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DOMAINE DE FORMATION : SCIENCES, TECHNOLOGIES, SANTE

Impact of Anthropogenic Pressure on the Behaviour of Barbary Macaques
(*Macaca sylvanus*) in Gibraltar

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ABSTRACT

Wildlife tourism is an increasingly widespread practice throughout the world. Primates are particularly popular with visitors because of their behavioural and physiological proximity to humans. In this study, we investigate the impact of anthropogenic pressure from visitors on the behaviour of Barbary macaques (*Macaca sylvanus*) in the Upper Rock Nature Reserve in Gibraltar. We collected data for 2 months from January to March 2025, on the number of tourists, vehicles, human-macaque interactions and noise intensity in 10 different sites, and on the impact of these anthropogenic pressures on the behaviour of 47 individuals (self-centred behaviour, agonistic behaviour and affiliative behaviour). The results showed a heterogeneous spatialisation of anthropogenic pressure according to the different sites. We showed a negative association between the number of visitors and the number of yawns, and a positive association between the number of vehicles and the number of yawns, as well as a positive associative trend between self-scratching and the number of visitors. These results suggest that certain self-directed behaviours, such as yawning and self-scratching, may be sensitive to specific indicators of anthropogenic pressure, while affiliative and agonistic behaviours appear to be less directly affected, highlighting a possible modulation linked to other factors (hierarchy, intra-group pressure, etc.). By highlighting the diversity of behavioural responses to gradients in tourist numbers, this study highlights the need for differentiated management of sites according to their level of exposure, in order to preserve the well-being of the macaques and promote sustainable cohabitation with visitors.

Key words: anthropised environments, wildlife tourism, human-macaque interactions, ethology, primatology

RÉSUMÉ

Le tourisme animalier est une pratique de plus en plus répandue dans le monde. Les primates sont particulièrement appréciés des visiteurs de par leur proximité comportementale et physiologique avec les humains. Dans cette étude, nous nous intéressons aux conséquences de la pression anthropique liée aux visiteurs sur le comportement des macaques de barbarie (*Macaca sylvanus*) dans la Upper Rock Nature Reserve de Gibraltar. Nous avons collecté des données pendant 2 mois de janvier à mars 2025, sur le nombre de touristes, de véhicules, d'interactions humains-macaques et d'intensité sonore dans 10 sites différents, et sur l'impact de ces pressions anthropiques sur le comportement de 47 individus (comportements auto-centrés, comportements agonistiques et comportements affiliatifs). Les résultats ont montré une spatialisation hétérogène de la pression anthropique en fonction des différents sites. Nous montrons une association négative entre le nombre de visiteurs et le nombre de bâillements, et une association positive entre le nombre de véhicules et le nombre de bâillements, ainsi qu'une tendance associative positive entre les comportements d'auto-grattage et le nombre de visiteurs. Aucune autre association significative entre le nombre de visiteurs et de véhicules n'a été trouvée avec les autres comportements. Ces résultats suggèrent que certains comportements auto-dirigés, comme le bâillement ou l'auto-grattage, peuvent être sensibles à des indicateurs spécifiques de la pression anthropique, tandis que les comportements affiliatifs et agonistiques semblent moins directement affectés, soulignant une possible modulation liée à d'autres facteurs (hiérarchie, pression intragroupe etc.). En soulignant la diversité des réponses comportementales face à des gradients de fréquentation touristique, cette étude met en lumière la nécessité d'une gestion différenciée des sites en fonction de leur niveau d'exposition, afin de préserver le bien-être des macaques et de favoriser une cohabitation durable avec les visiteurs.

Mots-clés : environnements anthropisés, tourisme animalier, interactions humain-macaque, éthologie, primatologie

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INTRODUCTION

Over the past century, the number of people engaging in recreational activities aimed at observing wildlife has grown considerably (Khanra et al. 2021). This growing interest reflects an increasing appreciation for nature, and coincides with intensified anthropogenic pressures on ecosystems, contributing to rising species extinction rates (Barnosky et al., 2011; Di Marco et al., 2018) and significantly altering animal behaviour (Ardiantiono et al., 2018; Bessa et al., 2017; Harris & Haskell, 2013; Pérez-Galicia et al., 2017). For example, both bottlenose dolphins (*Tursiops truncatus*) and grizzly bears (*Ursus arctos*) experience reduced foraging efficiency when exposed to human observers (Symons et al., 2014; Field et al., 2024). Similarly, anthropogenic presence in wildlife contexts—such as noise, roads, or artificial night lighting—has been shown to interfere with mating and parental care across species. Today, one of the most studied domain of anthropogenic disturbance is the effect of noise on marine mammals (Lakshnarayan Kumar Bhagarathi et al., 2024), as seen in the reef-dwelling fish *Acanthochromis polyacanthus*, whose exposure to motorboat noise leads to reduced paternal care (Nedelec et al., 2017).

Primates are particularly popular with tourists as they are social animals, entertaining to watch, and share physical and behavioural similarities with humans. Wildlife tourism is now very common with macaques and orangutans in Southeast Asia, mountain gorillas and chimpanzees in East Africa, and baboons in East and Southern Africa (McKinney, 2016). In Europe, the only place where monkeys can be observed in a free-ranging environment is in Gibraltar, where the Barbary macaques (*Macaca sylvanus*) have become a major tourist attraction, drawing visitors eager to observe and photograph free-ranging monkeys in close proximity. However, as tourism and human populations expand, so too does human presence in primate habitats. Rapid population growth and anthropogenic influences are largely responsible for the decline of many non-human primate species, 125 of which are classified as "endangered" on the IUCN Red List (2020), and 65 as "critically endangered" (Dirzo et al. 2014; Estrada et al. 2017). Among them is the Barbary macaque (*Macaca sylvanus*), the only macaque species found outside Asia, currently listed as endangered due to habitat loss, illegal trade, and increasing human–wildlife conflict (IUCN 2020). Wildlife tourism has greatly contributed to the increase in interspecies interactions between humans and nonhuman primates, leading to consequences for the latter's behaviors and ecology (McKinney, 2016).

The presence of tourists shapes the nature of interactions between humans and monkeys. Regardless of the interactions themselves, the mere presence of tourists increases the ambient noise level, which leads to an increase in threat behaviour in Tibetan macaques (*Macaca thibetana*; Ruesto et al., 2010). Indeed, when tourists actively participate in interactions, human engagement behaviours often provoke agonistic behaviours from monkeys (Ruesto et al., 2010; Xia et al., 2017; Mansell & McKinney, 2021). Specifically, provisioning from tourists leads to an increase in aggression in monkeys (Wheatley & Putra, 1994), and reduces their affiliative behaviours with conspecifics, such as allogrooming and social play (Chamove et al., 1988; de la Torre et al., 2000; O’Leary & Fa, 1993). More recently, in Southeast Asia, studies have highlighted that human presence alters grooming dynamics: grooming decreased under moderate disturbance, but increased under high-stress conditions (Marty et al., 2019), and grooming bouts were shorter, more fragmented, and less often reciprocated in contexts with frequent human–macaque interactions (Kaburu et al., 2019).

In anthropogenic contexts, not only do humans initiate interactions more often than primates do (Hsu et al. 2009; Sabbatini et al. 2006; Suzin et al. 2017), but they also tend not to adapt their actions in response to the behaviors of the latter (Sabbatini et al. 2006). Among visitors, tourists are the most likely to be intrusive (Behie et al., 2010), generating stress in primates through repeated and unpredictable exposure, which can in turn lead to aggression towards humans (Muehlenbein et al., 2012; Kaburu et al., 2019). Behavioural indicators such as self-directed behaviours (SDBs) offer a valuable proxy for evaluating anxiety levels in non-human primates (Wallace et al., 2019). SDB’s including self-scratching and yawning are widely recognized as markers of stress and anxiety (Maestripietri et al., 1992; Troisi, 2002), as shown for example as scratching increases after aggressive interactions in Japanese macaques (*Macaca fuscata*; Schino et al., 2004), following perceived threats in captive chimpanzees (*Pan troglodytes*; Baker & Aureli, 1997), and in long-tailed macaques under anxiolytic drug treatment (*Macaca fascicularis*; Schino et al., 1991). Yawning, likewise, has been observed to rise in contexts of social tension, such as during intergroup conflict or in the presence of dominant individuals (Castles et al., 1999; Baker & Aureli, 1997). In wild apes, it has been shown that human presence appears to elicit yawning (Goodall, 1968; Nishida et al., 1999).

Although previous studies have investigated injury rates involving humans and dietary variation through stable isotope analysis (Schurr et al., 2012), the effects of anthropogenic pressure on the

behavioural responses of Barbary macaques in Gibraltar—particularly affiliative, agonistic, and stress-related behaviours—have not yet been thoroughly examined, despite this population sharing much of its environment with humans.

In this study, we investigated a specific case of behavioural response to anthropogenic disturbance in the Barbary macaque population of Gibraltar, where individuals are frequently exposed to human visitors arriving by car, taxi, bus, cable car, or on foot. The Upper Rock Nature Reserve, a highly modified and tourist-frequented area, receives more than 700,000 visitors annually, with peaks during the summer months reaching over 72,000 monthly (Fuentes, 2007). Human presence is concentrated around key attractions—many of which are macaque viewing sites—resulting in intense and repeated human–macaque encounters. O’Leary and Fa (1993) documented up to 99.6 interactions per hour during peak periods, with macaques spending more than 13% of their time interacting with humans, most of whom are tourists.

We formulated the hypothesis that increasing levels of human disturbance—measured through the number of visitors and vehicles present—would significantly affect the behaviour of Barbary macaques in Gibraltar. Specifically, we expected that greater human and vehicle presence would be associated with a rise in self-directed behaviours, such as yawning and self-scratching.

We also hypothesised that the frequency of agonistic behaviours, including threats and aggression, would increase under higher levels of humans and vehicles.

Finally, we predicted that grooming behaviour, a key affiliative activity, would be negatively affected: not only would total grooming time decrease, but grooming would also occur in shorter, more fragmented bouts, reflecting a disruption in social cohesion due to human and vehicle presence.

MATERIAL & METHODS

Study Site, Species, Population, and Groups

The Barbary macaques from Gibraltar (36° 08' 24"E, 5° 21' 00"W) are divided into ten distinct troops of varying sizes (min: 4 individuals; max: ca. 55 individuals), numbering a total of about 230 individuals. All troops but one live in the Upper Rock Nature Reserve, a protected area of 2.44 km² that attracts a high level of tourism, with around 3,000 visitors a day. Each group of macaques is provisioned twice daily with peanuts, barley, fruits, and vegetables at feeding sites, though the exact feeding times vary. While it is officially forbidden to feed or touch the animals, these rules are not systematically respected by visitors nor strictly enforced by local authorities. Temperatures in the area range between 14 and 35 degrees Celsius throughout the year. We studied six groups of individually identifiable Barbary macaques in Gibraltar: Anglian Way (AW), Apes Den (AD), Middle Hill (MH), O'Hara's (OH), Prince Philip's Arch (PA), and Rock Gun (RG). These groups differ in their degree of exposure to humans—particularly tourists—ranging from no contact (MH) to sporadic or regular interactions for the other groups. This variation is primarily shaped by the geographic characteristics of each group's range, including its size, proximity to tourist areas, and intensity of human presence, such as the number of visitors and vehicles. The troops are distributed across distinct, though sometimes overlapping, locations within the Upper Rock Nature Reserve, including sites such as Ape's Den (also called Queen's Gate), Great Siege Tunnel, Middle Hill, O'Hara's Road, Prince Philip's Arch, St Michael Road, Charles V Wall Path, Princess Caroline's Battery, St Michael's Cave (Entry and Exit), where visitor pressure can vary greatly from site to site (see Figure 1 for details). These spatial and anthropogenic differences are likely to influence the frequency and nature of interactions between humans and macaques.



Figure 1. Map of location of different observations in Upper Rock Nature Reserve, Gibraltar (a). Photographies of macaque individuals in Ape's Den (b), and Prince Philip's Arch (c) (circled in red are visible interactions between macaques and visitors).

Data Collection and Extraction

The data collection for this project took place between January 10th and March 10th 2025. Two complementary approaches were used to investigate the effects of anthropogenic pressure on macaque behaviour: (1) event sampling to quantify anthropogenic variables across sites, and (2) individual focal follows (Altmann, 1974) to assess behavioural responses.

A total of 31 event sampling sessions were conducted across 10 distinct locations corresponding to the home ranges of the six studied groups (Ape's Den ($n = 6$), Charles V Wall Path ($n = 2$), Great Siege Tunnel ($n = 1$), Middle Hill ($n = 2$), O'Hara's Rd ($n = 1$), Prince Philip's Arch ($n = 3$), Princess Caroline's Battery ($n = 1$), St Michael Rd ($n = 6$), St Michael's Cave Entry ($n = 5$), and St Michael's Cave Exit ($n = 4$)). During each session, data on noise intensity using the Decibel X application (SkyPaw Co. Ltd., 2025), number of macaques, number of visitors, number of vehicles, and detailed human-macaque interactions were collected every five minutes over an approximative

one-hour period, within a defined geographical area whose size had been previously calculated using QGIS software (QGIS Development Team, 2023) with recorded GPS locations of the limits of each area. Across the study period, we obtained 64 one-hour focal follows (46.7 ± 2.31 minutes) on 47 adult individuals both male and female, during which behaviours were recorded every minute. The behaviours of interest were categorized into three groups: (1) grooming behaviour, measured as the total duration of grooming (given or received, undistinguished) per focal follow, and the number of distinct grooming bouts (defined by a pause of at least one minute); (2) agonistic behaviours (threats and aggression given); and (3) self-directed behaviours (self-scratching and yawning), as well as contextual variables including the number of tourists within 30 meters and within 3 meters of the focal individual, the number of visible conspecifics, and the number and details of interactions between macaques and humans. Details on behaviours can be seen in Table 1, which is adapted from the ethogram of O'Leary & Fa (1993). Both focal follows and event sampling were recorded using CyberTracker software (CyberTracker Conservation, 2022).

Behaviour	Definition
<i>Self-scratching</i>	Repetitive self-directed scratching using fingers/nails; not social; excludes grooming.
<i>Yawning</i>	Mouth opened wide; upper canines clearly visible; excludes partial or closed-mouth yawns.
<i>Agonistic</i>	A threat, chase or attack directed at another macaque or in a dyadic interaction with an infant.
<i>Grooming</i>	Allogrooming or being groomed by another individual.
<i>Interaction</i>	Any behaviour by a human that involves direct or indirect engagement with a macaque, including physical gestures, vocalisations directed toward the animal, attempts to touch or feed, or approaching within a distance that elicits a visible response (e.g., withdrawal, vigilance, or interruption of ongoing activity).

Table 1. Activity categories and interaction types (adapted from O'Leary and Fa, 1993)

Ethics Notes

During the research, particular care was taken not to interrupt the macaques, whether during their feeding or resting time, or during social interactions. A minimum observation distance was respected as much as possible. This project and methods were approved by the Ethics Board Committee of the Department of Archaeology from the University of Cambridge, and by the Gibraltar Macaques Management team.

Data Analyses

All statistical analyses were carried out using R software, version 4.4.0 (R Core Team, 2024).

First, we explored how anthropogenic pressure varied across the different sites by comparing the density (frequency per m² every 5 minutes) of visitors, vehicles, human–macaque interactions, and the noise levels between locations. To do so, we fitted four separate linear mixed models (LMM: models 1.1 to 1.4), each using one of these anthropogenic variables as the response variable and location as the fixed effect, using the *lme* function from the ‘nlme’ package (v. 3.1-164).

We then aimed to investigate how different indicators of human presence were related to one another, using data collected through event sampling. Specifically, we tested whether the number of human–macaque interactions was predicted by the number of visitors and vehicles using a generalized linear mixed model with Poisson structure (GLMM; model 2), using the function *glmer* of the R package ‘lme4’ (v. 3.1-164). In addition, we used a linear mixed model (LMM; model 3) to test whether noise intensity—considered a complementary environmental indicator of human pressure—was predicted by the number of visitors and vehicles, using the *lme* function from the ‘nlme’ package (v. 3.1-164). To explore whether behavioural responses to anthropogenic pressure differed between macaque groups, we fitted a set of generalized linear mixed models with Poisson structure (GLMM: models 4.1 to 4.6), in which behavioural variables — self-scratching, yawning, aggression (received or given), total grooming time, and the frequency of grooming bouts — were modeled as a function of group identity (home group as fixed effect).

We then assessed the effects of human density and vehicle density on the same behavioural variables using data collected during focal follows, by fitting a set of Poisson-structured GLMMs (models 5.1 to 5.6).

In all mixed-effect models, individual identity was included as a random effect in order to control for repeated-measures effects. We verified the absence of overdispersion in GLMM-type models with a Poisson distribution. The absence of collinearity between explanatory variables was verified using variance inflation factors (VIF), which remained below 2 (Fox & Monette, 1992). Where necessary, post hoc tests were performed, and significance levels were adjusted using the Bonferroni-Holm correction (Holm, 1979). The significance of fixed effects was established using likelihood tests (anova, test = “Chisq”), comparing the full model with a null model lacking the test predictors and keeping the same random effect structure (R function *drop1*; Dobson, 2008).

RESULTS

Descriptive Overview

During the 31 event sampling sessions, we recorded an average of 12.3 human–macaque interactions (mean $\pm$ SD: 12.3 ± 11.9 ; range: 0–47), 139.5 visitors (139.5 ± 104.0 ; range: 26–455), 13.7 vehicles (13.7 ± 13.2 ; range: 0–63), and a noise intensity of 54.0 decibels (54.0 ± 4.5 ; range: 45.9–66.6) per session. Event sampling sessions lasted on average 60.1 ± 2.17 minutes (range: 47–123).

In total, across 64 focal follow sessions on 47 individuals, we recorded 118 human–macaque interactions. Of these, 13.6% were initiated by macaques ($n = 16$), 61.0% by visitors ($n = 72$), and 21.2% by taxi drivers ($n = 25$), corresponding to a mean of 3.6 interactions per hour per individual. Focal follows lasted 46.7 ± 2.31 minutes on average (range: 1.8–66.8). On average, focal individuals were surrounded by 6.15 ± 7.39 visitors per minute, including 0.42 ± 1.38 within 3 meters, and 0.21 ± 0.84 vehicles.

Quantification of Anthropogenic Pressure

Effects of anthropogenic variables on spatial distribution

Relationship between four anthropogenic factors (human, vehicle, interaction density and noise intensity) and location

Full-null model comparisons for model 1.1 showed that human density was significantly affected by the test predictors (LRT: $\chi^2 = 61.72$, $d.f. = 9$, $p < 0.001$). The linear mixed-effects model revealed a strong effect of location site on human density (LMM: *marginal* $R^2 = 0.88$, $n = 31$, $p < 0.001$; Figure X). Post-hoc Tukey tests revealed 10 statistically significant pairwise comparisons after correction ($\alpha = 0.05$). The PPA site was significantly more frequented than all the other locations ($p < 0.001$) and other sites did not differ significantly from one another ($p > 0.05$). A visual representation of the spatial gradient of tourist frequency across sites is shown in Figure 2a, supporting the statistical findings.

Full-null model comparisons for vehicle density (model 1.2) revealed a significant effect of the test predictors (LRT: $\chi^2 = 65.33$, $d.f. = 9$, $p < 0.001$). The linear mixed-effects model showed that vehicle frequency significantly varied across observation sites (LMM: *marginal* $R^2 = 0.85$, $n = 31$, $p < 0.001$; Figure 2b). Post-hoc Tukey tests identified seven significant pairwise comparisons after correction ($\alpha = 0.05$). The results show that the PPA site differs significantly from seven other

locations in terms of vehicle presence: Ape's Den, Middle Hill, O'Hara's Battery Rd, St Michael Rd, Charles V Wall Path, as well as St Michael's Cave entrance and exit ($p < 0.01$ in all cases). Additionally, Princess Caroline's Battery differs significantly from the Charles V Wall Path ($p = 0.03$). No other significant differences were found between the remaining locations.

Full-null model comparisons for model 1.3 showed that human-macaque interactions were significantly affected by site location (LRT: $\chi^2 = 33.82$, $d.f. = 9$, $p < 0.001$). The linear mixed-effects model indicated a strong effect of location on the frequency of interspecies interactions (LMM: *marginal* $R^2 = 0.68$, $n = 31$, $p < 0.001$; Figure 2c). The Tukey post-hoc test results show that the PPA site exhibits significant differences in the number of interactions compared to six other sites: Ape's Den, Great Siege Tunnel, Middle Hill, St Michael Rd, Charles V Wall Path, and both the entrance and exit of St Michael's Cave ($p < 0.01$ for all except O'Hara's Rd with $p = 0.01$). Besides PPA, Middle Hill also differs significantly from Ape's Den ($p = 0.02$). No other significant differences were found between the remaining sites.

Full-null model comparisons for model 1.4 showed that noise intensity was significantly affected by site location (LRT: $\chi^2 = 51.45$, $d.f. = 9$, $p < 0.001$). The linear mixed-effects model indicated a strong effect of location on the frequency of interactions initiated by tourists towards macaques (LMM: *marginal* $R^2 = 0.83$, $n = 31$, $p < 0.001$; Figure 2d). Middle Hill differs significantly from Prince Philip's Arch ($p < 0.001$), Great Siege Tunnel ($p = 0.02$), as well as from the entrance ($p = 0.02024$) and exit ($p = 0.04$) of St Michael's Cave, with consistently lower noise levels. In addition, Prince Philip's Arch shows significantly higher noise levels than O'Hara's Rd ($p < 0.001$), Charles V Wall Path ($p < 0.001$), and St Michael Rd ($p < 0.001$). Charles V Wall Path differs significantly from Great Siege Tunnel ($p = 0.02$), Prince Philip's Arch ($p < 0.001$), and the entrance ($p = 0.02$) and exit ($p = 0.04$) of St Michael's Cave. No other pairwise comparisons were statistically significant.

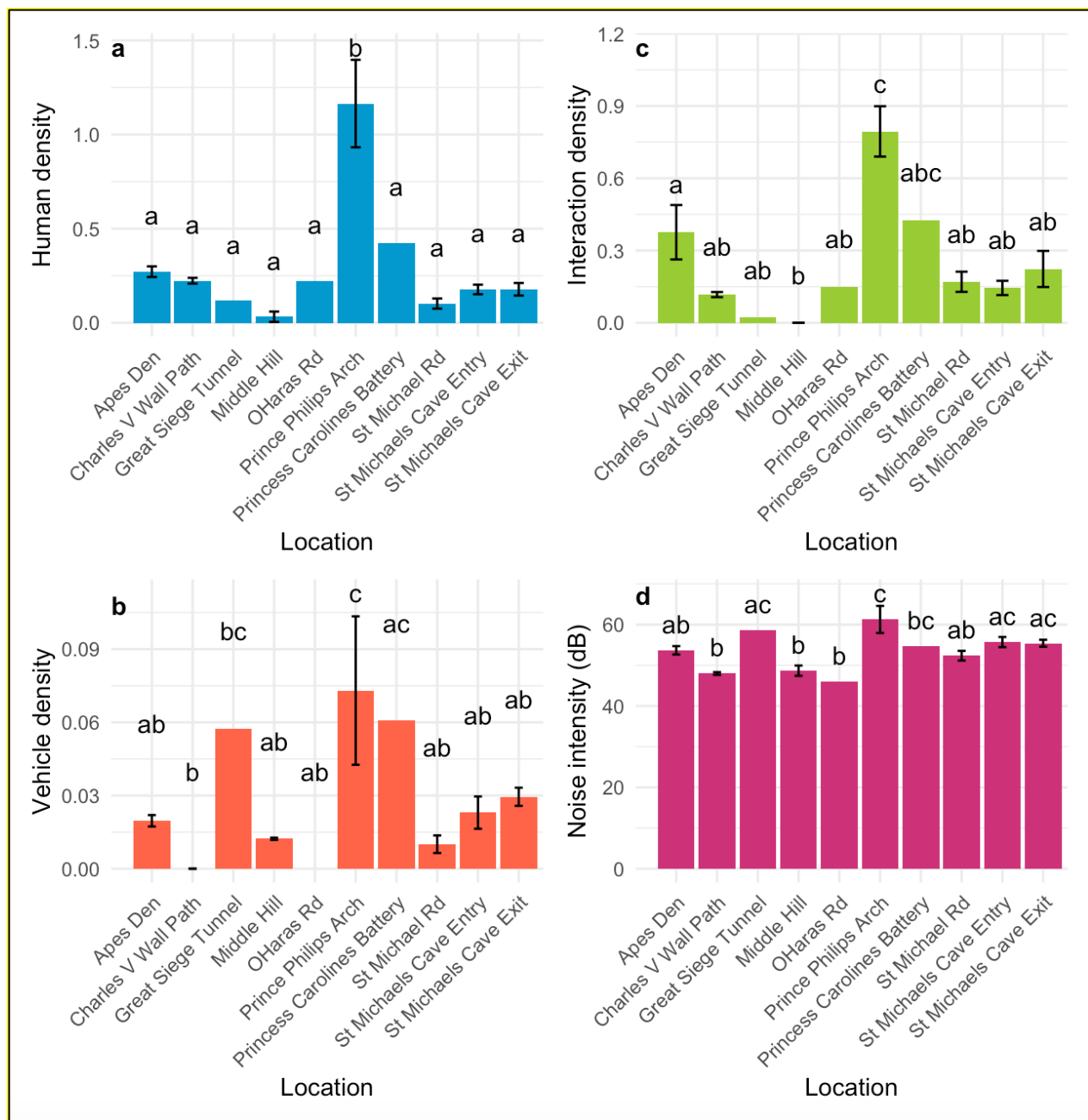


Figure 2. Anthropogenic pressure across locations. Barplots representing (a) human density (visitors per m² every 5 minutes), (b) vehicle density (vehicles per m² every 5 minutes), (c) interaction density (human–macaque interactions per m² every 5 minutes), and (d) noise intensity (in decibels) across different locations (see Material & Methods for sample sizes). Letters above bars indicate results of Tukey post hoc comparisons; groups that do not share a letter differ significantly ($p < 0.05$) (see text for statistical details). Bar heights represent mean values and error bars indicate standard errors of the mean ($\pm$ SE).

Relationship between human-macaque interactions and anthropogenic factors (human and vehicle density)

Full-null model comparisons for model 2 showed that the number of human-macaque interactions was significantly affected by the test predictors (LRT: $\chi^2 = 15.13$, $d.f. = 2$, $p < 0.001$). Generalized mixed models revealed significant positive associations between the number of human-macaque interactions and both human density (*estimate* $\pm$ SE = 0.378 ± 0.107 , $p < 0.001$; *marginal* $R^2 = 0.99$, $n = 31$; Figure 3a) and vehicle density (*estimate* $\pm$ SE = 0.284 ± 0.105 , $p = 0.007$; *marginal* $R^2 = 0.99$, $n = 31$; Figure 3b).

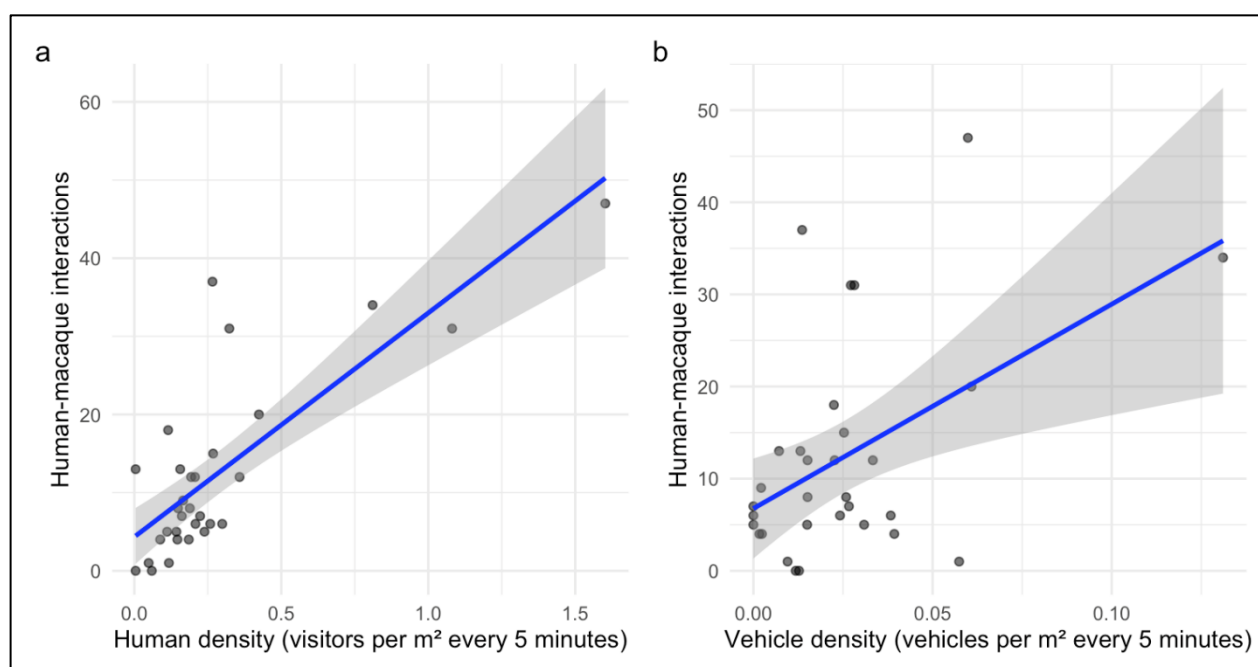


Figure 3. Anthropogenic influence on human-macaque interactions. Positive associations between the number of human-macaque interactions and (a) human density and (b) vehicle density. Regression lines are based on parameter estimates from linear mixed-effects models; shaded areas represent 95% confidence intervals (see text for details).

Relationship between noise intensity and anthropogenic factors (human and vehicle density)

Full-null model comparisons for model 3 showed that noise intensity was significantly affected by the test predictors (LRT: $\chi^2 = 13.07$, $d.f. = 6$, $p = 0.002$). Linear mixed models revealed significant positive associations between noise intensity and both human density (*estimate* $\pm$ SE = $1.87, \pm 0.76$, *marginal* $R^2 = 0.53$, $n = 31$, $p = 0.03$; Figure 4a) and vehicle density (*estimate* $\pm$ SE = 1.79 ± 0.7 , *marginal* $R^2 = 0.53$, $n = 31$, $p = 0.01$; Figure 4b).

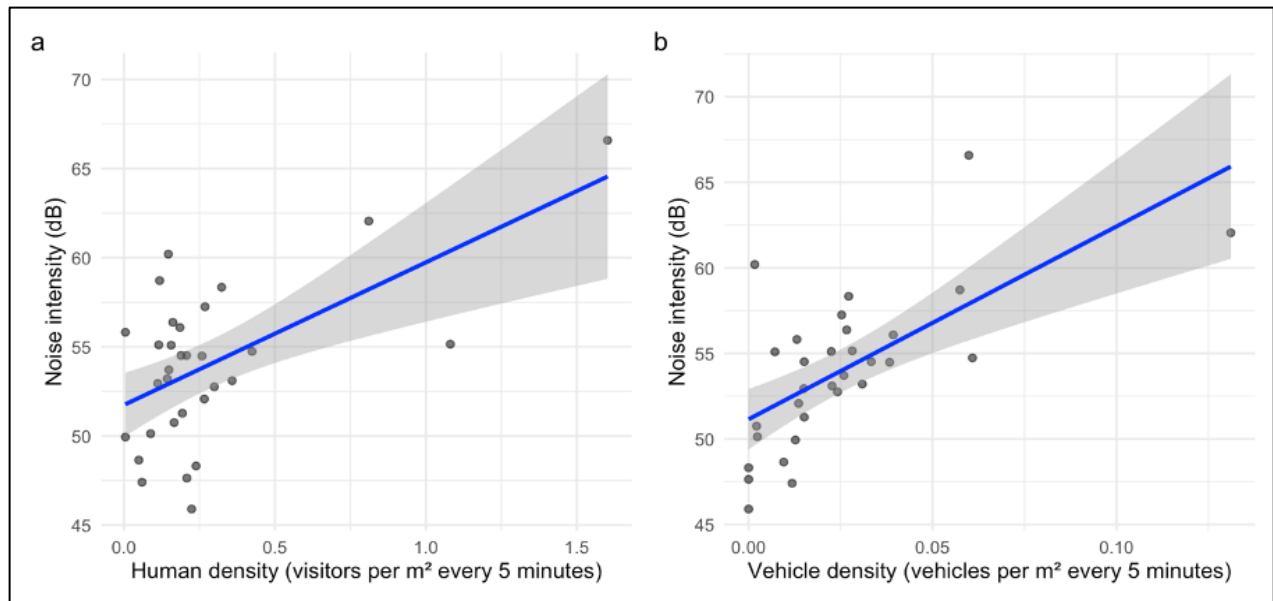


Figure 4. Noise as a proxy for human disturbance. Positive correlations between noise intensity and (a) human density and (b) vehicle density. Regression lines are based on parameter estimates from linear mixed-effects models; shaded areas represent 95% confidence intervals (see text for details).

Behavioural responses to anthropogenic pressure

Group variation in behavioural responses

Full-null model comparisons for models 4.1 to 4.6 showed that neither behaviours (self-scratch, yawning, aggression receive, aggression give, grooming (total and bouts)) were significantly affected by the group (model 4.1 LRT: $\chi^2 = 2.02$, $d.f. = 5$, $p = 0.85$, model 4.2 LRT: $\chi^2 = 8.83$, $d.f. = 5$, $p = 0.12$, model 4.3 LRT: $\chi^2 = 1.01$, $d.f. = 5$, $p = 0.6$, model 4.4 LRT: $\chi^2 = 4.8$, $d.f. = 5$, $p = 0.44$, model 4.5 LRT: $\chi^2 = 4.51$, $d.f. = 5$, $p = 0.48$, model 4.6 LRT: $\chi^2 = 5.22$, $d.f. = 5$, $p = 0.39$).

Influence of visitors and vehicles on behavioural metrics

Full-null model comparisons for Model 5.1 indicated that self-scratch occurrences were not significantly affected by human and vehicle density (LRT: $\chi^2 = 3.78$, $d.f. = 2$, $p = 0.15$), although the model showed a non-significant trend suggestive of a potential relationship that would require further investigation.

Full-null model comparisons for model 5.2 showed that the yawning occurrences were significantly affected by human and vehicle density (LRT: $\chi^2 = 18.53$, $d.f. = 2$, $p < 0.001$). Our GLMM analyses

revealed a significant negative association between human density and yawning occurrences, indicating that yawning decreased as human density increased ($estimate \pm SE = -0.6 \pm 0.18$, $\chi^2 = 10.87$, $p < 0.001$; Figure 5a). Conversely, we found a significant positive association between vehicle density and yawning occurrences, indicating that yawning increased with higher vehicle density ($estimate \pm SE = 0.42 \pm 0.16$, $\chi^2 = 6.91$, $p = 0.009$; Figure 5b).

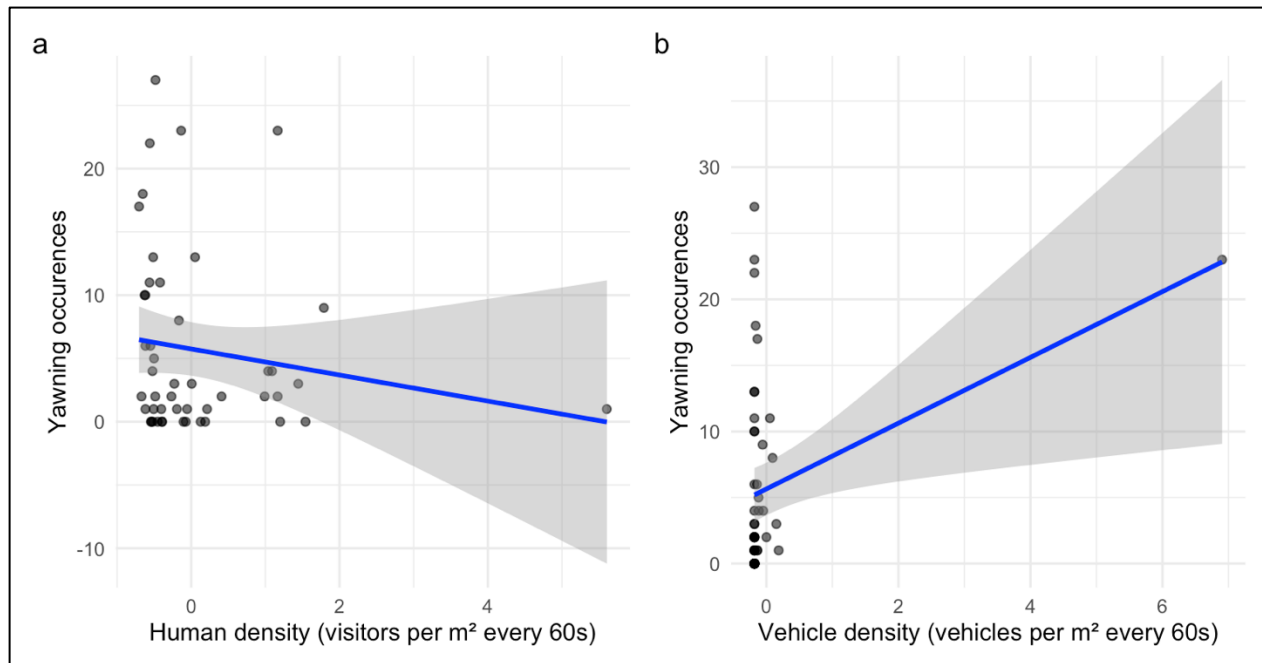


Figure 5. Yawning as a behavioural indicator of disturbance. Negative association between yawning occurrences and (a) human density. Positive association between yawning occurrences and (b) vehicle density. Regression lines are based on parameter estimates from linear mixed-effects models; shaded areas represent 95% confidence intervals (see text for details).

Full-null model comparisons for models 5.3 to 5.6 indicated that none of the affiliative or agonistic behaviours measured were significantly affected by human and vehicle density. Specifically, neither received nor given aggression occurrences were significantly predicted (model 4.3: $\chi^2 = 1.01$, $d.f. = 2$, $p = 0.60$; model 4.4: $\chi^2 = 0.27$, $d.f. = 2$, $p = 0.88$), nor were total grooming occurrences (model 4.5: $\chi^2 = 3.35$, $d.f. = 2$, $p = 0.19$) or grooming bout frequencies (model 4.6: $\chi^2 = 0.01$, $d.f. = 2$, $p = 0.99$).

DISCUSSION

This study provides new information into the effects of anthropogenic disturbance on the behaviour of a free-ranging primate population living in close proximity to humans. By focusing on the Barbary macaques of Gibraltar, this research contributes to a growing body of literature exploring how human presence—particularly in the context of wildlife tourism—can alter animal behaviour. Through the systematic observation of self-directed, affiliative, and agonistic behaviours under different levels of human activity, we tested the general hypothesis that increased human pressure disrupts macaque social dynamics and elevates behavioural markers of stress.

Quantification of Anthropogenic Pressure

Effects of anthropogenic variables on spatial distribution

The results reveal a spatially structured anthropisation gradient, marked by a systematic distinction between the Prince Philip's Arch (PPA) site and the nine other locations. This site is characterised by significantly higher levels of human density and vehicle traffic, an increased frequency of visitor-initiated interactions, and a higher noise intensity than that observed at the majority of the other sites. The fact that PPA was significantly different from the majority of the other sites in the models, but that the models did not differ significantly between them, suggests a hierarchy of affluence based on the dominance of an over-frequented site rather than a linear gradient. This clear distinction can be explained by the fact that PPA is an essential stop on tours organised by taxi drivers, who take tourists to the site and guarantee them the presence of a group of macaques accustomed to interacting with visitors, particularly in exchange for opportunities to make contact and take photographs. At this site, it is not uncommon to see a queue of several dozen taxis stopped, with visitors waiting to interact with the macaques, under the supervision of taxi drivers who reward the monkeys with food (see Figure 1c). The site is also easily accessible by cable car, which takes visitors up to the top of the hill.

Similarly, the Middle Hill site stands out for its low noise intensity compared with the other 9 sites, as well as its low frequency of interactions compared with Ape's Den, which can be explained in particular by the fact that it is a closed military site, not accessible to visitors, thus considerably reducing opportunities for interaction.

Justification of anthropogenic predictors for behavioural models

The results show that the number of visitors and the number of vehicles are significantly and positively associated with the human-macaque interactions, and with the noise level (ambient noise), showing that we observe more human-macaque interactions and the ambient noise is higher when there are more visitors and more vehicles. These two variables thus appear to be good predictors and therefore good proxies of human pressure. Visitors are a direct source of interaction, noise and visual disturbance, and vehicles are an indirect indicator of crowding, as well as an amplifier of noise (engines, traffic). Therefore, noise intensity and number of human-macaque interactions, although interesting, can be considered redundant with these two predictors, since they are correlated with both, we judge that it is not necessary to keep them as the main predictor, but rather to discuss it as a consequence of human pressure, as it is the result of the presence and activity of visitors. We therefore use these two predictors (number of visitors and number of vehicles) to model an anthropogenic gradient that makes it possible to anticipate areas and times at risk, since high visitor numbers seem to indicate a high frequency of human-macaque interaction.

Behavioural responses to anthropogenic pressure

Group variation in behavioural responses

The effect of group identity was tested on the three types of behaviour studied—self-directed (scratching, yawning), agonistic (aggression given and received) and affiliative (grooming)—but no significant variation between groups was found.

Consequently, group identity was not retained as a fixed or random factor in the final models. Adding this factor would have made the models unnecessarily complex without improving their quality or interpretability. These results suggest that behaviours related to stress or social interactions are more influenced by immediate contextual factors (such as human density or the presence of vehicles) than by membership of a given home group.

Influence of visitors and vehicles on behavioural metrics

Although the effect of the number of visitors on the frequency of self-scratching behaviours was not significant at the classic threshold, the results nevertheless suggest a notable positive trend that should be taken into account. This trend seems to indicate that the presence of visitors is associated with an increase in stress perceived by the macaques. The lack of a significant association with the

number of vehicles would reinforce the idea that direct human interaction is the main factor in triggering self-scratching responses.

Our results show a positive association between vehicle frequency and yawning behavior, and a negative association between the number of visitors and yawns. This suggests that vehicles may act as a source of stress for macaques, potentially due to their noise or unpredictable movement. Moreover, vehicles, particularly taxis, represent a real threat of collision, which may contribute to this stress response. At the same time, vehicles — and taxis in particular — can also represent an indirect food provisioning opportunity, as macaques must often approach drivers to receive food. This feeding context may enhance competition and lead to intra-group intimidation behaviors, such as yawning. In this sense, yawning may not solely reflect stress, but also serve a communicative function, particularly among dominant individuals. As described by Hall and DeVore (1965), the “secondary intimidating effect” of yawning may serve to expose large canines in a threatening display, a behavior notably observed in the Stumptail Macaque (*Macaca arctoides*; Bertrand, 1969). In contrast, interactions with tourists generally involve direct provisioning, with visitors often initiating contact and feeding macaques in groups. This more straightforward dynamic may reduce intra-group visibility and thus limit the expression of intimidation behaviors, such as “directed” yawns (Bertrand, 1965). While fewer yawns are observed in the presence of visitors, this does not necessarily imply an absence of disturbance. High human density may impair macaques’ ability to monitor their conspecifics due to reduced visual access, as visitors tend to surround the individuals, limiting their vision of their surroundings. If individuals cannot see one another well due to crowding, the use of directed yawns as intimidation signals loses its function.

Contrary to the hypotheses we had put forward, the results show no association between either agonistic behaviour (aggression receive, aggression give), or affiliative grooming behaviour and the frequency of visitors and vehicles. These results seem to show that these behaviours are less subject to the anthropogenic effect, or at least that they are modulated by other factors. Indeed, it has been shown in previous studies that grooming duration and reciprocity can be affected by factors such as group size and stability (Lehmann et al., 2007), kinship (Silk, 1982), bystander presence (Kaburu & Newton-Fisher, 2016) and dominance rank (Schino & Aureli, 2008). In this context, the apparent absence of an anthropogenic effect on affiliative and agonistic behaviours may reflect the influence of these internal factors. It is also possible that the mating season, during which

the data were collected, played a role: reproductive competition and sexual motivations may act as internal modulators of social interactions, potentially reducing individuals' sensitivity to external disturbances. In addition, social buffering plays an essential role in stress regulation in Barbary macaques in non-human environments: adult males with strong social bonds show attenuated physiological responses to stress (Hodgson et al., 2004). In a tourist context, the presence of an affiliated partner could also help to modulate the anxiogenic effects of close interactions with visitors (Maréchal et al., 2011). This could partly explain why affiliative behaviours such as grooming do not vary significantly with human or vehicle density: their regulatory function could be maintained or activated independently of the level of disturbance, with the aim of preserving group cohesion and well-being, especially in a context where they can access to areas and locations where they are less disturbed by people.

Recent literature examining the consequences of agonistic behaviour in an anthropogenic context shows that intra-group aggression rates are higher in the presence of high human density, notably because of the pressure to obtain anthropogenic food (Jaman & Huffman, 2013, Sinha & Mukhopadhyay, 2013). In our study, the absence of any significant difference between groups in Gibraltar frequenting areas that are very heavily disturbed by visitors, and those in areas that are less so, may also be explained by the fact that the macaques are fed twice a day by the Macaque Management Team, thus limiting the pressure to access anthropogenic food.

These findings suggest that the influence of anthropogenic pressure on affiliative and agonistic behaviours may be secondary to that of internal factors such as social dynamics and reproductive context. Moreover, there appears to be a trade-off between the stress induced by human presence and the opportunity to access anthropogenic food sources (Maréchal, 2016). This trade-off may complicate the interpretation of behavioural responses to anthropogenic pressure, as individuals may tolerate proximity to visitors and vehicles despite associated risks, in exchange for potential nutritional benefits.

Conclusion

Barbary macaques are the only free-living monkey population to be seen in Europe. Between 2022 and 2023, visitor numbers to the Gibraltar Rock Nature Reserve increased by 24%, reaching more than ten million visits throughout the year (Statistics Office, HM Government of Gibraltar, 2023).

This study highlights the complexity of macaques' behavioural responses to human pressure. While certain expected effects were confirmed—notably an increase in self-directed behaviour in the presence of visitors—other hypotheses, concerning agonistic and affiliative behaviour, were not verified. These results suggest that these behaviours may be more influenced by intrinsic or seasonal social factors, or modulated by stabilising affiliative relationships. In a context where human pressure varies greatly from one site to another, these results underline the need for differentiated management of tourist areas, by limiting the number of visitors in the busiest sectors in order to preserve the animals' well-being and encourage sustainable cohabitation, particularly given that macaques are the most numerous non-human primates living in close proximity to humans (Hubbard, 2023).

Limitations

The sample size—though sufficient to reveal some significant behavioural trends—remains relatively limited ($n = 31$ for event sampling, $n = 47$ for focal follows) which can reduce the statistical power to detect more subtle effects and limits the ability to incorporate individual-level variables such as dominance rank, sex, or group identity into the models. Data was collected between January and February 2025, during a period of relatively low tourist activity, limiting the ability to generalize findings to times of higher tourist density. Moreover, adverse weather conditions during data collection, including strong winds and frequent rain, restricted access to certain macaque groups situated in more elevated or difficult-to-reach locations, particularly Middle Hill. This uneven accessibility may have led to sampling bias and reduced the representativeness of the behavioural data across sites. This period coincides with the mating season, associated with natural fluctuations in social behaviours such as grooming and aggression, which could confound the interpretation of anthropogenic effects on macaque behaviour. Although some sites—most notably Prince Philip's Arch (PPA)—are normally easily accessible via the Cable Car, this facility was closed until the end of March, limiting the influx of tourists during the study period and potentially affecting macaque exposure to human presence. This may create temporal peaks in human presence that were not fully captured by the protocol, potentially influencing macaque behavior in ways not accounted for in the study.

Further studies could be carried out to assess seasonal variation in tourist pressure and its effects on macaque behavior, integrate individual-level variables such as rank or sex into the analysis, and ensure more balanced sampling across all group locations throughout the year.

Contribution

Jeanne Thiodet and Dr Sylvain Lemoine conceived the study; Jeanne Thiodet collected the data, created graphs and conducted statistical analyses; Dr Sylvain Lemoine supervised and contributed to the statistical analyses; Jeanne Thiodet wrote the report, Dr Sylvain Lemoine supervised the report.

Use of AI

ChatGPT (OpenAI, 2024) was used in this work to assist with data sorting and cleaning in R. DeepL (DeepL GmbH, 2024) was used to help translate and refine some sentence formulations.

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