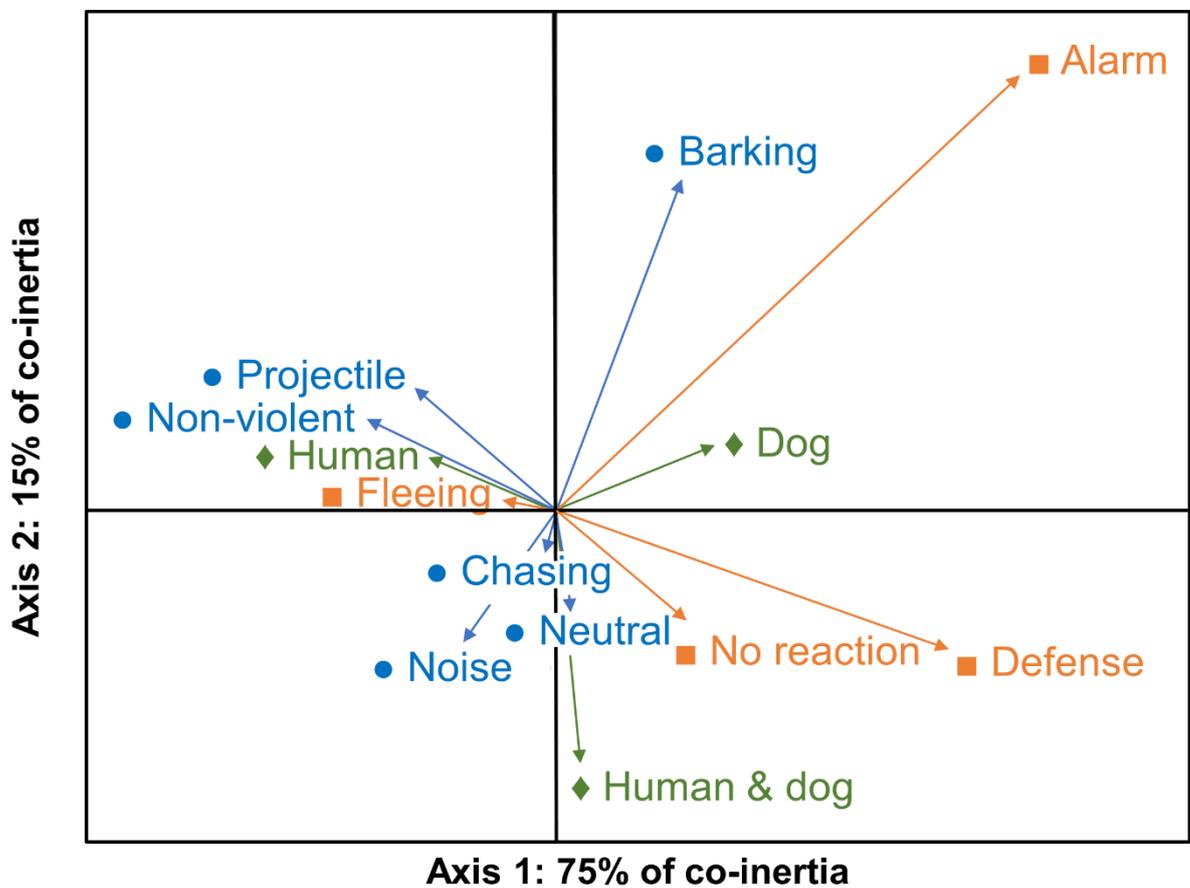
403

404 We retained the first two axes of the COA between anthropogenic encounters  
 405 and macaques' reactions (Figure 6). The first axis accounted for 75% of the total  
 406 covariance between the two tables, while the second axis accounted for 15%. The

407 correlation between the two tables was highly significant (Monte Carlo simulation,  $p =$   
408 0.001). The first axis opposes the encounters with dogs alone on the positive part, and  
409 with humans alone on the negative part (Figure 6). Fleeing was associated with the first  
410 axis on the negative part, as well as projectiles and non-violent interactions, although  
411 projectiles contributed more to the axis than non-violent interactions. This means that  
412 humans alone induced fleeing reactions when displaying overtly aggressive behaviors  
413 such as throwing projectiles, but also, to a lesser extent, when displaying non-aggressive  
414 behaviors such as trying to feed the macaques. By contrast, dogs alone tended to induce  
415 alarm calls, defense postures, or no visible reactions from the macaques. The second  
416 axis characterizes macaque reactions to noises, opposing barking dogs on the positive  
417 part to human noises on the negative part. Human noises, associated with neutral  
418 encounters, induced little reaction from the macaques, while barking dogs were strongly  
419 associated with alarm calls.

420         The linear regressions on the normed scores of the encounter events showed that  
421 distances fled were significantly negatively correlated with human encounters on the  
422 first axis (Linear regression:  $F_{1,205} = 43.69$ ,  $R^2_{\text{adj}} = 0.17$ ,  $p < 0.001$ ) but showed no  
423 significant correlation on the second axis ( $F_{1,205} = 0.003$ ,  $R^2_{\text{adj}} = -0.005$ ,  $p = 0.95$ ). This  
424 means that individual macaques fled further when encountering humans than dogs  
425 (when fleeing humans, mean: 17 m, range: 1-60 m; when fleeing dogs, mean: 9 m,  
426 range: 2-30 m), but that fleeing distance was not correlated with the types of  
427 anthropogenic noise. Time spent in cultivated areas by macaques also increased on the  
428 negative part of the first axis ( $F_{1,486} = 29.52$ ,  $R^2_{\text{adj}} = 0.05$ ,  $p < 0.001$ ), which confirms  
429 that when macaques spend more time in those areas, they receive more aggression from  
430 humans. Time spent by macaques in cultivated areas was not significantly correlated

431 with the second axis ( $F_{1,486} = 0.05$ ,  $R^2_{adj} = -0.002$ ,  $p = 0.82$ ) which means that time spent  
 432 in cultivated areas was not significantly correlated with barking dogs or human noises.  
 433 Time before resuming a normal activity after a disturbance (mean: 102 seconds, range:  
 434 5-3240 seconds) was not significantly correlated with any of the COA axes (Axis 1:  
 435  $F_{1,96} = 2.38$ ,  $R^2_{adj} = 0.01$ ,  $p = 0.13$ ; Axis 2:  $F_{1,96} = 0.17$ ,  $R^2_{adj} = 0.009$ ,  $p = 0.68$ ), meaning  
 436 that the type of anthropogenic disturbance did not influence the duration of macaque  
 437 responses.



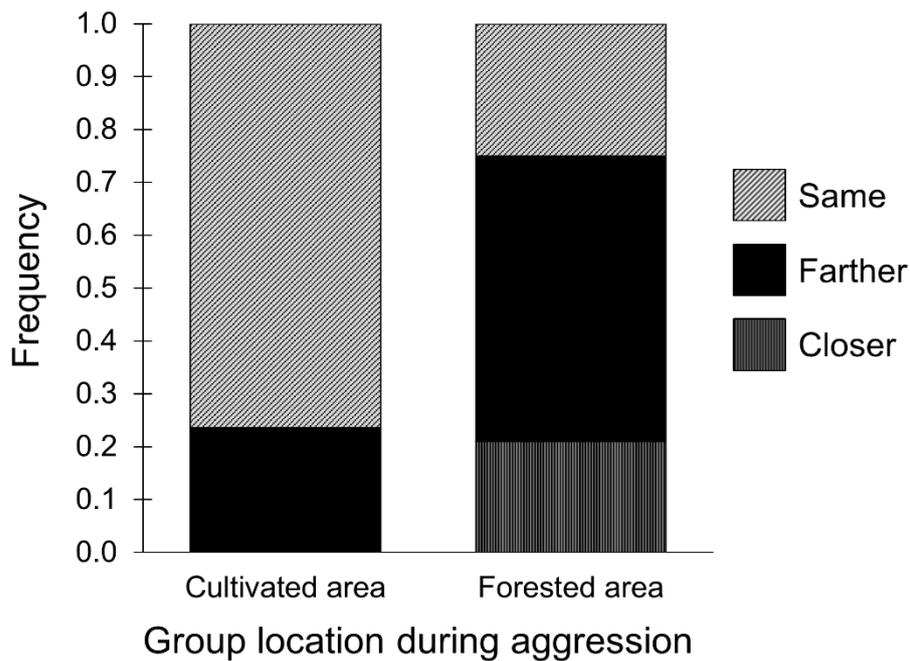
438

439 **Figure 6.** Graphical representation of a co-inertia analysis for Barbary macaque  
 440 responses to anthropogenic disturbances in Aïn Leuh, Morocco, in the fall of 2021 and  
 441 spring-summer of 2022. In green (♦) are the types of disturbers: Human: humans only;

442 Dog: dogs only; Human & dog: humans and dogs together. In blue (●) are the  
443 disturbers' behaviors: Projectile: humans throwing projectiles; Noise: humans directing  
444 loud noises at macaques; Non-violent: humans interacting non-agonistically with the  
445 macaques; Chasing: dogs chasing macaques; Barking: dogs barking at macaques;  
446 Neutral: humans and/or dogs passing by. In orange (■) are the macaques' reactions.

447

448         The macaques' distance to the cultivated areas one hour after receiving  
449 aggression from humans and/or dogs depended on their location at the time of the  
450 aggression (Chi-square test with Monte Carlo simulation:  $N=117$ ,  $\chi^2 = 32.95$ ,  $p <$   
451  $0.001$ ). When the macaques were in cultivated areas at the time of aggression, they were  
452 more likely to have remained in those areas one hour later than to have moved away  
453 from them (Figure 7). By contrast, when they were in forested areas at the time of  
454 aggression, they were more likely to have moved farther away from cultivated areas one  
455 hour later (mean: 97 m, range: 29-325 m) than to have moved closer. Human aggression  
456 towards macaques in forested rather than cultivated areas occurred mainly in May,  
457 when guards were monitoring the crops (percentage of human aggression in forested  
458 areas: 100% in May; 50% in June; 23% in July, 8% in August; 37% in October; 50% in  
459 November).



460

461 **Figure 7.** Frequency with which Barbary macaques were closer, farther, or at the same  
 462 distance from cultivated areas one hour after aggression compared to the time of the  
 463 aggression in Aïn Leuh, Morocco, in the fall of 2021 and spring-summer of 2022.

464

## 465 **Discussion**

466 Barbary macaques living at the edge of an agricultural landscape in Aïn Leuh,  
 467 Morocco, spent a large portion of their time in cultivated areas, particularly orchards.  
 468 They frequently encountered anthropogenic disturbers and received aggression from  
 469 both humans and dogs. They showed different activity patterns in the cultivated areas  
 470 compared to the forest. Contrary to our predictions, they did not avoid cultivated areas  
 471 when humans were present, and males did not use those risky areas more than females  
 472 or immatures. The macaques seemed more afraid of humans than dogs, as shown by

473 their greater fleeing responses. However, they generally did not leave the cultivated  
474 areas when attacked by either humans or dogs, but they did tend to move back into the  
475 forest when attacked before they entered the cultivated areas.

476

#### 477 **Macaque behavior in cultivated areas**

478         Barbary macaques in Ain Leuh used cultivated areas extensively, where they did  
479 not allocate as much time to resting and socializing as in the forest. This suggests that  
480 the macaques perceive cultivated areas as more dangerous than the forest, as  
481 minimizing the time devoted to activities which do not need to be performed in risky  
482 areas could be a strategy to reduce the risk of detection by humans. However, when in  
483 the orchards, they did spend a significant portion of their time resting (21.8%), which  
484 indicates that those areas are not used exclusively as foraging and feeding grounds.  
485 Macaques spent half as much time resting in the cereal field as they did in the orchards,  
486 which is unsurprising considering that Barbary macaques usually rest in trees, which  
487 were absent in the field.

488         Macaques used cultivated areas frequently and for long periods, especially  
489 orchards. While few studies have quantified the use of orchards by primates, our results  
490 are similar to those for robust capuchin monkeys (*Sapajus robustus*) in Brazil, which  
491 also spent a large proportion of their time in orchards in some months (Martins et al.,  
492 2022). In Malaysia, Southern pig-tailed macaques (*Macaca nemestrina*) visited oil palm  
493 plantations daily, with visits lasting 3 hours on average (Holzner et al., 2021). By  
494 contrast, primates typically only spend a short time in crop fields, for example under 3  
495 minutes for chacma baboons (*Papio hamadryas ursinus*) in graminoid fields in

496 Zimbabwe (Schweitzer et al., 2017), and on average 14 minutes for rhesus macaques  
497 (*Macaca mulatta*) in graminoid and vegetable fields in India (Anand & Radhakrishna,  
498 2022). These patterns of crop field use are quite different from those observed in Aïn  
499 Leuh, where Barbary macaques' average use of the cereal field lasted over one hour.  
500 Moreover, olive baboons in Nigeria minimized the risk of human detection by  
501 transporting cultivated foods out of the crop fields and eating them in safe locations  
502 (Warren et al., 2010), while we rarely saw macaques in Aïn Leuh transporting food  
503 from cultivated to forested areas. In South Africa, the core home range of a crop-  
504 foraging chacma baboon did not overlap with fields (Walton et al., 2021) whereas  
505 nearly 20% of the home range of Depog group in Aïn Leuh comprised cultivated areas  
506 (Figure 1; Neves et al., 2023a). Overall, those results suggest that Barbary macaques do  
507 not perceive cultivated areas as highly risky. In the cereal field, this finding could be  
508 explained by low levels of human retaliation and proximity to the forest edge. In the  
509 orchards, it could be explained by the fact that mature orchards resemble small forests,  
510 providing ample opportunities for macaques to hide from humans and dogs. However,  
511 these patterns of extensive crop-use can also be explained by the possibility that the  
512 benefits of crop-foraging outweigh the costs due to the scarcity of natural resources at  
513 our study site. While we did not quantify resource availability in Aïn Leuh, we observed  
514 clear signs of habitat degradation, particularly in the herbaceous layer which suffered  
515 from heavy grazing by sheep and goats. Overgrazing has dramatically increased in the  
516 Middle-Atlas over the last decades and is largely responsible for the high levels of land  
517 degradation in the region (Kouba et al., 2018).

518         The higher presence of females in the cereal field, relative to males and  
519 immatures, was contrary to our predictions. Typically, in primates, adult males, being

520 larger and stronger, tend to engage in riskier behaviors than other age-sex classes, which  
521 involves more crop visits (chimpanzees: Hockings et al., 2007; olive baboons: Strum,  
522 1994), spending more time in crops (vervets: Saj et al., 1999), and leading the group  
523 into crops (Buton macaques: Priston, 2005). However, in chacma baboons, both males  
524 and females initiate crop-foraging events (Schweitzer et al., 2017). In Sumatran  
525 orangutans (*Pongo abelii*), females were more likely to forage in crops than males  
526 (Campbell-Smith et al., 2011). It has been suggested that when crop-foraging risks are  
527 high, males are more likely to forage on crops than females (Humle & Hill, 2016).  
528 However, when levels of retaliation by humans are low, females may forage on crops as  
529 frequently or even more than males due to their higher needs to meet reproductive  
530 demands (Humle & Hill, 2016). In Aïn Leuh, the cereal field was not as important to  
531 farmers as the orchards. The fruits in the orchards were primarily grown for commercial  
532 purposes, making them a crucial source of revenue. In contrast, cereals were not sold.  
533 After harvesting, they remained in the field to feed passing herds of livestock. Farmers  
534 were thus less inclined to chase away macaques from the field than from the orchards,  
535 which could have led female macaques to feel relatively safe in the field. Additionally,  
536 the cereal field was directly adjacent to the forest, unlike the orchards which were  
537 separated from the forest by the road. If disturbed when foraging in the field, macaques  
538 thus had the possibility to quickly seek refuge in the forest, which likely contributed to  
539 the relative perceived safety of that area.

540         Contrary to our predictions, the macaques did not avoid cultivated areas during  
541 times of human activity. Agricultural workers, who worked primarily in the orchards,  
542 were usually present between 9am and 6pm. We expected the macaques to visit crops  
543 primarily outside of these hours, either just after dawn or before dusk, as observed in

544 long-tailed macaques (*Macaca fascicularis umbrosus*; Mishra et al., 2020). This would  
545 seem particularly feasible considering that the primary sleeping site of the main focal  
546 group, Depog, was near the orchards (Neves et al., 2023a). This pattern of high reuse of  
547 the same sleeping site contrasts with those of groups living in sites with no access to  
548 human resources, which usually avoid using the same sleeping site on consecutive  
549 nights to balance the costs and benefits of predation risk and proximity to food (Albert  
550 et al., 2011; Neves et al., 2023a). It is however commonly observed in primate groups  
551 which regularly use human resources (Almann & Muruthi, 1988; Neves et al., 2023a;  
552 Strum, 2010) and suggests that macaques in Aïn Leuh might choose to minimize  
553 security while maximizing energetic gains (Neves et al., 2023a).

554

#### 555 **Macaque responses to anthropogenic encounters**

556 Rates of anthropogenic encounters and aggression towards macaques were high  
557 in Aïn Leuh, and the macaques' reactions provided interesting information on their  
558 perceptions of risks. Throwing projectiles was effective to induce fleeing reactions, but  
559 the macaques also tended to flee when approached by humans who tried to feed them or  
560 take pictures. Interestingly, the macaques in Aïn Leuh never accepted food when we  
561 observed humans offering it to them, indicating that they do not perceive humans as a  
562 potential source of food but rather perceive them as inherently dangerous, even in the  
563 absence of overt aggression. Dogs induced fewer fleeing reactions from the macaques,  
564 likely because they were unable to reach the macaques when they were in trees. Despite  
565 their fear of humans, the macaques fled short distances when receiving aggression from  
566 humans and the aggression was not sufficient to drive them out of cultivated areas.

567 While in orchards, the macaques usually moved from tree to tree to avoid humans but  
568 did not leave the fruit trees. This suggests that chasing macaques away from the  
569 orchards once they have already settled in them is nearly impossible with the tactics  
570 currently used by farmers. However, pushing them away towards the forest before they  
571 enter seems effective. This tactic was used almost exclusively by guards who were hired  
572 to monitor crops in May and early June, before cherry harvesting. For financial reasons,  
573 those guards were employed only during this period of cherry maturation, considered by  
574 farmers as the most critical. The macaques spent the least time in cultivated areas during  
575 this period, which reinforces the conclusion that the guards' strategy is effective. This  
576 strategy consisted of monitoring the forest edges close to the cultivated areas and  
577 pushing macaques back to the forest when they approached. These findings align with  
578 studies that have shown the effectiveness of systematic crop-guarding against crop-  
579 foraging primates in other areas (Hill & Wallace, 2012; Koirala et al., 2021; Mekonnen  
580 et al., 2020). However, during the six months of observation in Aïn Leuh, we only  
581 observed continuous crop-guarding by employed guards for one month, while in the  
582 remaining five months, farmers sporadically attempted to chase monkeys away from  
583 small areas surrounding their houses. The high use of cultivated areas by Barbary  
584 macaques in the absence of guards supports the conclusion that guarding by farmers  
585 who are distracted by other tasks is not as successful as continuous monitoring by  
586 employed guards (Hill & Wallace, 2012). Although the financial implications must be  
587 considered, crop-guarding appears to be a suitable approach for Barbary macaques.

588           It is crucial to consider the potential negative impacts of violent methods used  
589 by guards. The use of slingshots to throw rocks at the macaques can result in serious  
590 injuries if the macaques are hit. Living in such a conflicted and stressful environment

591 can have significant implications for the demography of macaque groups. In the case of  
592 Depog group, many individuals disappeared during our study, particularly adult  
593 females, resulting in a mortality of 37%, in contrast to the <3% mortality observed in  
594 forest sites with low human pressure (Neves et al., 2023b). We therefore recommend  
595 throwing projectiles near the macaques, not directly at them to ensure safety while  
596 maintaining levels of intimidation. Crop-foraging deterrence should be viewed through  
597 the lens of optimal foraging theory, *i.e.* as a balance of costs and benefits (Hill, 2017).  
598 To be effective, deterrence must increase the costs or decrease the benefits of crop-  
599 foraging compared to natural foraging (Strum, 2010). When Endangered and protected  
600 species such as Barbary macaques are concerned, increasing the costs can only go so far  
601 without threatening the survival of individuals and populations. Therefore, efforts  
602 should also be put towards increasing the benefits of natural foraging, which requires  
603 changing current strategies of Barbary macaque habitat management, namely decreasing  
604 grazing and logging pressure and favoring more productive natural habitats.

605

## 606 **Conclusion**

607 There is an urgent need to develop safe and effective methods to deter Barbary  
608 macaques from crop-foraging while maintaining close collaboration with local farmer  
609 associations and official institutions. Prioritizing the conservation of this Endangered  
610 species while addressing the concerns of local farmers is crucial and requires effective  
611 crop-foraging deterrents which do not jeopardize the macaques' survival. We showed  
612 that despite frequent aggressive encounters with humans and dogs, Barbary macaques  
613 do not avoid the riskiest habitats and are able to use crops extensively. Trying to chase

614 them away after they have settled inside the orchards is unlikely to succeed, while  
615 monitoring the crops' edges and pushing them away before they enter is much more  
616 effective. Those insights into Barbary macaque behavioral responses to conflicts with  
617 humans and crop-foraging deterrence are important for the development of effective  
618 crop-protection methods and ultimately for human-Barbary macaque coexistence.  
619 Future research will include interdisciplinary analyses involving both ecological and  
620 socio-economical models which are expected to result in a range of potential deterrents  
621 to be tested on Barbary macaques in Ain Leuh. In the broader global context of  
622 increasing land-use change and human-wildlife conflicts, research of this nature holds  
623 significant importance.

#### 624 **Supporting Information**

625 Supporting Information is available online.

#### 626 **Acknowledgments**

627 Financial support for this study came from the NGO AAP (Animal Advocacy  
628 and Protection, Morocco and Netherlands), the French ANR project COHUMAG ANR-  
629 22-CE03-0008-01, the CNRS (Centre National de la Recherche Scientifique, France).  
630 Our study was conducted in close partnership with the “Agence Nationale des Eaux et  
631 Forêts” and the Director of the Ifrane National Park, Morocco. We thank L. Oukannou  
632 who helped us in the choice of the study site in Morocco, the team of the Ifrane  
633 National Park who assisted us in the field, and the local farmers who let us work on  
634 their lands. We are very grateful to Ellen Merz, Gilbert de Turkheim and Guillaume de  
635 Turkheim (La montagne des singes, France) who kindly hosted N. Ménard and E.

636 Neves and provided valuable assistance in identifying the age and sex of Barbary  
637 macaques. We thank the Associate Editor Addisu Mekonnen, the Editor-in-chief Joanna  
638 Setchell, as well as two anonymous reviewers, for their suggestions which greatly  
639 improved this manuscript. This is a scientific production of UMR CNRS 6553/OSUR,  
640 University of Rennes.

#### 641 **CRedit authorship contribution statement**

642 EN, NM and PLG conceived and designed the study, developed the methodology and  
643 wrote the manuscript. EN, NM and CD collected the data. EN analyzed the data. SIC,  
644 NM, PLG and EN acquired funding. SIC and ZA administered the project and provided  
645 essential resources. All authors read and approved the final manuscript.

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