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Tourism encounters with macaques: A comparative analysis of human–wildlife interactions in Gibraltar

Bethany Maxwell[1,*], Matt Reed[2] & Julia E Fa[3]

[1]Research Unit, University of Gibraltar, Gibraltar
[2]Countryside and Community Research Unit, University of Gloucestershire, Cheltenham, UK
[3]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK and University of Gibraltar
*Corresponding author, e-mail: bethany.gadd@unigib.edu.gi

ABSTRACT Human-wildlife interactions, particularly in tourism-dominated environments, significantly impact primate behaviour, yet how these pressures vary across different ecological settings remain relatively understudied. This study aimed to investigate the influence of tourist presence on Barbary macaque, *Macaca sylvanus* Linnaeus, 1758 (Primates Cercopithecidae) behaviour at two distinct sites within the Upper Rock Nature Reserve (URNR) in Gibraltar: Prince Phillip's Arch (PPA) and St Michael's Cave (SMC). The research enhanced our understanding on how factors such as habitat structure and varying tourist pressures shape macaque activity patterns, social interactions, and stress-related behaviours. Through behavioural observations, we recorded macaque state behaviours (grooming, foraging, vigilance, etc.) and interactions (agonistic, anthropogenic, etc.) across both sites over a 6-month period. A comparison between the two sites revealed that PPA, characterised by confined spaces and high tourist traffic, had significantly higher grooming and vigilance behaviours, while macaques at SMC exhibited more foraging and movement, likely due to more open terrain and dispersed tourist presence. Self-directed behaviours, indicators of stress, were notably higher at PPA. Anthropogenic interactions, including feeding by visitors, were common at both sites but more frequent at SMC. The findings suggest that tourist density and site-specific habitat structures significantly influence macaque behaviour, with PPA macaques showing higher stress and aggression levels due to spatial limitations and visitor proximity. These results highlight the importance of implementing site-specific management strategies, including regulating tourist access, enforcing no-feeding policies, and enhancing habitat design, to mitigate stress on wildlife.

KEY WORDS Management/wildlife management; *Macaca sylvanus*; primate tourism; human-macaque interactions; primate behaviour.

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INTRODUCTION

In recent decades, human-wildlife interactions have gained popularity in tourism settings (Bateman & Fleming, 2017; Dou & Day, 2020; Duffus & Dearden, 1990). Unlike consumptive activities like hunting or fishing, this non-consumptive interaction entails engaging with wildlife for recreational purposes without removing or permanently affecting the animals (Duffus & Dearden, 1990). These interactions, from observation to more intimate engagements like feeding and touching, offer humans a memorable experience driven by aesthetic pleasure and emotional connection to the animals (Duffus & Dearden, 1990; Curtin, 2009). Wildlife tourism fulfils people's desire to appreciate nature and brings economic benefits to host communities (Tisdell, 2012; Mmbaga, Tarimo & Modest, 2024). Despite some debate, wildlife tourism is viewed as a practice contributing to wildlife conservation, aligning with the Sustainable Development Goals (SDGs) proposed by the United Nations (UN), emphasising the significance of biodiversity in sustainable development (United Nations, 2017).

Human-wildlife interactions in tourism settings exert diverse impacts on target animals. These effects range from behavioural changes, such as habituation to human presence and alterations in natural behaviours, to physiological consequences like increased stress levels and potential dependency on human-provided food (Saiyed et al., 2024). Habitat disruption due to tourist infrastructure and altered social dynamics within animal communities are also common outcomes. The risk of injury or death, especially when tourists approach too closely or attempt to interact physically, poses direct threats to wildlife and tourists alike (Maréchal et al., 2016; Bertrand et al., 2022). Furthermore, human activities may contribute to a decline in reproductive success, impacting birth rates and overall population health (O'Leary & Fa, 1993).

Additionally, introducing tourist diseases through direct contact or waste disposal can pose a serious threat to wildlife populations lacking immunity to such pathogens (Engel et al., 2008). Likewise, wildlife can also be a reservoir for serious diseases that could be infectious for humans. For example, *Plasmodium knowlesi* Sinton et Mulligan, 1893, also known as "monkey malaria" in southeast Asia can be transmitted to humans from infected monkeys through mosquito bites (Collins, 2012). Recognising and addressing these impacts is crucial for developing and promoting responsible tourism practices that prioritise the conservation and wellbeing of wildlife.

Research exploring the dynamic interaction between wildlife and human systems has captured considerable attention across diverse disciplines, including tourism, leisure studies, environmental science, conservation, wildlife biology and ethnoprimatology (Sponsel, 1997; Cong et al., 2017). Notably, wildlife-tourist contacts, particularly involving primates, have become increasingly prevalent globally (Mallapur, 2013; Sengupta et al., 2021). A historical example of this is the Barbary macaque population, *Macaca sylvanus* Linnaeus, 1758 (Primates Cercopithecidae), inhabiting the Rock of Gibraltar, whose interactions with Gibraltar's human population dates to 1915 and earlier (Sawchuk & Tripp, 2019). These monkeys were introduced from their natural range in North Africa, likely before the 1700s (Majolo et al., 2013; Sawchuk & Tripp, 2019; Tripp & Sawchuk, 2021). The presence of these non-human primates on the Rock persists due to a blend of historical tradition and, more recently, the recognition of economic benefits associated with maintaining them as a tourist attraction. This poses a conflict between ensuring the wellbeing of the macaque population and the interests of the various stakeholder groups wishing to use the animals as a source of income (Fa, 1984b; Fuentes et al., 2007; Schurr et al., 2011). The Barbary macaques are a unique and cherished feature of Gibraltar, but their presence in urban and tourist areas has led to various forms of interaction, both positive and negative (Radford et al., 2018). Close encounters between humans and macaques in Gibraltar have been typical in Gibraltar since at least the 1960s when tourism in Spain began to rise (Fa, 1986).

While numerous studies have examined the interactions between Gibraltar macaques and tourists (Fa, 1992; O'Leary & Fa, 1993; Fuentes, 2006; Fuentes et al., 2007; Unwin & Smith, 2010; Saiyed et al., 2024), there is a notable gap in research documenting variations in the level, frequency, and types of interactions in different macaque troops. Understanding these contrasts is crucial for developing effective management strategies that fully consider the complexities of human-macaque interactions in a tourism site like Gibraltar. Differences in interaction levels can indicate varying degrees of acclimation to human presence, which can affect the macaques' stress levels and natural behaviours. Additionally, variations in the frequency and types of interactions can provide insights into the adaptability and resilience of different macaque troops to tourism-related activities.

By identifying differences in responses of monkeys to visitors it is possible to tailor management strategies that not only recognise the unique characteristics and needs of each macaque troop but allows conservationists and wildlife managers to implement site-specific interventions. These measures can reduce potential stressors and alleviate adverse effects on the macaques, thus enhancing conservation efforts. This more nuanced understanding of these diverse interactions allows management strategies to be more precise and adaptive, fostering responsible tourism practices that benefit the macaques and the visiting public. In this paper, we describe state and event behaviours in two macaque troops in Gibraltar during the same study period. We then highlight the contrasting interactions with tourists and natural behaviours exhibited by each troop and explore how differences may be attributed to the site's geographic layout, the types and intensities of visitor interactions, competition for resources, and pressures from neighbouring troops.

This study aims to examine the factors influencing macaque behaviour in two distinct tourist sites in Gibraltar by focusing on the balance between ecological conditions, social dynamics, and human presence. Four specific objectives guide the research:

Assessing consistency in daily activity patterns. The study explores whether macaques at both sites exhibit similar daily activity patterns - including feeding, resting, and movement - under comparable ecological and management conditions. Identifying such consistencies would suggest that environmental and operational stability contributes to predictable behavioural rhythms across locations.

Exploring the stability of social interactions A key objective here is to evaluate whether the two troops' social behaviours such as grooming, aggression, and play remain consistent. These interactions are expected to be shaped by internal dynamics such as hierarchy, kinship, age, and sex. Demonstrating such stability would reinforce the idea that macaque social structures are resilient and primarily governed by intrinsic social organisation.

Investigating the influence of tourism pressure on behaviour. The study examines how varying levels of tourism affect macaques' social and ecological behaviour. By correlating visitor numbers with behavioural changes, this objective aims to reveal how human presence alters natural activity patterns and social interactions.

Understanding the interplay between ecological and human factors. Finally, the study integrates insights from the previous objectives to develop a broader perspective on how ecological variables and human disturbances collectively shape macaque behaviour. This integrated approach seeks to identify how internal and external forces interact, offering a nuanced understanding that can inform future wildlife management and conservation efforts.

MATERIAL AND METHODS

Study area

The study was undertaken within the Upper Rock Nature Reserve (URNR), an area spanning 2.33 km^2 in Gibraltar. Gibraltar is a British jurisdiction in the southernmost tip of the Iberian Peninsula (Fig. 1).

The URNR was established in 1993 under Gibraltar's Nature Protection Act 1991 (Gibraltar Nature Reserve Management Plan, 2019) and expanded further in 2013. The URNR provides protection to a wide range of terrestrial and marine species and habitats. The reserve is mostly covered by Mediterranean matorral, composed of wild olive (*Olea europaea* var. *oleaster* Hoffmgg. et Lk.), lentisc (*Pistacia lentiscus* L.), and other shrub species (Perez & Bensusan, 2005). This vegetation is thick and largely impenetrable, except in areas opened as firebreaks or on the cliffs along the spine of the Rock.

Gibraltar has a typical Mediterranean climate; summers are warm and dry, and winters cool and wet. Temperatures range from on average 13.4 °C to 24.2 °C (56.1 °F to 75.6 °F). Annual rainfall is about 768 mm (30.2 in). Clouds, locally known as the "Levanter", often form a cap over the Rock during the dry summer months, when moisture-laden easterly winds are forced upward by the Rock's eastern cliffs. These clouds provide moisture to the vegetation in the dry periods of the year.

Study species and study groups

The current Barbary macaque population roams freely within the URNR and surrounding areas. At the time of the study, eight multi-male, multi-female troops were in the URNR. The macaques mostly live in the upper parts of the Rock but may wander into the lower reaches where the town is located. When this happens, the macaque management team, responsible for feeding and overall care of the monkeys will encourage them back into the reserve grounds with their authoritative presence, and harmless "darts" that fire small rocks to scare them off. Feeding (consisting of cultivated fruits and vegetables) of the macaques is undertaken daily and ponds have been built in various sites of the URNR as drinking sources.

Visitors to Gibraltar often seek out the macaques to watch and photograph them in their natural habitat. However, negative interactions also arise when macaques intrude into urban areas, where they raid houses in search of food or take household items, leading to conflicts with residents. Instances of macaques raiding garbage bins, stealing food from tourists, or causing damage to property can also lead to clashes with humans (Radford et al., 2018). Additionally, people approaching monkeys to feed or touch them can provoke aggression, posing risks to humans and disrupting the monkeys' natural behaviours (Fa, 1992).

Public awareness campaigns in Gibraltar have informed residents and visitors of the importance of avoiding direct contact with the macaques and to refrain from feeding them (Perez & Bensusan, 2005; Thinking Green Digest, 2016; Gibraltar Nature Reserve Management Plan, 2019; Monkeytalk-Gibraltar, n.d.). However, enforcement of regulations prohibiting feeding or harassment of macaques have been limited. Infrastructure improvements, such as secure waste bins and barriers to restrict macaque access to certain areas, has mitigated macaque-human conflicts (Thinking Green Digest, 2016).

In this study, we focused on two macaque troops at Prince Philip's Arch (PPA) and St. Michael's Cave (SMC) (Fig. 1). These two troops are widely visited by large numbers of tourists on the URNR.

The PPA range (approx. 7,828.33 m²), is located near the top cable car station (Figure 1) where tourists come to enjoy the panoramic views from the top of the Rock (around 500 m elevation). This area is frequented by several macaque troops which compete for resources and space. Additionally, a narrow road connecting St. Michael's Cave to the cable car station passes through PPA, which leads to high human and vehicle traffic.

Tourists and guides at PPA frequently feed and touch the macaques. The SMC range (approx. 13,160.48 m²) is one of the most visited tourist sites in Gibraltar since it offers access to a renowned tourist attraction on the Rock, St Michael's Cave. This area is occupied by only one troop, the Royal Anglian Way troop. Unlike PPA, SMC is surrounded by extensive scrubland. Most tourists here are more interested in visiting St. Michael's Cave than in observing the monkeys. The site's layout includes upper and lower roads, with the feeding area and pond situated away from the main tourist activity centre.

Age-sex composition of both study troops is given in Table S1. Age groups were classified according to Burton (1972) (Adult females = AF, Adult males = AM, Subadults = SA, Juveniles = JUV). This classification (see Table S2) has been employed in other studies of the species such as in Simonds (1973), Burton & Sawchuk (1974), Fa, 1984a and Paul & Thommen (1984).

Methods

This study was conducted in compliance with protocols approved by the Research and Research Degrees Committee (RRDC) at the University of Gibraltar (Ethics ID: 003/2022/UniGib). The study followed the ASP Code of Best Practices for Field Primatology (https://www.asp.org/resources/docs/Code%20of_Best_Practices%20Oct%202014.pdf). Furthermore, all research activities adhered to the legal requirements of the country in which the study was conducted.

To accurately categorise and analyse macaque behaviours, we first developed an ethogram (Tables S3 and S4). This ethogram was informed by previous studies (Sha et al., 2009; McFarland & Majolo, 2011; Tkaczynski, 2017) and supplemented by our own field observations.

Observations took place between February - July 2023 between 8:30 am and 12:30 pm up to four times a week. This time period covered peak and non-peak tourist seasons but excluded the macaque mating season. The latter period was deliberately omitted since males often roam between troops seeking mating opportunities, potentially leading to confrontations with other males, significantly altering troop dynamics.

We recorded "states" (behaviours), and "events" (interactions) (Altmann, 1974). We used scan samples to document every instance of state behaviours for all monkeys observed during the scan; sex and approximate age were known. Scan samples were conducted at 10–minute intervals for

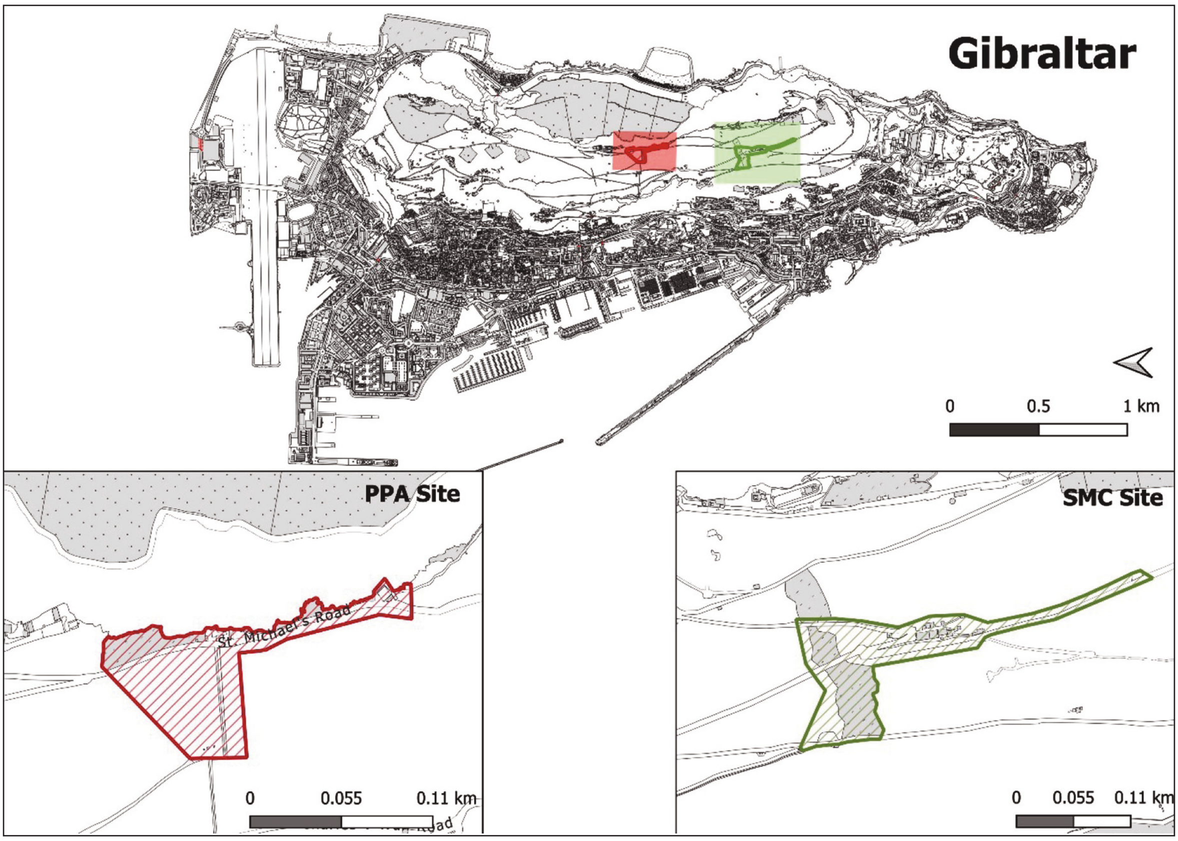

Figure 1. Map of Gibraltar with the two study site locations. PPA = Prince Phillip's Arch and SMC = St Michael's Cave.

an hour at each site. This involved a site walk-through to record behaviours of all visible macaques, along with visitor numbers and vehicles using the site. Between scan samples, we recorded interactions/event during a period of 10 minutes, which included all occurrence sampling of macaques visible and their interactions (with other macaques and visitors), as well as visitor numbers and vehicles present. The observer was stationed at a single vantage point on the site that offered the most comprehensive view of as many macaques as possible. Details of state and event behaviours recorded in the study are given in S3 and S4.

To assess the normality of the data, we utilised both visual inspection and the Kolmogorov-Smirnov test (Mohd Razali & Yap, 2011). Given that the data did not follow a normal distribution, we employed non-parametric tests (Conover, 1999).

To facilitate cross-comparisons between age-sex classes and sites, we converted count data into proportions. Specifically, we calculated the proportion of monkeys engaging in each behaviour by dividing the number of individuals observed performing a given behaviour at a site during each observation period by the total number of recorded instances of that behaviour across all observations. These proportions were used in the statistical analyses. The proportion data for each age sex class and site were combined and then divided by the total number of behaviours exhibited by that specific age-sex class to create a summary of activity patterns during the observation period. For example, to determine the proportion of time that males spent grooming at a particular site, we divided the number of grooming records for males by the total number of all recorded behaviours exhibited by males at that site.

A Welch two sample t-test was used to compare visitor and macaque numbers per observation across the two sites. To assess differences in behaviour counts between different age sex classes and sites we employed a Mann-Whitney U test (Mann & Whitney, 1947). We used Spearman's rank tests (Spearman, 1987) to explore potential impacts of visitor numbers (NOV) on observed behaviours and interactions. Before fitting the data into these statistical tests, the data were log-transformed to equalise variances between the datasets and allow for better comparison between sites and age sex classes.

RESULTS

A total of 210 scan samples of state behaviours and 2100 minutes of 10-minute interactions/event observations were collected during the study period at each site (Figs. 2, 3). This resulted in a total of 420 scan samples of state behaviours and 4200 minutes of event/interaction observations for the entire study period (see also Figs. 4–7 and Supplementarys Tables). Table 1 summarises the intra-troop and intra-site differences in behaviours and interactions between age-sex classes and sites.

We classified interactions into two types: grouped and isolated. Grouped interactions included broader behavioural categories, such as agonistic interactions, which included specific actions like 'chase with contact' and 'chase without contact'. In contrast, isolated interactions referred to individual behaviours within these categories that yielded significant results in our analysis.

Our results indicate significant differences between the PPA and SMC sites in both macaque and visitor numbers, with fewer visitors and more monkeys at PPA. Behaviours such as grooming, foraging, and movement varied significantly across sties and among age-sex classes. Additionally, the composition and frequencies of social and self-directed interactions within troops also varied significantly.

At SMC, there was a positive correlation for vigilance (p= 0.003***), eating (p= 2.659e-08***), and movement (p= 0.0027**). These results suggest that as the number of visitors rise, vigilance, eating, and movement behaviours also increase.

In contrast, at PPA, all tested behaviours showed weak correlations with the number of visitors. However, grooming was positively correlated with visitor numbers (p= 0.052*).

At SMC there was a notable decrease in agonistic interactions and vocalisations with more numbers of visitors (p= 7.829e-4***). Facial displays were also negatively correlated with visitor numbers (p= 0.001***). Conversely, at PPA, only self-directed behaviours were negatively correlated with numbers of visitors (p=0.005**).

At both sites, anthropogenic interactions were positively correlated with number of visitors (p= 2.2e-16***), as expected given the increased opportunities for macaques to interact with visitors.

DISCUSSION

Previous research has highlighted the role of environmental variables, such as habitat type and human presence, in shaping primate behaviour patterns and activity budgets (Fuentes & Gamerl, 2005; Thierry, 2007; Bertrand et al., 2022). Our results showed there were significant differences between behaviours and interactions exhibited by macaques across two URNR sites.

Macaque behaviours between two sites

Grooming behaviours, essential for social bonding (Shutt et al., 2007; Roubová et al., 2015; Duboscq et al., 2016), were significantly higher at PPA, with AF grooming more; this is consistent with observed sex and age-related patterns in rhesus macaques (*Macaca mulatta*) (Kapsalis & Berman, 1996). High tourism activity and traffic at PPA may increase cortisol levels, leading to more grooming for stress relief (Sonnweber et al., 2015). Grooming also supports social bonds, hierarchy, and affiliation (Shutt et al., 2007; Roubová et al., 2015; Berthier & Semple, 2018). Due to competition from neighboring troops, strong grooming relationships at PPA may play a crucial role in alliance formation and support during confrontations (Arseneau-Robar et al., 2016). In contrast, the dispersed layout of SMC may contribute to lower grooming frequencies.

Variations in foraging behaviour may reflect differences in resource availability or habitat structure between study sites, as found in other primate studies on ecology and resource use studies (e.g., Rothman et al., 2009). In the SMC site, macaques can engage in more natural foraging in the adjacent sloping terrain with less dense *matorral* vegetation. Conversely, the PPA site presents challenges, since steep cliffs on one side and competition from troops of macaques below, renders the area less appealing as a natural foraging location. This disparity between sites likely contributes to comparatively less

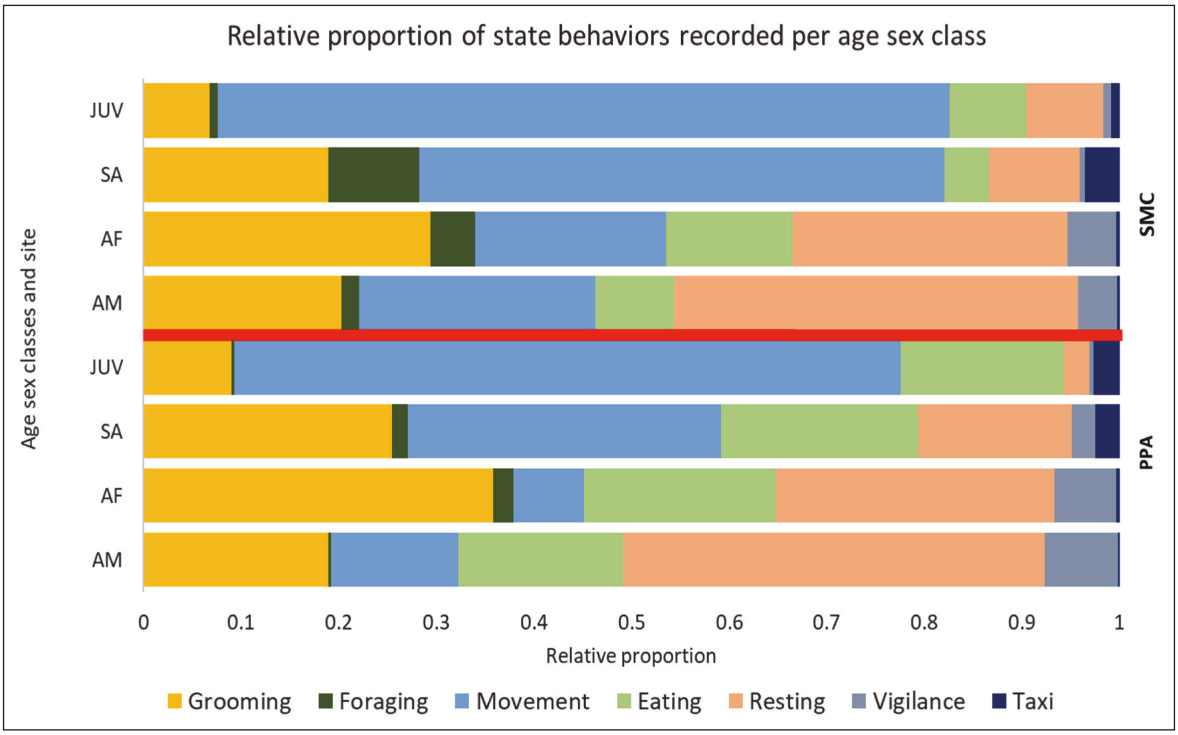

Figure 2. Relative proportion of state behaviours recorded per age sex class across the two sites during the study period. Results collected from state sampling.

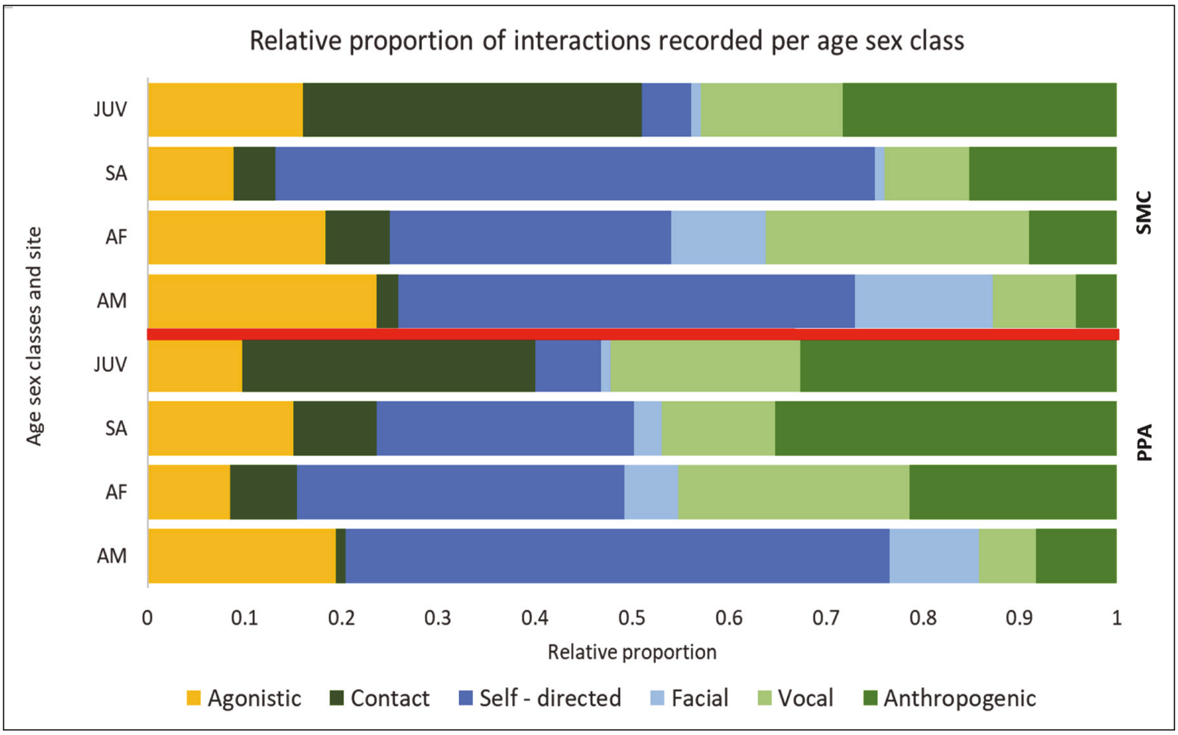

Figure 3. Relative proportion of events/interactions and behaviours recorded per age sex class across the two sites during the study period. Results collected from events sampling.

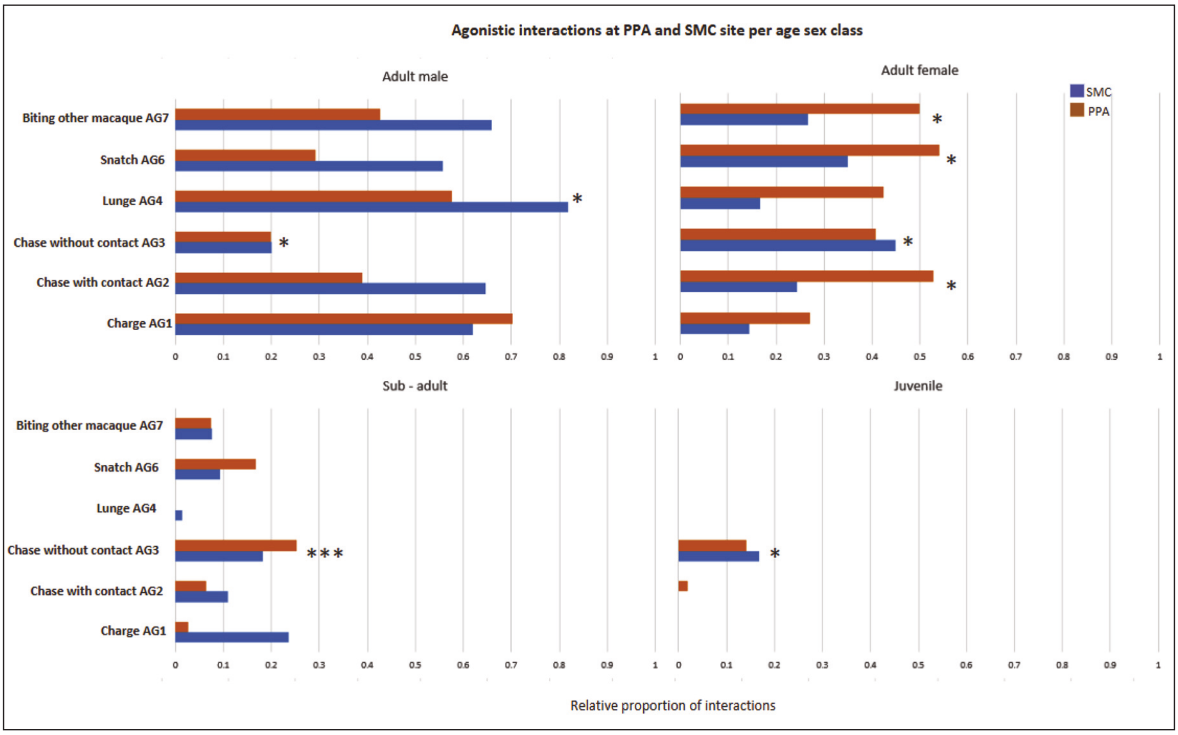

Figure 4. Proportion of agonistic interactions per age sex class and site.
Significance levels as follows: *** : p=<0.001, ** : p=<0.01, * : p=<0.05.

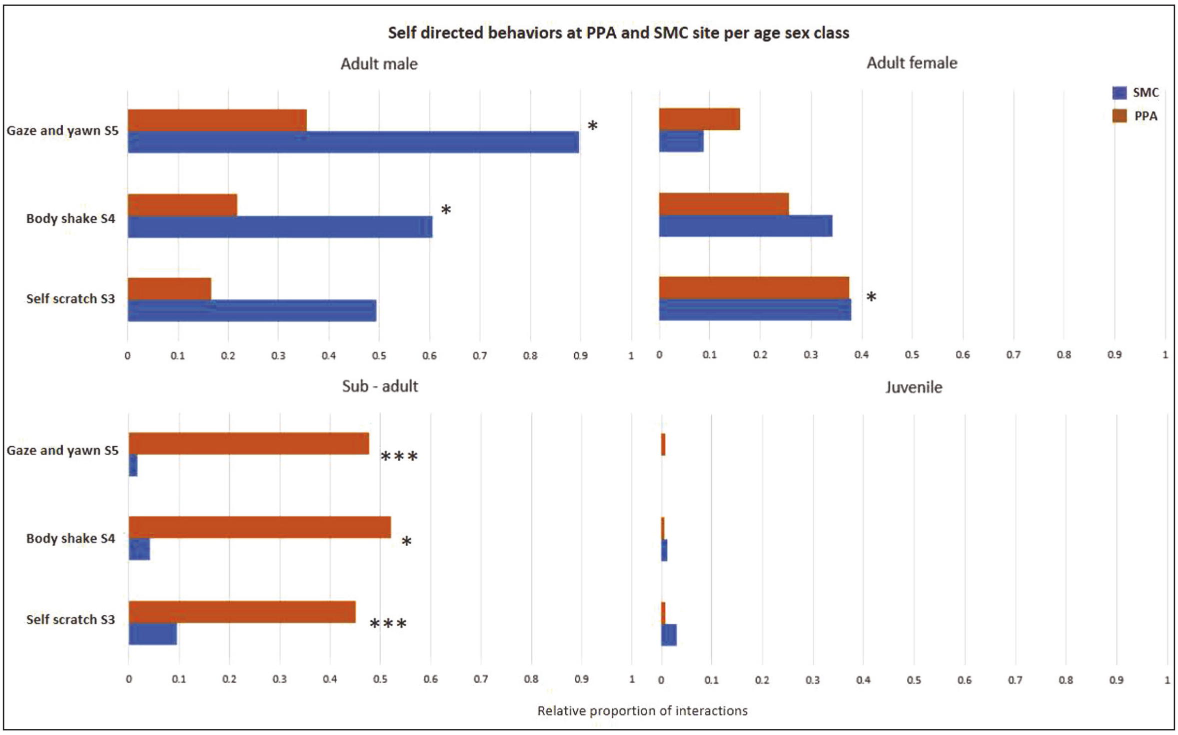

Figure 5. Proportion of self-directed behaviours per age sex class and site.
Significance levels as follows: *** : p=<0.001, ** : p=<0.01, * : p=<0.05.

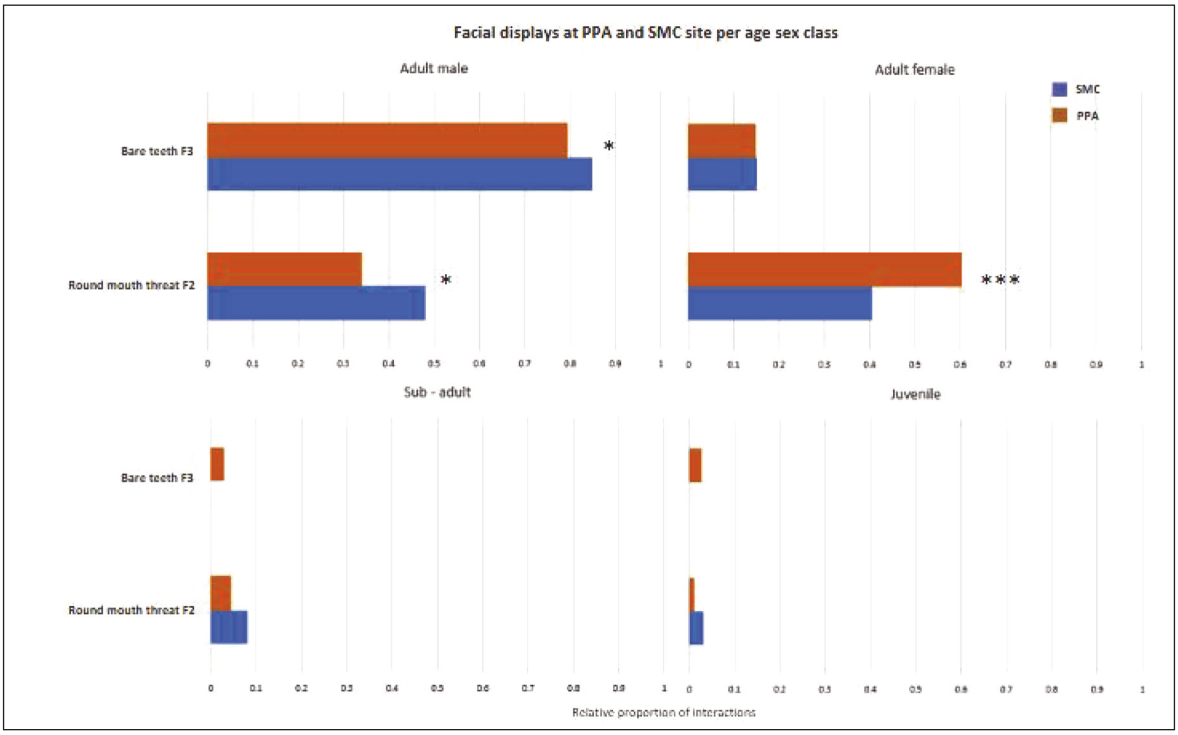

Figure 6. Proportion of facial displays per age sex class and site.
Significance levels as follows: *** : p=<0.001, ** : p=<0.01, * : p=<0.05.

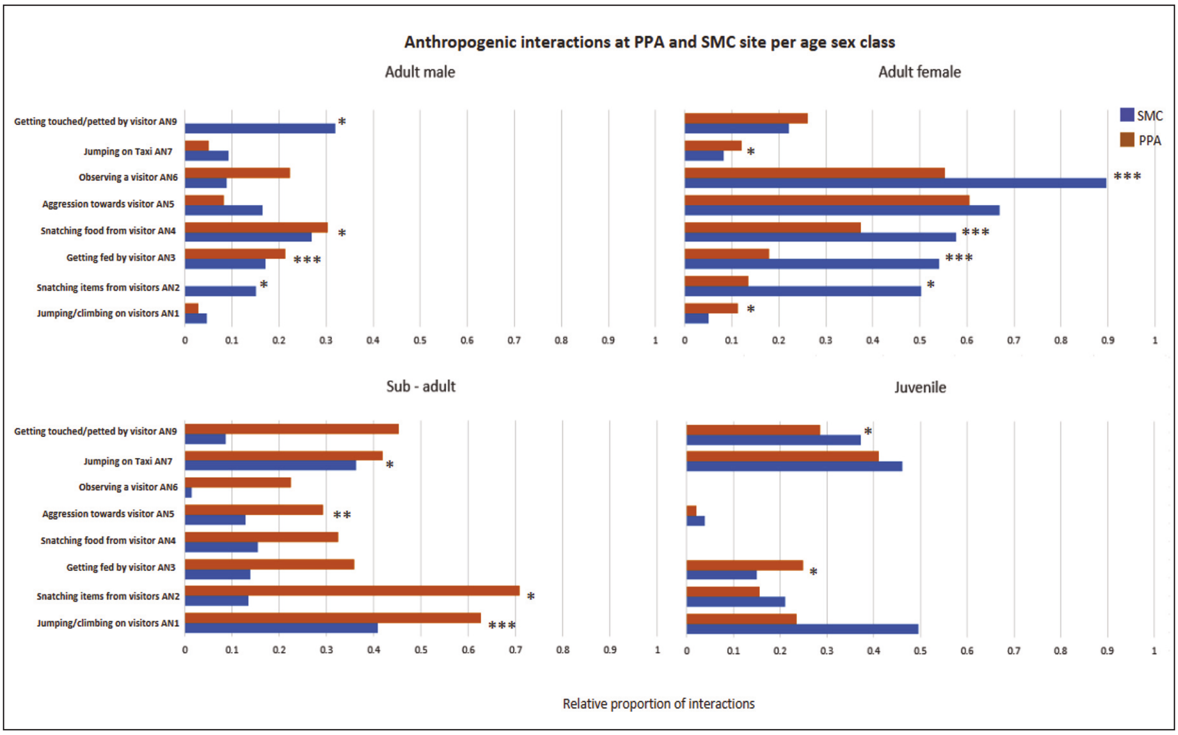

Figure 7. Proportion of anthropogenic interactions per age sex class and sites.
Significance levels as follows: *** : p=<0.001, ** : p=<0.01, * : p=<0.05.

Variable	Intra-troop	Inter-site
Site composition		
Visitor numbers	NA	Significant differences between the sites (t=10.664, df=1866.6, p=2.2e-16***). Less visitors at PPA (7.18 ± SD 9.37, range 1–55) than in SMC (12.59 ± SD 13.51, range 1–110).
Macaque numbers	NA	Significant differences between the sites (t=24.04, df= 1855.6, p=2.2e-16***). More monkeys at PPA (15.80 ± SD, range 3–41), lower numbers at SMC (9.85 ± SD 4.54, range 2–30).
Activity patterns		
Grooming	AF groomed more compared to other age groups.	Grooming between AF (p=0.026*), and SA (p=7.03e-5), (SA) were significantly different across the two sites (p=0.026*), with a higher proportion observed at PPA.
Foraging	SA foraged the most in SMC, and AF foraged the most in PPA.	Foraging frequency of SA differed significantly (p=0.017**), with more foraging observed at SMC. Overall, foraging varied significantly across the two sites; there was more foraging behaviour observed at SMC (p=5.927e -06***).
Movement	Movement was highest in SA and JUV across both sites.	Movement was significantly different across all age-sex classes between the sites (AM: p=0.003*, AF: p=0.0001***, SA: p=0.155*, and JUV: p=0.014**), with more movement observed at SMC.
Eating	Eating was relatively equal across all age-sex classes at PPA, and varied more at SMC, with AF displaying the most eating behaviours.	Eating was significantly different across all age-sex classes between the sites (AM: p=4.2e-6***, AF: p=2.824e-4***, SA: 3.557e-12***, JUV: p=0.001***) and higher at PPA.
Resting	Resting counts were higher amongst male and female adults at both sites.	Resting counts were significantly different among SA (p=2.25e-5), with higher resting observed at PPA.
Vigilance	Vigilance was higher amongst AM and females at both sites.	Vigilance varied between sites for AM (p=3.869e-4***), AF (p=0.017**), and SA (p=0.004**), with vigilance being most observed, and higher amongst AF PPA.
Grouped interactions		
Agonistic interactions	Agonistic interactions were consistently high across all age-sex classes, with a slight increase among adults.	Agonistic interactions were significantly different between both study troops for all age-sex classes except AM (AF: p=1.232e-12***, SA: p=1.699e-09***, JUV: p=0.001***).
Contact	Contact interactions were most common among SA and JUV, likely due to their frequent physical play.	Contact interactions were significantly different across all age-sex classes (AM: p=0.034*, AF: p=0.106., SA: p=1.217e-13*** JUV: 0.018*), with SA having the highest observed contact interactions.
Self-directed	Self-directed interactions were prevalent in all age classes except JUV.	Self-directed behaviours were also significantly different across all age-sex classes except in JUV (AM: p=8.70e-5***, AF: p=3.256e-4***, SA: p=1.961e-122***), with higher occurrences at SMC.

Facial displays	Facial displays were higher across AM at both sites, closely followed by AF.	Facial displays were more frequent at SMC for all age-sex classes except JUV (AM: p=6.006e-4***, AF: p=9.5e-6***, SA: p=0.035*).
Vocalisations	Vocalisations were dominated by females, SA and JUV at both sites.	Vocalisations were significantly higher among SA at PPA (p=2.177e-09***).
Anthropogenic interactions	Anthropogenic interactions were primarily observed in SA and JUV.	Anthropogenic interactions were significantly different across all age-sex classes except JUV (AM: p=0.014*, AF: p=2.240e-09***, SA: p=2.5e-6***), with higher instances at PPA.
Isolated interactions		
Chasing with and without contact	Chasing with and without contact was most common amongst AM and females across both sites.	Chase without contact was significantly more frequent at PPA across all age-sex classes (AM: p=1.15e03**, AF: p=3.67e-06***, SA: p=2.12e-09***, JUV: p=2.03e-03**).
Snatching and biting	Snatching at other macaques, and biting other macaques was most common amongst AM and females at both sites.	Snatching and biting were significantly higher at PPA among AF (p=6.81e-3* and p=2.9e-02*).
Self-scratching	Self-scratching was a common self-directed behaviour amongst AM, females and SA.	Significantly more frequent at SMC among AF (p=4.24e-05*) and significantly more frequent at PPA among SA (p=4.31e-112***).
Body shakes and yawns	Body shakes and yawns were also higher at PPA (AM: p= 2.74e-02*, SA: p=4.22e-20***).	Body shakes were significantly higher at SMC for AM (p=2.74e-02*) and for yawns (p=8.69e-06*) but body shakes were higher at PPA for SA (p=2.98e-06) and for yawns (p=4.22e-20***).
Round mouth threat and bare teeth	Both facial displays were most common amongst AM and females.	The round mouth threat was significantly higher at SMC for AM (p=2.34e-03*) and PPA for AF (p=2.51e-08***). The bare teeth display was significantly higher at SMC for AM (p=4.34e-02*).
Interactions with visitors		
Jumping/climbing on visitors	Jumping/climbing on visitors was most commonly seen across SA and JUV at both sites.	Jumping/climbing on visitors exhibited significant differences observed among AF (p=0.012*) and SA (p=1.13e-06***), with instances of this interaction being higher at PPA site.
Snatching items from visitors and snatching food from visitors	The incidence of snatching items and food from visitors was highest across AF and SA at both sites.	The snatching of items was significantly higher at SMC for both AM (p=2.52e-02***) and AF (p=3.15e-02*), and higher at PPA for SA (p=1.81e-02*). Snatching food items was higher at PPA for males (p=1.12e-02*), but higher at SMC for females (1.51e04***).
Getting fed and petted by a visitor	AF and SA showed the highest frequencies of getting fed by visitors at both sites. SA and JUV were the most common age-classes that visitors engaged in petting with at both sites.	The interaction of getting fed by visitors was significantly higher amongst males (p=3.83e-04***) and JUV (p=3.56e-2*) at PPA but was significantly higher at SMC for females (p=2.45e-14). AM (p=1.42e02*) and JUV (p=1.94e-02*) were getting touched/ petted by visitors more frequently at SMC site.

Aggression towards visitors and observation	Aggression towards visitors and observation was most observed amongst AF at both sites.	Significant variation between sites only among SA (p=2.09e03*), with aggression being higher at PPA. The behaviour of observing a tourist was highly significant amongst females (p= 3.65e-08***), with a higher frequency of this behaviour recorded at SMC exclusively.
Jumping on taxis	The jumping on taxis was most observed amongst SA and JUV across both sites.	Jumping on taxis at the two sites were significantly different amongst AF (p=5.41e-03*) and SA (p=2.40e-02*), with both being significantly higher at PPA.

Table 1. Comparisons of intra-troop and inter-site behaviours and interactions. Results of the Mann-Whitney U tests.

foraging at the PPA site. Despite this, natural foraging was infrequent at both sites, as has been observed in other macaque studies in Gibraltar (Fa, 1984a; El Alami et al., 2012). Such lower levels of natural foraging proportions are related to the fact that the monkeys in Gibraltar are provisioned; non-provisioned troops exhibit higher foraging rates (Unwin & Smith, 2010). Although foraging was higher at SMC, the SMC monkeys were also more frequently fed by visitors, and food snatching from them occurred more often (Fig. 7). Moreover, peanuts and seeds are scattered in a sloped area near Spur Battery, a disused WWII gun emplacement, away from the main tourist hub. This may contribute to the observed increase in foraging activity. This practice is absent at PPA site, and macaques there are provisioned in the centre of the tourist hub.

Differences in movement proportions between sites may be attributable to increased feeding by tourists at the SMC site. AF are more inclined to receive or pilfer food from tourists (O'Leary & Fa, 1993). JUV and SA across both sites exhibited the highest movement counts, consistent with findings suggesting that these age groups are the most mobile (Wong, 2019). Higher incidences of movement were also correlated with increased visitor numbers at SMC, indicating greater disturbance as macaques may need to relocate to avoid large tourist groups typical of the SMC site.

The higher feeding counts at PPA could be attributed to the site layout. In this site, a feeding area situated at the center of the site invites visitors to observe and wander around the feeding macaques. Here, higher-ranking individuals were observed dominating these spaces, attracting tourists eager to capture photos and offering ample opportunities for access to anthropogenic food. Females exhibited the highest eating frequencies at both sites, suggesting their dominance in accessing available food resources, likely attributable to their elevated social rank within macaque hierarchies (Saito, 2017). At the SMC site, eating behaviours primarily stem from provisioned peanuts, seeds, or anthropogenic foods, as the macaque feeding site remains secluded from the main tourist areas. The analysis of tourist pressure revealed that as NOV increased, eating behaviours decreased, indicating potential disruptions to feeding activities in the presence of visitors, consistent with findings from previous studies of the effects of tourist presence on the Gibraltar macaques (O'Leary & Fa, 1993; Maréchal et al., 2016). The act of eating is inherently an action that can place an individual primate in a vulnerable situation (e.g., Brügger et al., 2023) - in the presence of potential threats, increased vigilance may result in reduced feeding.

Notably, intra-specific variation in vigilance among troops in Gibraltar have been previously documented (Unwin & Smith, 2010). The increased levels of aggression at the PPA site could necessitate higher vigilance levels among macaques to ensure their safety. Additionally, the dense tourist presence in this narrow and confined site might further elevate vigilance counts. In contrast, at the SMC site, macaques are more dispersed, with reduced competition, potentially leading to lower vigilance counts. Analysing the effect of tourist pressure revealed that macaques may heighten their vigilance in response to increased human activity, a phenomenon observed in other macaque species (Fuentes, 2011; Riley & Ellwanger, 2013). Interestingly, this correlation was not evident at the PPA site, indicating that macaques there may have adapted to cope with stress factors associated with tourist presence. Despite environmental and intra-specific differences favoring the SMC site, macaques there appear to be more sensitive to tourist pressures.

These differences suggest that, despite similar ecological conditions and management practices, other factors such as site-specific tourist pressures and habitat structures can greatly influence Barbary macaque activity patterns.

Macaque interaction comparisons between the PPA and SMC sites

Agonistic interactions play a pivotal role in establishing dominance hierarchies and resolving social conflicts among primates (de Waal, 1986). These interactions provide valuable insights into levels of intraspecific competition, troop tensions, and aggression within primate groups (Dennen, 1995; Thierry, 2007; Roth & Cords, 2016; Amici et al., 2021). The elevated levels of agonistic interactions observed at the PPA site indicate a higher degree of inter-individual aggression, consistent with the site's heightened competition, limited space, and increased stress impacts resulting from its geographical layout.

Significant differences in self-directed interactions, often indicative of stress or anxiety in primates, were observed between the two sites. Overall, self-directed behaviours were more frequently observed at the PPA site amongst SA, suggesting higher stress and anxiety levels, consistent with previous studies (e.g., Kaburu et al., 2012). It is plausible that SA may be facing pressures from both competition for rank and tourist interactions. Self-scratching, known to be a robust indicator of anxiety, was particularly prominent among SA at PPA. Given that SA often occupy lower ranks within macaque hierarchies, which has been associated with emotional costs in some species, the heightened levels of stress and anxiety among this demographic may manifest as increased self-scratching behaviours (Kaburu et al., 2012).

The prevalence of round mouth threat and bare teeth facial displays are commonly associated with aggression directed towards other macaques (Preuschoft et al., 1998; Wiper & Semple, 2007; Maréchal et al., 2011). We show that AF displayed the highest counts of facial displays at PPA and almost consistently as high as AM in SMC. This aligns with findings from previous studies indicating that female macaques tend to direct more aggressive behaviours towards other troop members (Westergaard et al., 2003). Increased aggression could potentially lead to behavioural contagion, wherein bystanders become more likely to initiate aggressive interactions themselves after witnessing such behaviours (Blood & Semple, 2023). This heightened aggression also poses a greater threat to tourists visiting the site.

Although laws and fines exist to deter contact interactions in Gibraltar, macaques jumping on tourists or being encouraged onto visitors' shoulders by local guides for photo opportunities occurs often. In our study we observed these behaviours more often at PPA among AF, though SA and JUV were the most common age-sex classes interacting with humans, as has been observed in previous studies (O'Leary & Fa, 1993). Increased touch encounters, such as jumping/climbing, pose threats to both macaques and tourists. For example, macaques and humans may be at risk of exchanging pathogens (i.e., human to macaque anthropozoonotic diseases and macaque to human zooanthroponotic diseases) (Fuentes, 2006).

The prevalence of feeding by visitors and snatching of food items was significantly higher at the SMC site. This may be linked to the greater food availability within the vicinity of the SMC site, since it includes a café frequented by macaques and where there are opportunities for tourists to purchase food to feed the monkeys. Increased feeding of anthropogenic foods has been associated with sex-related body weight differences, heightened obesity levels overall (Saiyed et al., 2024), as well as an increased incidence of diabetes (Maréchal et al., 2016).

Interestingly, there was only a difference in aggression displayed towards visitors at both sites amongst SA, despite this interaction being commonly recorded at each location, indicating a high level of aggression towards visitors. AF were seen to have the highest rate of aggression towards visitors. This phenomenon has been observed previously in Gibraltar (Fa, 1992), along with age-sex differences in directed aggression among macaques. Such aggression also poses physical threats to tourists, potentially leading to injuries requiring medical treatment. These uncontrolled interactions also impact people's perceptions of macaques, consequently affecting conservation efforts.

The behaviour of jumping on taxis was significantly higher at the PPA site, which is expected given the nature of tourism present at this site. Although taxis were present at both sites, the PPA site exclusively allows taxis as the only form of vehicular transport, while the SMC site features a mix of coaches and taxis. SA and JUV were most likely to be observed jumping and playing on taxis, consistent with findings from O'Leary and Fa (1993), who found JUV to be the most common age class in contact with vehicles.

While grooming behaviours were significantly higher at PPA and agonistic interactions varied between sites, many social behaviours such as vigilance and self-directed interactions showed site-specific differences. This suggests that while intrinsic factors like social hierarchy and kinship influence social interactions, external pressures such as tourist activity and site layout also play crucial roles, as social structures remain somewhat stable, but external environmental factors introduce variability.

Do number of visitors influence macaque behaviours and interactions?

Four significant associations between behaviour counts and the number of visitors (NOV) were identified, with three pertaining to the SMC site. This could suggest potential differences in habituation levels across the two sites, prompting a reconsideration of our understanding of tolerance to tourism, a topic explored in previous studies (e.g., Bertrand et al., 2022). Given the SMC site's usable space, macaques have the option to disperse themselves from tourists more easily, resulting in less interest for the macaques to linger around the site. Consequently, an increase in visitor numbers appears to have a more pronounced effect on their behaviour. In contrast, at the PPA site, the consistently high levels of tourists and limited escape routes due to the site's geographical layout may lead to higher habituation levels and consequently, less impact on behaviour in response to visitor numbers.

Data from the SMC site revealed a notable pattern between NOV and state behaviours. Similarly, the SMC site showed the highest significant associations. All correlations were negative, meaning that as NOV increases, the incidences of agonistic, self-directed, facial, and vocal interactions decrease. This shows that NOV seem to affect shorter, interactive behaviours rather than behavioural states, thereby altering the short-term social dynamics of the sites.

At SMC, where tourist numbers were higher, macaques exhibited increased movement, as well as higher levels of visitor interactions such as food snatching and being fed by tourists. Conversely, at PPA, the confined site layout and dense tourist presence led to higher incidences of grooming and vigilance behaviours. These findings underscore the significant impact of tourism on macaque activity patterns and social interactions, highlighting the need for effective management strategies to mitigate negative impacts of tourism on macaque behaviour in Gibraltar.

RECOMMENDATIONS AND CONCLUSIONS

Based on the results, several recommendations can be made to improve the welfare of the Gibraltar macaques and manage human-wildlife interactions effectively. Firstly, regulating tourism intensity, particularly at the PPA site, can reduce stress and aggression among macaques. Implementing designated viewing areas and limiting tourist proximity to macaques can help alleviate the pressures of high visitor density. Educating tourists on appropriate behaviour, such as refraining from feeding macaques and avoiding direct contact, will mitigate negative interactions and reduce the risk of pathogen transmission. Additionally, providing natural foraging opportunities and reducing provisioning at both sites can encourage natural behaviours and improve the macaques' diet quality. Enforcement of existing laws and fines regarding human-macaque interactions should be strengthened to ensure compliance.

The interaction of site-specific ecological features (e.g., habitat layout, resource availability) with varying levels of human activity (e.g., tourism pressure, food provisioning) creates distinct behavioural patterns in macaque troops at both the PPA and SMC sites. For instance, the higher grooming and vigilance at PPA can be attributed to both the site's confined space and intense tourist presence, whereas the increased foraging at SMC relates to the broader foraging range and further distance between tourists and macaques. Therefore, a comprehensive approach to conservation that considers both ecological and anthropogenic factors in influencing primate behaviour is recommended. This holistic view is essential for formulating well-rounded conservation strategies that address both ecological and anthropogenic factors affecting macaque populations.

Lastly, our study also highlights the need for site-specific macaque management plans in the conservation and management efforts concerning Barbary macaques in Gibraltar. Even though interaction studies have been carried out in the past, studies of specific comparisons between sites in Gibraltar has only been done once before. By emphasising the significance of tailoring strategies to the distinct ecological and anthropogenic contexts of each site, we advocate for a holistic approach that acknowledges and accommodates the variability in macaque behaviour and interactions. This refined perspective not only enhances the efficacy of conservation initiatives but also contributes to the advancement of scientific understanding and informed decision-making in primate management practices.

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SUPPLEMENTARY TABLES

S1. Population size and composition of one macaque troop that utilises PPA site and one macaque troop that utilises SMC. Numbers are approximate and accurate as from February-July 2023. Data collected by Bethany Maxwell (2023).

Name of troop	Site	Population Size					Total size
		Adult male	Adult female	Subadults	Juveniles	Infants	
Cable Car (CBC)	PPA	12	16	6	5	1	40
Royal Anglian Way (RAW)	SMC	8	11	4	4	0	27

S2. Age classifications used in this study during macaque observations. Adapted from: Burton, F.D. (1972).

Age class	Age	Size
Adult male	5+ years	Characterised by large size, with fully developed features indicative of sexual maturity
Adult female	5+ years	Characterised by large size, with fully developed features indicative of sexual maturity, and the presence of anogenital swelling, and the presence of breasts.
Sub adults	3-4 years old	Characterised by a smaller size, and not fully sexually mature. Gender difficult to identify unless genitals are visible.
Juveniles	1-3 years old	Characterised by a small size, as well as their playful behaviours.
Infants	Birth to 1 year	Characterised by their dark fur when born, and small size

S3. Ethogram of state Behaviours.

State Behaviour	**Abbreviation**	**Definition**
Travel	TRA	Macaque is moving and does not appear to be moving to food source or other macaques. This includes short bouts of sitting and looking in-between
Climbing an inanimate object	CLI	Macaque is seen to be climbing an object. i.e tree, wall, pole, Cliffside
Swinging on an inanimate object	SWI	Macaque is seen to be swinging on an object. i.e tree, vine, pole
Rest	RES	Macaque is stationary and not doing any other behaviour
Feed	FEE	Macaque is ingesting food; putting food in mouth and chewing it
Foraging	FOR	Macaque is breaking stems, stripping leaves from twigs, turning over rocks and moving dirt. Macaque is not feeding
Give groom	GGR	Macaque grooms fur of the other, it watches the groomed place on the subject's body, using its fingers or mouth
Receive groom	RGR	Macaque is receiving grooming of the fur from another macaque

Groom simultaneous	GSI	Macaque is both grooming another macaque and being groomed by another macaque
Self-groom	SGR	Macaque grooms its own fur, it watches the groomed place, using its fingers and mouth
Playing	PLA	Macaque is play fighting or chasing another macaque. No aggression evident in the activity
Vigilance	VIG	Macaque is checking the area around itself, may be scanning for conspecifics or potential threats outside of the group
Sitting on taxi	TAXI	Macaque sitting on taxi which is stationary or moving

S4. Ethogram of event (interactions) Behaviours.

Events	**Interactions**	**Description**
Contact/proximity behaviours	Embrace C1	A macaque embraces another individual, often as a gesture of affiliation or social bonding.
	Present for grooming C2	A macaque presents itself to another individual for grooming, indicating a desire for social interaction and grooming.
	Mock bite C3	A mock bite involves a macaque making biting motions towards another individual without causing harm, often used as a playful or submissive gesture.
	Submission C4	Submission behaviour involves a macaque displaying submissive postures or gestures towards a dominant individual, indicating deference and social hierarchy within the group.
	Touching C5	Touching behaviour involves physical contact between macaques, such as grooming, grooming solicitation, or other forms of tactile interaction, facilitating social bonding and communication.
Agonistic	Charge AG1	A macaque charges towards another individual, often as a threat display or during aggressive encounters.
	Chase with contact AG2	A macaque chases another individual while maintaining physical contact, typically during aggressive interactions or pursuit.
	Chase without contact AG3	A macaque chases another individual without making physical contact, often as a display of dominance or territorial behaviour.
	Lunge AG4	A macaque makes a sudden forward movement towards another individual, often as an aggressive or threatening gesture.
	Mount AG5	Mounting behaviour involves one macaque mounting or climbing onto another individual, typically during social interactions or mating displays.
	Snatch AG6	A macaque snatches or grabs an item or food from another individual, often as a competitive or assertive behaviour.
	Biting other macaque AG7	A macaque bites another individual, typically during aggressive encounters or social conflicts.

Sexual Behaviours	Present sex SB1	A macaque presents itself for sexual interaction or mating, displaying receptive behaviours towards a potential mate.
	Reject sex SB2	A macaque rejects sexual advances from another individual, displaying avoidance or refusal behaviours.
	Reach back SB3	A macaque reaches back towards a potential mate or sexual partner, engaging in courtship or mating behaviours.
	Start copulation SB4	A macaque initiates copulation or sexual intercourse with a mate, beginning the mating process.
	Finished copulation SB5	A macaque completes copulation or sexual intercourse with a mate, concluding the mating process.
	Unfinished copulation SB6	Copulation between macaques is interrupted or remains incomplete, possibly due to external disturbances or social factors.
Solitary behaviour	Tree/item shake S1	A macaque shakes a tree or item in its environment, possibly as a sign of dominance.
	Masturbate S2	Masturbation behaviour involves a macaque engaging in self-stimulatory genital manipulation, often observed as a solitary activity.
	Self-scratch S3	A macaque scratches itself using its hands or feet, typically to alleviate itching, grooming needs, or as a sign of stress
	Body-shake S4	A macaque performs a body shake, involving rapid movements of its body, limbs, or head, yo dry off after rain, itch, or as a sign of awkwardness.
	Gaze and yawn S5	A macaque gazes into the distance and yawns, possibly as a sign of boredom, relaxation, or physiological arousal, or stress.
Facial displays	Stare F1	A macaque stares at another individual or object, often as a form of social communication or threat display.
	Open mouth (O threat) F2	A macaque opens its mouth, displaying teeth or vocalising, typically as a threat or warning signal during social interactions.
	Bare teeth F3	A macaque bares its teeth, exposing its canines, often as a threat or aggressive display towards another individual.
	Eyebrow lift F4	A macaque lifts its eyebrows, often accompanied by facial expressions or postures, indicating emotional states such as surprise, submission, or threat.
Vocalisations	Lipsmack V1	A macaque produces rapid, repeated smacking sounds with its lips, often used as a friendly or affiliative gesture during social interactions.
	Teeth chatter V2	A macaque produces rapid, rhythmic teeth chattering or grinding sounds, typically as a friendly or affiliative gesture during social interactions.
	Fear scream V3	A macaque emits a loud, high-pitched scream or vocalisation in response to perceived threats, danger, or fear-inducing stimuli.

	Aggression scream V4	A macaque emits a loud, harsh scream or vocalisation during aggressive encounters or conflicts with conspecifics.
	Long call V5	A macaque produces a long, loud vocalization or call, often used as a form of long-distance communication to convey information about territory, social status, or reproductive readiness.
	Grunt V6	A macaque emits a short, low-pitched grunt or vocalisation, often used as a form of communication during social interactions or to express contentment.
	Pant V7	A macaque breathes rapidly and audibly, producing panting sounds, often observed during physical exertion, stress, or excitement.
Anthropogenic interactions	Jumping/climbing on visitors AN1	A macaque jumps or climbs on visitors, often as a form of play, exploration, or social interaction in captive or tourist settings.
	Snatching items from visitors AN2	A macaque snatches or takes items such as food or belongings from visitors, exhibiting opportunistic or food-seeking behaviour.
	Getting fed by visitor AN3	A macaque receives food directly from visitors, often in captive or tourist settings where human feeding occurs, influencing macaque behaviour and ecology.
	Snatching food from visitor AN4	A macaque snatches food directly from visitors, exhibiting bold or assertive behaviour in human-macaque interaction contexts.
	Facial display towards visitor AN5	A macaque exhibits facial displays such as threats, stares, or aggressive postures towards visitors, possibly as a response to perceived threats or interactions.
	Observing a visitor AN6	A macaque observes or watches visitors from a distance, exhibiting curiosity or vigilance towards human presence in their environment.
	Jumping on Taxi AN7	A macaque jumps or climbs on vehicles such as taxis or cars, possibly in search of food, shelter, or as a form of exploration or play behaviour.
	Aggression towards visitor AN8	A macaque displays aggressive behaviours such as threats, lunges, or vocalisations towards visitors, potentially in response to perceived threats, territorial disputes, or social interactions.
	Getting touched/petted by visitor AN9	A macaque allows visitors to touch or pet it, often in captive or tourist settings where human-macaque interactions occur, influencing macaque behaviour and socialization.

S5. Composition of macaque and visitor numbers at each site during the study period.

Descriptive statistics	Number of macaques				Number of visitors			
	PPA Events	PPA States	SMC Events	SMC States	PPA Events	PPA States	SMC Events	SMC States
Mean	15.80	15.87	9.85	9.75	7.18	6.42	12.59	14.29
Standard Error	0.20	0.44	0.14	0.27	0.29	0.66	0.42	1.08
Median	14.00	15.00	10.00	10.00	4.00	3.00	10.00	10.00
Mode	12.00	12.00	10.00	10.00	1.00	1.00	1.00	1.00
Standard deviation	6.62	6.41	4.54	3.91	9.37	9.52	13.51	15.64
Sample Variance	43.83	41.10	20.59	15.30	87.75	90.59	182.42	244.56
Kurtosis	0.31	0.25	3.07	2.63	8.08	9.70	10.97	7.01
Skewness	0.67	0.55	1.27	0.81	2.76	3.08	2.48	2.10
Range	38.00	37.00	28.00	26.00	55.00	50.00	109.00	110.00
Minimum	3.00	4.00	2.00	2.00	0.00	0.00	1.00	0.00
Maximum	41.00	41.00	30.00	28.00	55.00	50.00	110.00	110.00
Sum	16590.00	3348.00	10324.00	2047.00	7538.00	1349.00	13207.00	3000.00
Count	1050.00	211.00	1048.00	210.00	1050.00	210.00	1049.00	210.00
Largest(1)	41.00	41.00	30.00	28.00	55.00	50.00	110.00	110.00
Smallest(1)	3.00	4.00	2.00	2.00	0.00	0.00	1.00	0.00
Confidence Level(95.0%)	0.40	0.87	0.28	0.53	0.57	1.29	0.82	2.13

S6. Mann-Whitney U test results comparing Behaviours between age-sex classes across different sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Behav	***Age_gender***	***Site1***	***Site2***	***P_Value***	***Sig.***	***Median1***	***IQR1***	***Median2***	***IQR2***
Grooming	*AM*	*PPA*	*SMC*	*0.3914735*		0.000	0.080	0.000	0.087
	AF	*PPA*	*SMC*	*0.0266719*	*	0.128	0.154	0.095	0.201
	SA	*PPA*	*SMC*	*0.0000703*	***	0.000	0.087	0.000	0.000
	JUV	*PPA*	*SMC*	*0.0997439*		0.000	0.000	0.000	0.000
	ALL			*1.60338e-19*	***				
Foraging	*AM*	*PPA*	*SMC*	*0.4693941*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*0.0000121*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*0.0168451*	**	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*0.6601229*		0.000	0.000	0.000	0.000
	ALL			*5.927306e-06*	***				
Movement	*AM*	*PPA*	*SMC*	*0.0039765*	*	0.000	0.049	0.000	0.103
	AF	*PPA*	*SMC*	*0.0001633*	***	0.000	0.040	0.000	0.118
	SA	*PPA*	*SMC*	*0.1553573*	*	0.000	0.095	0.000	0.141
	JUV	*PPA*	*SMC*	*0.0145023*	**	0.057	0.118	0.080	0.154
	ALL			*8.382217e-07*	***				
Eating	*AM*	*PPA*	*SMC*	*0.0000042*	***	0.000	0.080	0.000	0.000
	AF	*PPA*	*SMC*	*0.0002824*	***	0.061	0.105	0.000	0.095
	SA	*PPA*	*SMC*	*3.556900e-12*	***	0.000	0.072	0.000	0.000
	JUV	*PPA*	*SMC*	*0.0018305*	***	0.000	0.000	0.000	0.000
	ALL			*1.60338e-19*	***				
Resting	*AM*	*PPA*	*SMC*	*0.9822697*		0.095	0.110	0.095	0.167
	AF	*PPA*	*SMC*	*0.4912972*		0.095	0.135	0.105	0.182
	SA	*PPA*	*SMC*	*0.0000225*	***	0.000	0.043	0.000	0.000
	JUV	*PPA*	*SMC*	*0.1357764*		0.000	0.000	0.000	0.000
	ALL			*0.1443599*					
gi la nc	*AM*	*PPA*	*SMC*	*0.0003869*	***	0.000	0.000	0.000	0.000

	AF	*PPA*	*SMC*	*0.0178514*	**	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*0.0041859*	**	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*0.9904902*		0.000	0.000	0.000	0.000
	ALL			*1.376758e-06*	***				
Taxi	*AM*	*PPA*	*SMC*	*0.5618460*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*0.7202898*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*0.4014994*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*0.0595113*		0.000	0.000	0.000	0.000
	ALL			*0.1475086*					

S7. Spearman rank correlation results for macaques' state Behaviours and number of visitors. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, : 0.05 < p-value ≤ 0.1.

Site	**Variables tested**	**S statistic**	**P-Value**	**Rho (ρ) estimate**
SMC	Grooming $ NOV	1496832	0.6633	0.03021293
PPA	Grooming $ NOV	1355560	0.05163*	0.1341706
SMC	Foraging $ NOV	1713182	0.1121	-0.1099582
PPA	Foraging $ NOV	1524800	0.7065	0.02607262
SMC	Movement $ NOV	1225954	0.002741***	0.2057133
PPA	Movement $ NOV	1625381	0.5814	-0.03817085
SMC	Vigilance $ NOV	1231084	0.00322***	0.2023895
PPA	Vigilance $ NOV	1708510	0.1866	-0.09126715
SMC	Eating $ NOV	2117932	2.659e-08***	0.3721928
PPA	Eating $ NOV	1781036	0.0491	-0.1375914
SMC	Resting $ NOV	1306689	0.02622	0.1534053
PPA	Resting $ NOV	1534286	0.7726	0.02001358

S8. Results of Mann- Whitney u test between age groups and sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, : 0.05 < p-value ≤ 0.1.

Behav	Age_gender	Site1	Site2	P_Value	Sig.	Median1	IQR1	Median2	IQR2
Agonistic	AM	PPA	SMC	0.3771842		0.000	0.000	0.000	0.000
	AF	PPA	SMC	1.232217e-12	***	0.000	0.000	0.000	0.000
	SA	PPA	SMC	1.699416e-09	***	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	0.0012723	***	0.000	0.000	0.000	0.000
	ALL			1.60338e-19	***				
Contact	AM	PPA	SMC	0.0345828	*	0.000	0.000	0.000	0.000
	AF	PPA	SMC	0.1060427	.	0.000	0.000	0.000	0.000
	SA	PPA	SMC	1.217368e-13	***	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	0.0180397	*	0.000	0.000	0.000	0.000
	ALL			5.73256e-11	***				
Self-directed	AM	PPA	SMC	0.0000870	***	0.000	0.061	0.000	0.095
	AF	PPA	SMC	0.0003256	***	0.000	0.062	0.000	0.095
	SA	PPA	SMC	1.961916e-122	***	0.045	0.095	0.000	0.000
	JUV	PPA	SMC	0.5440888		0.000	0.000	0.000	0.000
	ALL			1.454686e-19	***				
Facial	AM	PPA	SMC	0.0006006	***	0.000	0.000	0.000	0.000
	AF	PPA	SMC	0.0000095	***	0.000	0.000	0.000	0.000
	SA	PPA	SMC	0.0350471	*	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	0.7424660		0.000	0.000	0.000	0.000
	ALL			2.917633e-09	***				
Vocal	AM	PPA	SMC	0.0758155	.	0.000	0.000	0.000	0.000
	AF	PPA	SMC	0.0417412	*	0.000	0.047	0.000	0.000
	SA	PPA	SMC	2.177002e-09	***	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	0.7481766		0.000	0.000	0.000	0.000
	ALL			0.0000016	***				
Anthropogenic	AM	PPA	SMC	0.0137353	*	0.000	0.000	0.000	0.000
	AF	PPA	SMC	2.240030e-09	***	0.000	0.000	0.000	0.000
	SA	PPA	SMC	0.0000025	***	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	0.2493449		0.000	0.000	0.000	0.000
	ALL			0.0114062	*				

S9. Spearman rank correlation results for macaques' events/interactions and number of visitors. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Site	**Variables tested**	**S statistic**	P-Value	Rho (ρ) estimate
SMC	Agonistic $ NOV	212906095	0.0007829***	-0.1034987
PPA	Agonistic $ NOV	192554127	0.9487	0.001986128
SMC	Contact $ NOV	200889474	0.182	-0.04121623
PPA	Contact $ NOV	184240763	0.1444	0.04507454
SMC	Self directed $ NOV	197539620	0.44	-0.02385383
PPA	Self directed $ NOV	209452069	0.005513*	-0.08559642
SMC	Facial $ NOV	211704526	0.001601***	-0.09727097
PPA	Facial $ NOV	201786466	0.1375	-0.04586537
SMC	Vocal $ NOV	226410816	1.53e-08***	-0.1734941
PPA	Vocal $ NOV	199056529	0.3045	-0.03171602
SMC	Anthropogenic $ NOV	125818311	2.2e-16***	0.3478799
PPA	Anthropogenic $ NOV	123713232	2.2e-16***	0.3587906

S10. Mann-Whitney U test results comparing agonistic interactions between age-sex classes across different sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Behav	*Age_gender*	*Site1*	*Site2*	*P_Value*	*Sig.*	Median1	IQR1	Median2	IQR2
Charge	*AM*	*PPA*	*SMC*	*1.89E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*6.00E-02*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*4.12E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*NaN*	*NA*	0.000	0.000	0.000	0.000
Chase with contact	*AM*	*PPA*	*SMC*	*6.37E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*1.45E-05*	*	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*4.16E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*3.18E-01*		0.000	0.000	0.000	0.000
Chase without contact	*AM*	*PPA*	*SMC*	*1.15E-03*	**	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.67E-06*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*2.12E-09*	***	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*2.03E-03*	**	0.000	0.000	0.000	0.000
Lunge	*AM*	*PPA*	*SMC*	*2.42E-02*	*	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.18E-01*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*3.18E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*NaN*	*NA*	0.000	0.000	0.000	0.000
Snatch	*AM*	*PPA*	*SMC*	*8.35E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*6.81E-03*	*	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*8.31E-02*		0.000	0.000	0.000	0.000

	JUV	PPA	SMC	NaN	NA	0.000	0.000	0.000	0.000
Biting another macaque	AM	PPA	SMC	5.09E-01		0.000	0.000	0.000	0.000
	AF	PPA	SMC	2.90E-02	*	0.000	0.000	0.000	0.000
	SA	PPA	SMC	5.65E-01		0.000	0.000	0.000	0.000
	JUV	PPA	SMC	NaN	NA	0.000	0.000	0.000	0.000

S11. Mann-Whitney U test results comparing self-directed Behaviours between age-sex classes across different sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Behav	Age_gender	Site1	Site2	P_Value	Sig.	Median1	IQR1	Median2	IQR2
Self-scratch	AM	PPA	SMC	4.19E-01		0.000	0.028	0.000	0.000
	AF	PPA	SMC	4.24E-05	*	0.000	0.048	0.000	0.091
	SA	PPA	SMC	4.31E-112	***	0.037	0.083	0.000	0.000
	JUV	PPA	SMC	2.03E-01		0.000	0.000	0.000	0.000
Body shake	AM	PPA	SMC	2.74E-02	*	0.000	0.000	0.000	0.000
	AF	PPA	SMC	7.09E-01		0.000	0.000	0.000	0.000
	SA	PPA	SMC	2.98E-06	*	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	1.00E+00		0.000	0.000	0.000	0.000
Gaze and yawn	AM	PPA	SMC	8.69E-06	*	0.000	0.000	0.000	0.000
	AF	PPA	SMC	8.97E-01		0.000	0.000	0.000	0.000
	SA	PPA	SMC	4.22E-20	***	0.000	0.000	0.000	0.000
	JUV	PPA	SMC	1.57E-01		0.000	0.000	0.000	0.000

S12. Mann-Whitney U test results comparing facial displays between age-sex classes across different sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Behav	***Age_gender***	***Site1***	***Site2***	***P_Value***	***Sig.***	Median1	IQR1	Median2	IQR2
Round mouth threat	*AM*	*PPA*	*SMC*	*2.34E-03*	*	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*2.51E-08*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*3.26E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*9.96E-01*		0.000	0.000	0.000	0.000
Bare teeth	*AM*	*PPA*	*SMC*	*4.34E-02*	*	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.65E-01*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*3.18E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*3.18E-01*		0.000	0.000	0.000	0.000

S13. Mann-Whitney U test results comparing anthropogenic interactions between age-sex classes across different sites. The significance codes indicate the level of significance based on the p-values as follows ***: p-value ≤ 0.001, **: 0.001 < p-value ≤ 0.01, *: 0.01 < p-value ≤ 0.05, .: 0.05 < p-value ≤ 0.1.

Behav	*Age_gender*	*Site1*	*Site2*	*P_Value*	*Sig.*	Median1	IQR1	Median2	IQR2
Jumping/climbing on visitors	*AM*	*PPA*	*SMC*	*4.16E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*1.23E-02*	*	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*1.13E-06*	***	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*8.37E-01*		0.000	0.000	0.000	0.000
Snatching items from vistitors	*AM*	*PPA*	*SMC*	*2.52E-03*	***	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.15E-02*	*	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*1.81E-02*	*	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*7.69E-01*		0.000	0.000	0.000	0.000
Getting fed by visitors	*AM*	*PPA*	*SMC*	*3.83E-04*	***	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*2.45E-14*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*9.73E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*3.56E-02*	*	0.000	0.000	0.000	0.000
Snatching food from visitors	*AM*	*PPA*	*SMC*	*1.12E-02*	*	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*1.51E-04*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*1.02E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*NaN*	*NA*	0.000	0.000	0.000	0.000
Aggression towards visitor	*AM*	*PPA*	*SMC*	*6.83E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.24E-01*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*2.09E-03*	**	0.000	0.000	0.000	0.000

	JUV	*PPA*	*SMC*	*6.54E-01*		0.000	0.000	0.000	0.000
Observing a visitor	*AM*	*PPA*	*SMC*	*3.38E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*3.65E-08*	***	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*4.14E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*NaN*	*NA*	0.000	0.000	0.000	0.000
Jumping on a taxi	*AM*	*PPA*	*SMC*	*1.84E-01*		0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*5.41E-03*	*	0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*2.40E-02*	*	0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*2.70E-01*		0.000	0.000	0.000	0.000
Getting touched/petter by a visitor	*AM*	*PPA*	*SMC*	*1.42E-02*	*	0.000	0.000	0.000	0.000
	AF	*PPA*	*SMC*	*5.82E-02*		0.000	0.000	0.000	0.000
	SA	*PPA*	*SMC*	*9.99E-01*		0.000	0.000	0.000	0.000
	JUV	*PPA*	*SMC*	*1.94E-02*	*	0.000	0.000	0.000	0.000

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