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submitted for a Master's Degree
Predictive and integrative animal biology (PRIAM)

**Behavioural Adaptations and
Tourist-Macaque Interactions:**
*A Comparative
Study of Social Learning in Gibraltar's Barbary
Macaques*

by

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I. Introduction

Over the past few decades, the intensification of human activity has transformed many natural environments, leading to increasingly frequent and complex interactions between humans and wildlife. This phenomenon, characteristic of the Anthropocene, has not only reshaped habitats but also introduced new behavioural pressures on free-ranging animal populations (Barnosky et al., 2011; Dirzo et al., 2014). Non-human primates are particularly impacted by anthropogenic pressures as their social visibility, close relations with us and charismatic nature make them disproportionately exposed to human attention, often placing them at the frontline of wildlife tourism and human–wildlife conflict.

The Barbary macaque (*Macaca sylvanus*), a gregarious Old World monkey species, represents a particularly interesting subject in this domain. It is the only macaque species naturally found outside Asia and the only non-human primate found in Europe. Once widespread, its native range is now restricted to fragmented forests in the mountainous regions of Morocco and Algeria. In these habitats, deforestation, livestock farming, and illegal capture for the pet trade continue to degrade population viability (Modolo et al., 2008; IUCN, 2024). Consequently, the species is currently listed as Endangered on the IUCN (The International Union for Conservation of Nature) Red List.

In contrast to its declining North African counterparts, the population of Barbary macaques introduced into Gibraltar benefits from legal protection and high visibility. Approximately 230 individuals inhabit the Upper Rock Nature Reserve, a 2.44 km² protected area that receives over 800,000 visitors annually (Fuentes, 2007). Here, macaques live in close proximity to humans, with frequent opportunities for visual and physical contact. Tourists travel on foot or via car, taxi, minibus, or cable car, and often gather at known macaque hot spots such as Apes' Den, Prince Philip's Arch, and St Michael's Cave.

These daily and repeated encounters between humans and macaques create a unique social and ecological interface, marked by interaction patterns that are rarely observed in more secluded primate habitats. Visitors often attempt to photograph, touch, feed, or vocalise at macaques. Behaviours that, while seemingly harmless or playful, constitute unpredictable and often stressful stimuli for the animals. O'Leary and Fa (1993) reported up to 100 human–macaque interactions per hour during peak tourist seasons, with macaques spending more than 13% of their activity budget engaged with people. Unlike macaques in other contexts, Gibraltar's individuals cannot escape to inaccessible refuges, which may compound their exposure to anthropogenic stimuli and intensify behavioural repercussions.

Prior studies have highlighted elevated physiological stress caused by human presence on Moroccan Barbary macaque such as increased cortisol levels and behavioural signs of emotional arousal, including self-directed behaviours like yawning and self-scratching (Maréchal et al., 2011; Troisi, 2002). These behaviours are recognised as reliable, non-invasive indicators of anxiety and stress in macaques, especially in response to ambiguous or repeated external disturbances. Beyond stress indicators, anthropogenic exposure can also influence social dynamics. Studies on other macaque species have shown that provisioning, crowding, and unpredictable human proximity can disrupt grooming patterns, increase intra-group aggression, and shift dominance interactions (Kaburu et al., 2019). Such effects may vary across groups depending on habitat microstructure, group composition, or frequency of exposure, factors especially relevant in Gibraltar, where macaque groups occupy different traffic zones of tourists within the reserve.

The frequency and intensity of human-macaque interactions in Gibraltar offer a context for understanding how primates navigate persistent anthropogenic disturbance. Such repeated encounters do not only alter day-to-day behavioural patterns, they may also shape long-term strategies of social and ecological adaptation. In particular, macaques are known for their behavioural plasticity, an evolutionary advantage that may allow them to cope with unpredictable environments, but which also risks promoting maladaptive tendencies when shaped by unnatural conditions (McKinney, 2016). For instance, individuals repeatedly exposed to human feeding may exhibit excessive aggressive behaviours, increased food solicitation, or reliance on anthropogenic resources, all of which can affect group cohesion and inter-individual dynamics (Maréchal et al., 2016)

In the Upper Rock Nature Reserve, macaques have been observed engaging in complex interactions with tourists, often involving intentional approaches, gestural communication such as staring at tourists to express discomfort, or spatial monitoring of human movement. These patterns may reflect learned behaviours or social facilitation, whereby individuals mimic or follow the responses of conspecifics, especially in uncertain or high-reward contexts (O’Leary & Fa, 1993). As such, anthropogenic pressures do not operate in isolation: they are modulated by social structure, prior experience, group identity, and the microecology of each site.

Building on this, the present study focused on four distinct macaque groups distributed across various zones of the reserve, each exposed to different levels of tourist pressure and environmental complexity. While some areas attract dense and continuous visitor flows, others are more exposed to sporadic flow of visitors. This variability allowed for a comparative framework through which the behavioural consequences of tourist presence can be investigated. The study also integrated an experimental component to investigate problem solving capacity as a socially learned capacity. It also allowed testing of potential inter-individual and inter-group differences, reflecting local enhancement by humans and as a result, local adaptations to specific types of interactions. These included structured trials using transparent pencil case containing peanuts (most common food given by the reserve management and the tourists and locals). Positioned at visible but variable distances, these devices offered macaques the opportunity to engage with anthropogenic stimuli in a semi-standardised format, permitting fine-grained observations of approach behaviour, hesitation, success, and potential imitation or social learning.

These trials are conducted alongside location sampling, in which a suite of interactions between macaque and human are recorded including pillage when a macaque is looking and stealing food from a human, aggressive behaviours, voluntary given food from human and any other type of interaction that might happen.

By systematically analysing these patterns, the thesis seeks to contribute to a deeper ethological understanding of how one endangered primate species *Macaca sylvanus* responds to high-density anthropogenic exposure. In doing so, it explores broader questions of behavioural flexibility, intergroup variation, and the cognitive capacities of wild primates living under intense and persistent human influence. Although the Barbary macaques of Gibraltar have been the subject of several descriptive studies over the past decades, most focus either on population structure, health or direct aggression toward visitors. Far less is known about the ways in which macaques and human interact under varying levels of human presence. In a context where space is limited, human macaque interactions are often initiated by tourists and as a result behavioural flexibility becomes a key mechanism through which macaques navigate their environment.

The objective is to characterise the variability of individual and group behaviours across different contexts of anthropogenic pressure. By incorporating both naturalistic and experimental data collection, this work allows for the examination of not only problem-solving strategies, but also broader patterns of interaction with novel objects. Specifically, the study considers both the likelihood of engaging with a task and the strategies used to solve it, offering a more comprehensive view of exploratory and social tendencies. To guide the study design and analytical framework, the research was driven by several core questions: how tourist density and group composition influence the frequency and duration of human–macaque interactions across sites; whether food-related behaviours such as provisioning and pillaging vary systematically between groups; how individual problem-solving performance relates to group origin, sex, and social context, particularly the presence of conspecifics and associated stress; and whether certain manipulation strategies, such as using the zipper tab, are more frequent among individuals exposed to specific anthropogenic contexts, potentially reflecting localised behavioural adaptations.

This study therefore contributes to a better understanding of the ecological and behavioural plasticity of Barbary macaques living in human-modified environments, and more broadly to the study of wildlife resilience in the face of intensifying anthropogenic influences.

II. Material and Methods

Study Site, and Groups

The study was conducted on the Barbary macaques (*Macaca sylvanus*) inhabiting the Upper Rock Nature Reserve in Gibraltar. This protected area of approximately 2.44 km² attracts considerable tourism, with daily visitor numbers reaching around 3,000. Temperatures in the region vary from 14°C to 35°C throughout the year. The macaques are provisioned twice daily with peanuts, barley, fruits, and vegetables, though feeding schedules vary, and despite official regulations prohibiting visitors from feeding or touching the animals, these rules are most often not enforced effectively. We studied four different groups of Barbary macaques (*Macaca sylvanus*) out of the ten present in the Upper Rock Nature Reserve in Gibraltar: Royal Anglian Way, Apes Den, Prince Philip's Arch, and Cable Car, see Figure 1 for a map of their respective localisations. As those four groups are those with a well-known composition, and are located along the anthropogenic gradient, offering a good comparative perspective. These groups live in areas that partly overlap, but each group spends most of its time in a specific zone. The number of tourists and the type of human-macaque interactions vary a lot between these zones, which may influence the macaques' behaviour.

The Royal Anglian Way group, made up of around 22 adult individuals, is usually found near the entrance of Saint Michael's Cave. This area includes a restaurant where tourists often stop to eat or rest. Because of this, macaques have many chances to get food from visitors, especially during lunch hours and early afternoon when the place is busy. Items like ice cream, sold nearby, are common targets for pillaging.

The Apes Den group includes about 25 adults and subadults, it is the original first group from which the others group are from. This group lives in an area that can be either calm or quite busy. Tourists usually stop here for a short time to take photos of the view and the monkeys. Taxi drivers often bring visitors but do not stay very long, same for larges buses that stop regularly.

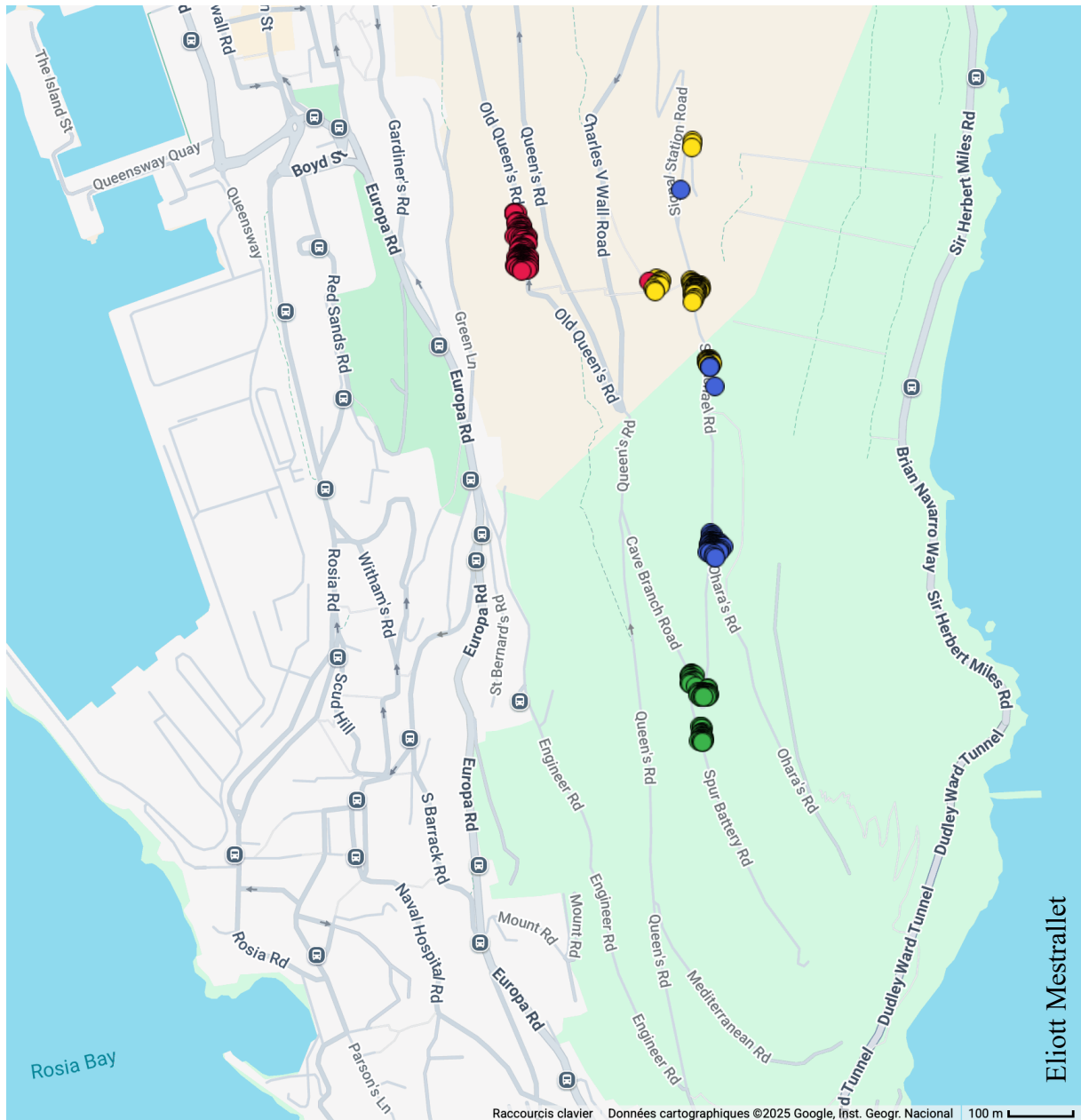


Figure 1. Map of the Upper Rock reserve with locations of the four group, Apes Den in red dots, Cable Car in yellow dots, Prince Philip Arch in blue dots and Royal Anglian Way in green dots

The Prince Philip's Arch group has around 18 adult individuals. They live in a narrow area that partly overlaps with the Cable Car group. This area is mainly a path used by tourists walking from Saint Michael's Cave to the top of the Rock. Visitors stop briefly here to catch their breath before continuing.

The Cable Car group is the largest, comprising over 40 individuals. They inhabit the summit of the Rock near the cable car station (which remained closed during the study period) and frequent the Prince Philip Arch feeding platform, a hotspot for tourist activity due to frequent taxi stops. Despite the cable car being out of service, the area remained busy, with taxis bringing groups of tourists who often fed the macaques and encouraged them to climb on people for photographs (Figure 2; Figure 3). In the late afternoon, the Cable Car group typically moves to a different area, and the Prince Philip Arch group ascends to the top. Although occasional conflicts occur, this transition generally happens with minimal aggression. The Prince Philip Arch feeding platform is occasionally shared by individuals from the Prince Philip, Apes Den, and Cable Car groups. However, it is primarily used by the Cable Car group, and the frequent human presence at this site generates interactions that can affect all three groups.

Data Collection and Extraction

Fieldwork was conducted from January 10 to March 10, 2025. Data collection followed two complementary approaches: location sampling and an experimental task designed to test problem-solving behaviour.

Location sampling was carried out using the CyberTracker software across 48 observation sessions distributed among four groups of wild Barbary macaques in Gibraltar: Apes Den ($n = 16$), Cable Car ($n = 12$), Prince Philip Arch ($n = 9$), and Royal Anglian Way ($n = 11$). A total of 571 observations were collected, with data recorded every five minutes about the number of conspecifics and the number of people, for approximately one hour per session, supplemented by additional entries *ad libitum* when an interaction happened, with a detailed description of the interaction. A custom-designed CyberTracker form was created on a computer and deployed to mobile devices via QR code, ensuring structured and consistent data collection in the field. Each observation included the group identity, number of visitors present, number of conspecifics nearby, the presence of food in the interaction (binary), descriptive information such as the description of the interaction (was written while the interaction where happening), identity and category of people involved (adult, child, taxi driver...), as well as object-related information such as the type of object obtained. This detailed ecological sampling framework allowed for tracking of the macaques social and environmental context, enabling robust interpretation of their behavioural and cognitive responses in an anthropogenic environment.

The experimental protocol involved presenting individual Barbary macaques with a transparent plastic pencil case containing three monkeynuts (peanuts in shell) to assess their problem-solving abilities in an anthropogenic context. A total of 48 experimental trials were conducted across the four groups. Trials were alternated between groups to ensure balanced sampling, and only adult individuals were selected for testing. Whenever possible, individuals were tested only once; if a subject was tested more than once, trials were separated by several days. Each trial began with the discreet placement of the pencil case near a focal macaque, ideally when the subject was distant from conspecifics to reduce social interference. Care was taken to ensure that the focal individual was the first to notice the object.



Figure 2. Picture of the access to Cable Car group's location, crowded with taxis waiting to deposit their tourists



Figure 3. Picture of tourists and taxi driver interacting with Cable Car group

The task required subjects to open the case, ideally using the zipper mechanism (Figure 4), although alternative strategies were also observed. Each trial was video-recorded, beginning when the subject noticed the case and ending once the monkey had finished eating all three monkeynuts or clearly disengaged. This ensured that the entire problem-solving sequence was captured. The consumption of all nuts indicated that the macaque had successfully gained full access to the contents, regardless of the method used (e.g., tearing, biting, or manipulating the zip), and had completed the task in its own way.

A detailed coding protocol was used to generate a dataset that included: trial number, group, individual ID, age class and sex, interaction occurrence, task success, use of the zipper, time to success, approach description, self-directed behaviours (as stress proxies), presence of conspecifics, contextual notes, and date.

Ethical Considerations

All procedures were designed to minimise disturbance to the macaques and their environment. Observers kept appropriate distances and avoided interfering with natural behaviours, particularly during sensitive activities such as feeding, resting, or social interactions. The experimental setup using a transparent pencil case containing three peanuts was validated prior to deployment to ensure it posed no risk or significant disruption to the animals.

The full research protocol, including both observational and experimental components, was reviewed and approved by the Department of Archaeology, University of Cambridge. It also received authorisation from the Gibraltar Macaques Management Team. This ensured that all data collection adhered to ethical standards for research involving wild primates.

Data Analyses

All statistical analyses were conducted using R version 4.4.0 (R Core Team, 2024). The analytical strategy was designed to address the study's predefined research questions concerning group-level differences in exposure to anthropogenic pressure, variation in food-related behaviours, and inter-individual problem-solving performance under varying social contexts.

For the location sampling data, we employed generalised linear mixed models (GLMMs) and linear mixed models (LMMs), depending on the distributional properties of each outcome variable. Models were fitted using the *lme4*, *glmmTMB*, and *brglm2* packages. Random effects were incorporated to account for repeated observations within individuals (for behavioural outcomes) or within locations and dates (for session-level data).

Initial analyses examined differences between groups in key indicators of anthropogenic pressure such as hourly interaction rates (number of interactions per hour), presence of food-related behaviours (interactions with food involved, separated in provisioning or pillaging), and visitor density. These variables were modelled using LMMs or GLMMs with group identity as a fixed effect and session or group as a random intercept where appropriate. Session was included as a random effect to account for non-independence of observations within sampling events and to control for unmeasured variability associated with temporal or contextual factors.



Figure 4. Coco an Adult Male from Cable Car with his hand in the pencil case after successfully opening it using the zipper tab

Post hoc comparisons were conducted using the *emmeans* package with Tukey correction for multiple testing.

To explore inter-individual and group-level differences in engagement and problem-solving during the experimental task, we constructed a series of generalised linear mixed models (GLMMs) and linear mixed-effects models (LMMs), tailored to each dependent variable. Initial full models included group of origin, sex class, standardised self-directed behaviours (as a proxy for stress), and the number of nearby conspecifics (also standardised) as fixed effects. Individual identity was included as a random intercept to account for repeated measures. However, preliminary diagnostic checks highlighted strong multicollinearity among certain predictors, particularly between group origin and sex class, and between stress behaviours and conspecific presence. These redundancies affected both model convergence and the interpretability of parameter estimates.

To improve model stability and interpretability, we adjusted our modelling approach based on both statistical and theoretical considerations. The variable *sex class* was removed selectively only from models where it did not contribute meaningfully to explaining the outcome or caused convergence issues. Specifically, in the models for interaction and latency, removing *sex class* improved model fit (lower AIC) or had no impact on explanatory power (LRT $p > 0.9$), justifying its exclusion for parsimony. However, for the zipper success model, including *sex class* improved fit ($\Delta\text{AIC} \approx -30$; LRT $p = 0.064$), and it was therefore retained in the final version of that model.

Additionally, *stress-related behaviours* and *conspecific density* were never included together, due to high collinearity and overlapping conceptual meaning. To decide between them, we ran a preliminary linear model regressing self-directed behaviour (stress proxy) on conspecific density, confirming a strong positive association. Given this redundancy and the theoretical salience of social context for zipper use, we retained *conspecific presence* in models of success and interaction. Conversely, *stress* was retained in the latency model, where individual motivation and arousal may play a larger role.

We fitted three primary models to the experimental dataset. First, a binomial generalised linear mixed model (GLMM) with a logit link function was used to predict the probability of interacting with the pencil case, regardless of task outcome. Second, we applied a linear mixed-effects model (LMM) to examine latency to task completion (in seconds) among individuals who successfully retrieved all food rewards. Third, task success itself defined as retrieving all three monkeynuts was modelled as a binary outcome using another binomial GLMM. Across all models, group origin and either stress or conspecific density were included as fixed effects, while individual identity was included as a random intercept to account for repeated measures.

The use of the zipper was considered a separate behavioural outcome and analysed with an additional binomial GLMM. Repeated trials were spaced across multiple days to minimise temporal dependencies. We assessed model fit via likelihood ratio tests comparing each full model against its corresponding null, and explored trends further using pairwise post hoc comparisons and penalised logistic regression (ridge). All visualisations were produced using the *ggeffects* and *ggplot2* packages in R. This modelling framework allowed us to evaluate how group identity and immediate social context shaped individuals' engagement with the task and their problem-solving strategies, while controlling for individual variability.

III. Results

Location sampling analysis :

Descriptive Statistics for the location sampling data

Given the exploratory nature of this dataset, which was based on real-time field descriptions of individuals and behaviours, the analysis focused on descriptive patterns and keyword frequencies rather than inferential statistics. Overall, most individuals involved in human-macaque interactions were adult tourists, with males and females almost equally represented (140 and 134 out of 451 total individuals, respectively). Male taxi drivers also made up a notable portion of the sample ($n = 64$), likely reflecting their regular involvement in facilitating macaque encounters.

At the group level, as shown on figure 5, Apes Den recorded the highest number of people involved in interactions, notably dominated by adult tourists (80 males and 68 females). It also had a high number of teenagers and children, and moderate involvement from taxi drivers ($n = 14$). Cable Car came next, with a balanced mix of adult tourists (33 males, 30 females) and a relatively high number of taxi drivers ($n = 18$). Anglian Way involved fewer individuals overall but still included both tourists and local participants, notably 8 taxi drivers. Prince Philip showed the lowest total number of individuals, yet had the highest concentration of male taxi drivers ($n = 24$), which may reflect local practices: at this site, taxi drivers frequently stop their vehicles and allow macaques to approach car windows, offering food while tourists take photos, this being the main entrance to the reserve where macaques are often seen for the first time. In contrast, taxis rarely stop at Royal Anglian Way despite its location upstream on the same road.

Regarding object transfers, interactions were strongly food-oriented, with peanuts (especially salted) being by far the most commonly retrieved item, consistent with routine provisioning by taxi drivers. Other popular objects included biscuits, apples, bananas, and ice cream. The presence and variety of food items confirm the central role of human provisioning in shaping macaque behaviour.

When specifically analysed by group and as visible on figure 6, Cable Car had the highest total number and diversity of object transfers, including 32 instances of peanut acquisition and a variety of other items such as biscuits, ketchup sauce, and even clementines. Apes Den followed with 16 peanut events and smaller quantities of items like banana, bread, and pasta. Prince Philip recorded fewer total objects but a more diverse and atypical list, including blueberries, chocolate biscuits in a plastic bag, and a bouquet of flowers—indicating occasional, less systematic provisioning. Royal Anglian Way had fewer total interactions involving objects but stood out as the only group where ice cream was obtained, supporting the observation that this item is more accessible there due to the presence of a designated tourist refreshment stop.

The qualitative keywords extracted from interaction descriptions further illustrate patterns of contact and provisioning. Across the full dataset, the most frequent term was “gave”, highlighting the centrality of human-initiated feeding. Other common terms included “bag”, “car”, and “touched”, which point to macaques’ opportunistic foraging and the physical closeness often encouraged by tourists. On figure 7 and when specifically by group, we can see that Cable Car had the highest count for the keyword “gave” ($n = 38$), reflecting intense provisioning activity. Apes Den followed with high values for “touched” ($n = 16$) and “bag” ($n = 12$), suggesting not only feeding but also close-range interactions. Interestingly, “car” was

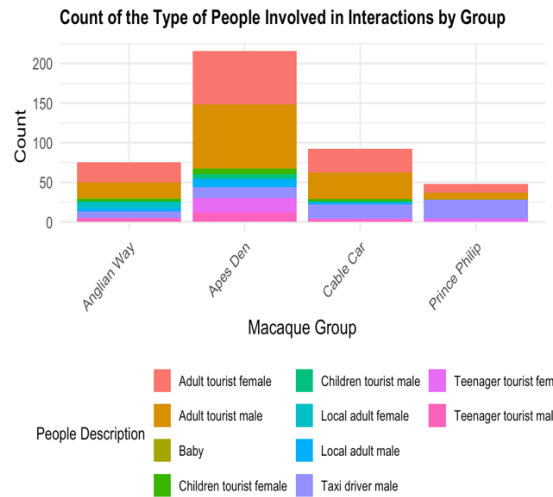


Figure 5. Bar plot of the count of the type of people involved in interactions by group

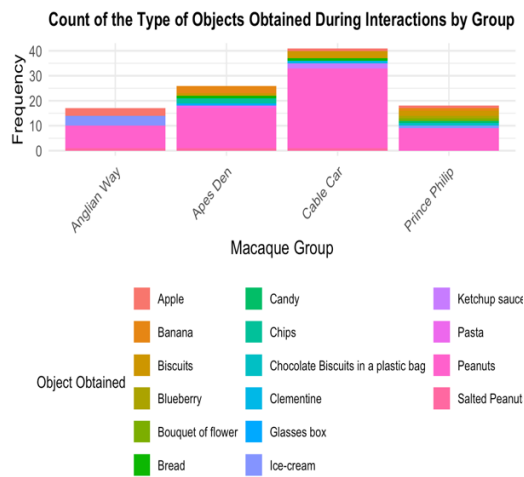


Figure 6. Bar plot of the count of the type of objects obtained during interactions by group

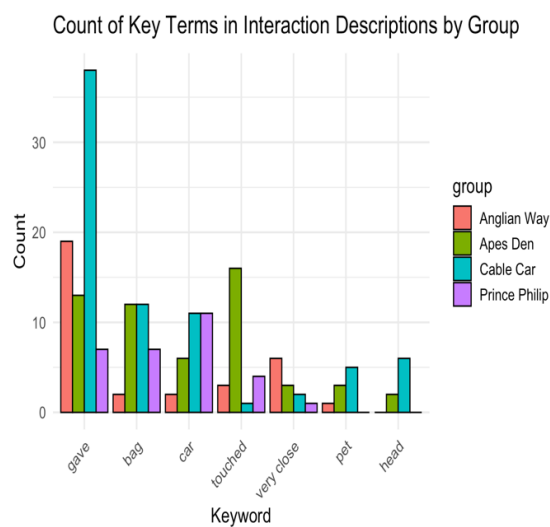


Figure 7. Bar plot of the count of the key terms in interaction descriptions by group

reported frequently at both Cable Car and Prince Philip ($n = 11$ each), indicating macaques approaching or climbing onto vehicles in those locations. Anglian Way showed lower overall keyword frequencies, though it still had notable mentions of “gave” ($n = 19$) and “very close” ($n = 6$), possibly reflecting briefer but still engaged interactions. Terms such as “pet” and “head” were rare across all groups, suggesting that overt physical contact was less typical than food-based exchanges.

Interaction Rates Across Groups

Figure 8 displays the mean hourly interaction rates across the four macaque groups. Descriptive statistics indicated that the Cable Car group exhibited the highest mean interaction rate, (mean = 10.0, SD = 13.77, $n = 10$), followed by Apes Den (mean = 7.50, SD = 6.24, $n = 12$), Anglian Way (mean = 6.14, SD = 4.71, $n = 7$), and Prince Philip (mean = 4.67, SD = 5.43, $n = 9$). However, a one-way ANOVA revealed no statistically significant difference in interaction rates between groups ($F(3, 34) = 1.35$, $p = 0.275$). Post hoc pairwise comparisons using Tukey’s HSD confirmed this result: all groups shared the same significance letter (“a”), and the 95% confidence intervals of their means overlapped substantially. These results suggest that, although there was variation in observed means, the frequency of human-macaque interactions per hour was statistically comparable among the four sites during the study period.

Modelling the Predictors of Human-Macaque Interaction Rates

To assess the influence of crowd and macaque number on the frequency of human-macaque interactions, a Poisson generalized linear mixed model (GLMM) was first implemented with group as a random effect and observation time as an offset. This initial model revealed that the number of people significantly increased interaction rates ($p < 0.001$), while the number of macaques had no detectable effect ($p = 0.866$). However, diagnostic checks revealed substantial overdispersion (dispersion ratio = 7.45, $p < 0.001$), violating the assumptions of the Poisson distribution.

To address the issue of overdispersion observed in the Poisson model (dispersion ratio = 7.45, $p < 0.001$), a negative binomial GLMM was fitted using the same predictors and random structure (group as a random intercept; observation time as an offset). This model provided a substantially better fit (AIC = 225.0 vs. 356.2) and revealed a significant positive effect of visitor density on the frequency of human-macaque interactions (Estimate = 0.0577, SE = 0.0260, $z = 2.22$, $p = 0.0266$). In contrast, macaque number did not significantly affect interaction frequency (Estimate = 0.0158, SE = 0.0591, $z = 0.27$, $p = 0.7896$), see figure 9 for effects plots. The random intercept variance for group was negligible ($\approx 7.97e-10$), indicating that most variation in interaction rates was explained by visitor numbers rather than group identity or location.

As shown in Figure 10, model diagnostics supported the robustness of this fit. A Kolmogorov-Smirnov test on simulated residuals confirmed that the model met distributional assumptions ($D = 0.103$, $p = 0.802$). These results validate the use of the negative binomial model and underscore that tourist density is the primary driver of interaction frequency. While a weak trend was observed for macaque presence, it was not statistically supported.

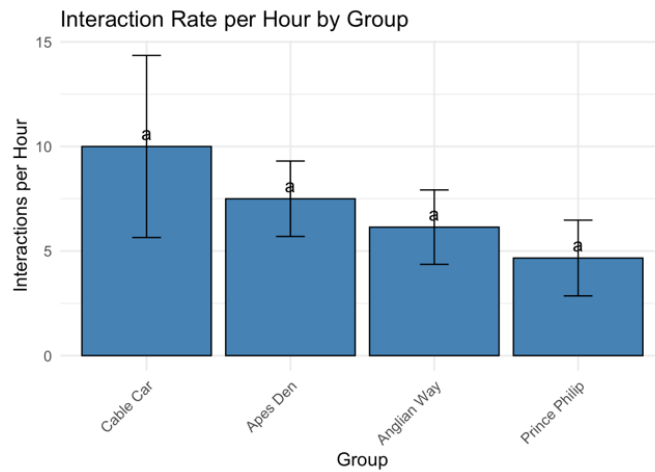


Figure 8. Bar plot of interaction rate per hour across macaque groups

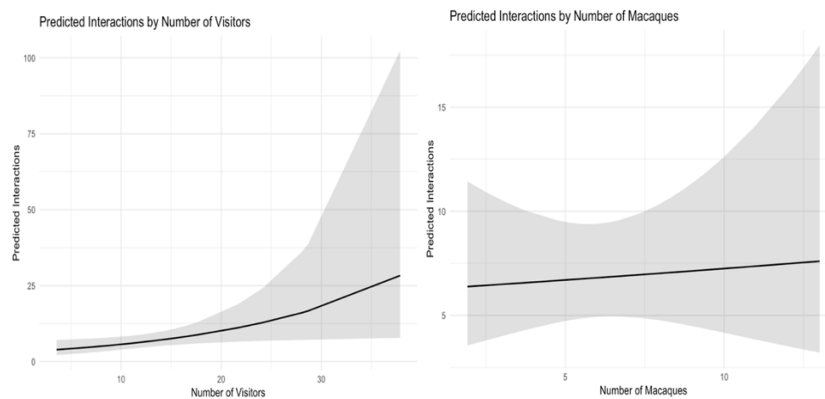


Figure 9. Effect plots from the negative binomial GLMM showing predicted number of interactions per session as a function of visitor density (left) and macaque density (right), with 95% confidence intervals.

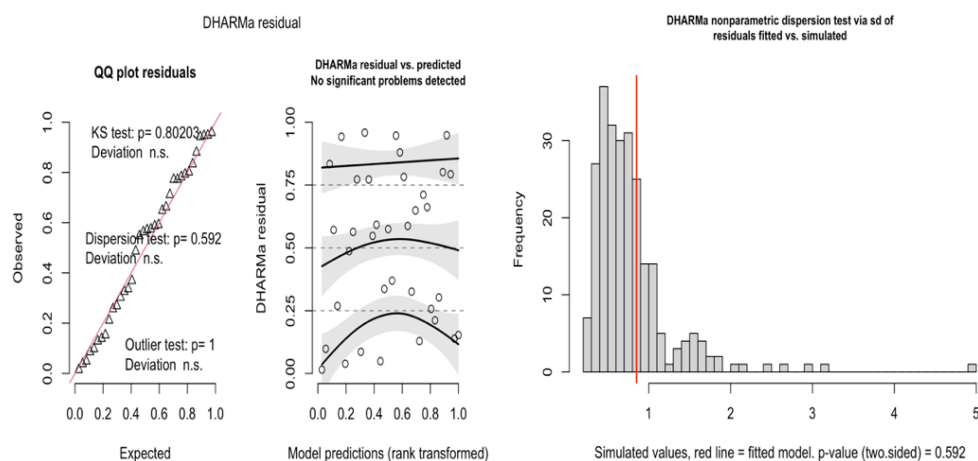


Figure 10. Residual Diagnostics for the Negative Binomial GLMM (This figure combines two diagnostic plots from the DHARMA package. The left panel presents a QQ plot of residuals and simulation-based tests. The right panel displays a histogram comparing the disper

Relationship Between Number of People and Interaction Duration

To formally examine the predictors of interaction duration, we fitted a linear mixed-effects model (LMM) with interaction duration as the response variable, and the number of people, number of macaques, and group identity as fixed effects. A random intercept for individual macaque identity was included to account for repeated measures. Model comparison using a likelihood ratio test revealed that the full model (including group identity) provided a significantly better fit than the reduced model without it ($\chi^2(3) = 34.0, p = 0.011$).

Among the predictors, the number of macaques present had a significant positive effect on interaction duration (Estimate = 5.28 ± 2.07 , $t = 2.55$), suggesting that interactions tend to last longer when more conspecifics are present. In contrast, the number of people did not significantly influence interaction duration ($p = 0.076$), as visible in figure 11. Regarding group-level differences, interactions were significantly shorter at Prince Philip Arch compared to Anglian Way (Estimate = -64.91 ± 25.58 , $t = -2.54$), while durations at Apes Den and Cable Car did not differ significantly from those at Anglian Way.

Together, these results suggest that social context, especially conspecific presence, have more influence on interaction duration than visitor numbers. Nonetheless, the model's explanatory power was limited (residual SD = 110.2), pointing to other unmeasured social or environmental factors shaping interaction dynamics.

To assess whether interaction duration differed between macaque groups, we conducted a one-way ANOVA with group as a fixed effect. The analysis revealed a significant group-level difference in interaction durations ($F(3, 271) = 4.63, p = 0.0035$). Post hoc Tukey tests indicated that interactions involving the Prince Philip's Arch group were significantly shorter than those recorded at both Apes Den ($p = 0.0016$) and Cable Car ($p = 0.038$), while differences between other pairs of groups were not statistically significant. As shown in Figure 12, Apes Den exhibited the longest interactions (mean = 136 seconds), followed by Cable Car and Anglian Way. Prince Philip had the shortest average interaction duration (70 seconds). These findings suggest that macaques at Prince Philip are engaged in quicker encounters with humans, potentially reflecting faster-paced tourist movement through that zone or lower levels of provisioning. In contrast, the extended durations at Apes Den and Cable Car may reflect settings where visitors stay longer, allowing more time for any kind of interactions.

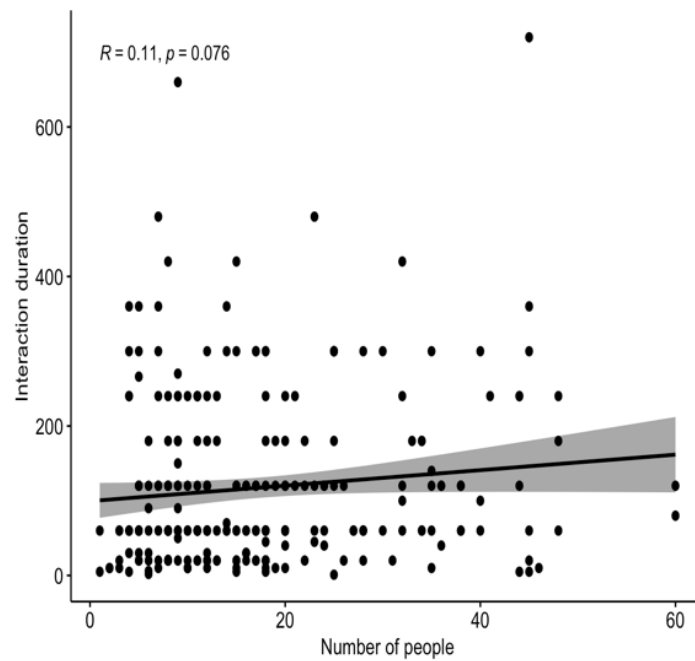


Figure 11. Scatterplot of the relationship between number of people and interaction duration

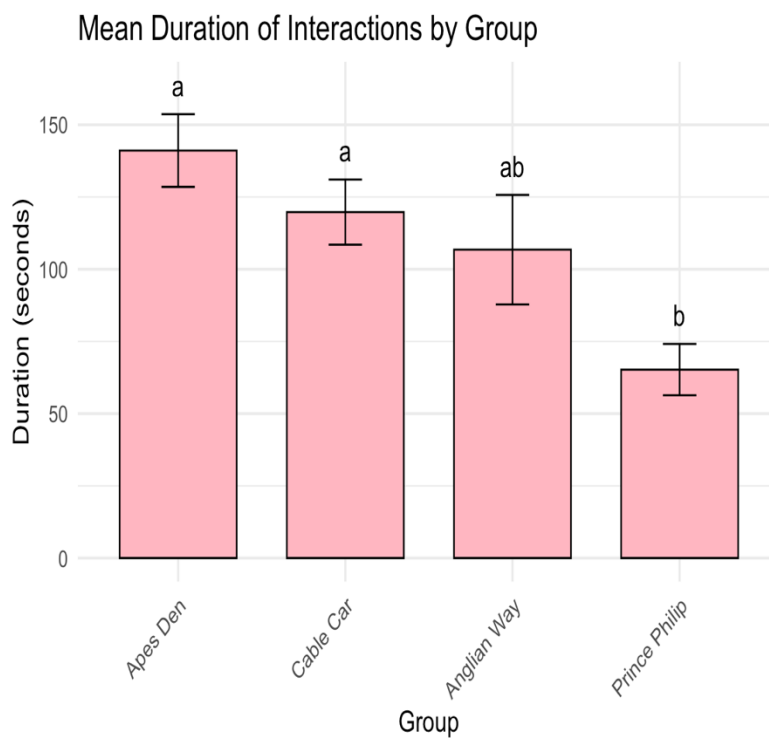


Figure 12. Bar plot of the mean duration of interactions by group with Tukey letters

Group Differences in the Nature of Human-Macaque Interactions

To better understand the qualitative nature of human–macaque interactions across the four studied groups, we analysed the proportion of interactions involving food, and among those, the more specific one that involved intentional feeding by visitors (i.e., active offering of food or taxi drivers giving food to the macaques in order for them to climb on tourists). These metrics allow for a more refined interpretation of anthropogenic pressure beyond interaction frequency alone.

As shown in Figure 13 and 14, the Cable Car group displayed the highest level of food-related interactions, with 66.7% of all interactions involving food and 59.6% being actively encouraged by visitors. This contrasts sharply with Apes Den, which had a similarly high number of total interactions ($n = 90$) but the lowest proportion of food-related (33.3%) and intentional feeding events (28.9%).

To evaluate differences in food-related behaviours across macaque groups, we fitted two separate one-way ANOVAs using group as a fixed effect. The first model assessed the proportion of interactions involving food (coded as 0 or 1), and the second assessed the rate of intentional feeding. Both models revealed significant effects of group identity (food involvement: $F(3, 269) = 7.48, p < 0.001$; intentional feeding: $F(3, 269) = 7.50, p < 0.001$).

Post hoc Tukey HSD tests were conducted to identify pairwise group differences based on the fitted models. These tests showed that the Cable Car group significantly differed from Apes Den for both food involvement (*Tukey group*: b vs. a) and intentional feeding (*Tukey group*: b vs. a). Anglian Way and Prince Philip occupied an intermediate statistical position (*group ab*), not differing significantly from either Cable Car or Apes Den.

Descriptively, Cable Car exhibited the highest proportion of food-involved interactions (66.7%) and intentional feeding (59.6%), while Apes Den had the lowest rates (33.3% and 28.9%, respectively). Intermediate levels were observed in Anglian Way (52.4%, 40.5%) and Prince Philip (50.0%, 31.0%). These patterns likely reflect site-specific dynamics in tourist behaviour, provisioning tendencies, and the spatial context of interactions.

Group	Total Interactions	Food Interactions	Intentional Feeding	% Food Involved	% Intentional Feeding	Tukey Group (Food)	Tukey Group (Intentional)
Cable Car	99	66	59	66.7	59.6	b	b
Anglian Way	42	22	17	52.4	40.5	ab	ab
Prince Philip	42	21	13	50.0	31.0	ab	a
Apes Den	90	30	26	33.3	28.9	a	a

Figure 13. Summary of food-related interactions across macaque groups

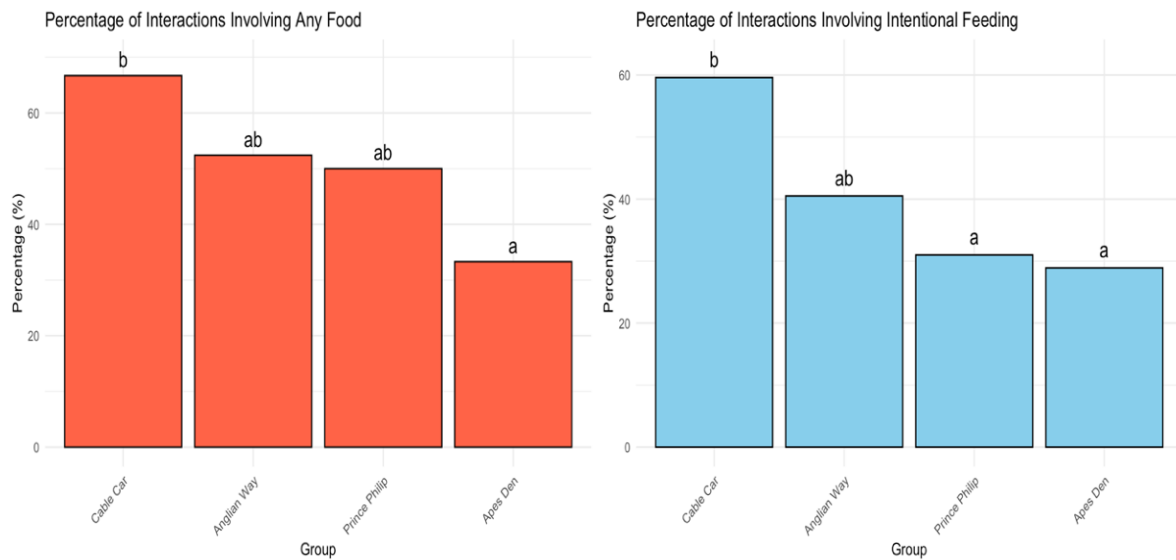


Figure 14. Histograms of proportion of interactions involving any food (left) and intentional food provisioning (right) across macaque groups with Tukey's post hoc comparisons shown with letters

Pillaging Rates and Success Across Groups

To examine group-level differences in foraging-related conflict behaviours, we analysed the proportion of interactions involving pillaging as well as pillage success rate, using separate one-way ANOVAs with group as the fixed factor, followed by Tukey's HSD post hoc comparisons.

The proportion of interactions involving pillaging varied significantly between groups as shown in Figure 15. Prince Philip's Arch exhibited the highest proportion of pillaging, with 33.3% of all interactions involving an attempt to steal food. This was significantly greater than in Cable Car, where only 12.1% of interactions involved pillaging ($p < 0.05$). Anglian Way and Apes Den showed intermediate values of 18.6% and 15.6%, respectively, and did not differ significantly from either Prince Philip's Arch or Cable Car. These results continue to indicate that while total interaction frequency may be high across groups, the nature of these interactions particularly food-related conflict differs depending on the site.

We also evaluated pillage success rates, defined as the proportion of attempted pillages that resulted in the macaque acquiring food. Although the ANOVA revealed no significant effect of group, descriptive statistics indicate notable variation across sites. Prince Philip's Arch again ranked highest, with a success rate of 78.6%. While these differences were not statistically significant, they suggest that individuals in Prince Philip's Arch may experience a higher probability of success once a pillaging attempt is initiated.

Initiation Dynamics and the Role of Food in Human–Macaque Interactions

Figure 16 shows the proportion of observed interactions initiated by macaques across the four studied groups. The Prince Philip group displays a significantly higher percentage of macaque-initiated interactions (68%) compared to the other three groups, which all fall below 40%. Error bars indicate standard error, and a significant group difference is denoted by the significance star (ANOVA, $p < 0.05$).

Analyses of interaction initiation revealed significant variation among groups (ANOVA, $p < 0.05$), with the Prince Philip group showing a higher proportion of macaque-initiated interactions compared to Anglian Way, Cable Car, and Apes Den. This finding may reflect the unique context of Prince Philip's Arch, where tourist flow is less structured and the tourists don't stop there, possibly encouraging macaques to adopt more proactive strategies to obtain food or attention. In contrast, groups like Cable Car or Royal Anglian Way experience more predictable tourist stops and structured feeding contexts, which may reduce the need for macaques to initiate interactions themselves.

Figure 17 pictures the comparison between the proportion of food-related interactions initiated by humans (61.3%) versus macaques (30.4%). The difference is statistically significant, as indicated by the triple asterisk ($p < 0.001$, Chi-squared test). When focusing specifically on food-related interactions, humans were found to be twice as likely as macaques to initiate them (61.3% vs. 30.4%). This highlights the strong role of human behaviour in driving provisioning dynamics across all sites, regardless of group. Despite frequent concerns about macaque aggressiveness, these results underline that many food-based interactions originate with human actions through deliberate feeding.

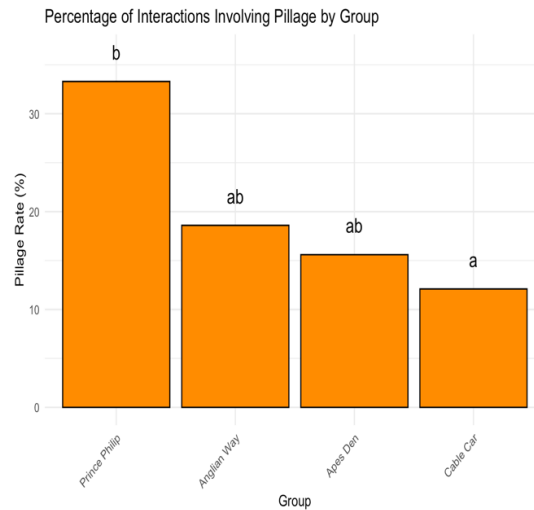


Figure 15. Histogram of proportion of human-macaque interactions involving pillage behaviour by group

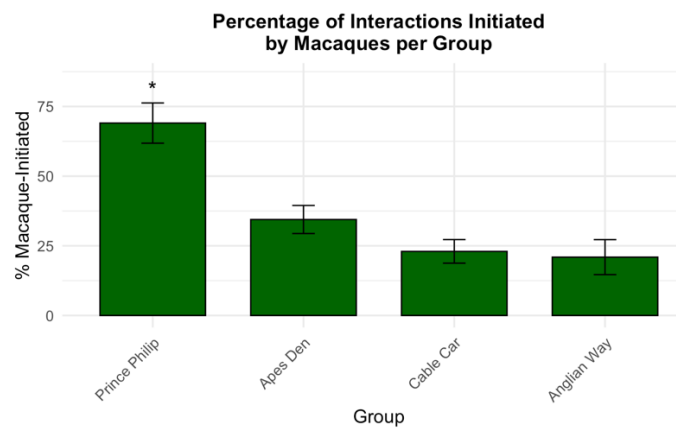


Figure 16. Histogram of the percentage of interactions initiated by macaques across groups

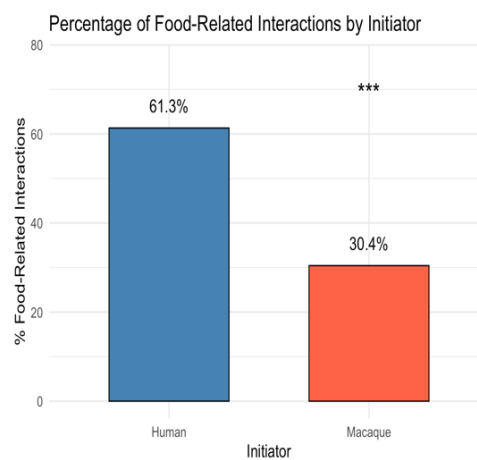


Figure 17. Histogram of the percentage of food-related interactions initiated by humans vs. food-related interactions initiated by Macaques

Experimental data results:

Qualitative observations

We analysed behavioural keywords extracted from the qualitative observation notes. Figure 18 displays the frequency of commonly observed actions during task engagement. The most frequently coded behaviour was "bite" ($n = 37$), followed by "left hand" ($n = 18$), "zipper tab" ($n = 17$), and "soft part" ($n = 11$) which corresponds to the easiest part to rip of the pencil case, suggesting that subjects used both exploratory and targeted manipulation behaviours. The frequent mention of "zipper tab" confirms the relevance of zipper use or that the macaque noticed the zipper tab as a key strategy to open the pencil case.

Additional coded behaviours included attention and stress-related terms (Figure 19). The keyword "MON" (monitoring around, $n = 42$) was the most common, followed by "self-scratch" ($n = 10$) and "stare" (staring at a conspecific to tell him to leave, $n = 6$). The frequent mention of MON shows the awareness of macaques when doing a task while "stare" and "self-scratch" show that some individuals were indeed stressed during the time of the task.

Random Effects Structure

Across all experimental models, a random intercept for individual ID was included to account for repeated measures on the same individuals. However, in nearly all models, variance estimates for the random effect were either extremely small or resulted in singular fits, indicating that between-individual variability was negligible once fixed effects were included. Despite this, the random structure was retained throughout for consistency in model specification and to ensure appropriate estimation of standard errors. This pattern was consistent across interaction, latency, success, and strategy models, suggesting that most of the variability in performance stemmed from fixed factors rather than stable individual traits. As such, individual differences did not meaningfully influence outcomes in the current dataset.

Engagement with the Experimental Task

To assess general motivation, we modelled the probability of interacting with the pencil case using a binomial GLMM. The final model included group origin and conspecific presence as fixed effects, and a random intercept for individual identity ($n = 48$ trials). No fixed effect emerged as significant (all $p > 0.4$), and the model failed to outperform a null model ($\Delta AIC = +0.1$), indicating limited explanatory value. These results suggest that engagement with the task was not systematically influenced by group membership or social context. Instead, interaction with the object appeared sporadic and idiosyncratic, with some individuals approaching the pencil case while others did not, regardless of their background. Exploratory behaviour in this context therefore seemed variable but not clearly driven by demographic or situational factors.

Influence of Social Context and Stress

To understand whether the social environment influenced emotional state, we tested if macaques showed more signs of stress when more group members were nearby. We ran a linear model predicting the number of self-directed behaviours (e.g., scratching, monitoring, yawning) from the standardised number of nearby conspecifics ($n = 48$). The result showed a significant

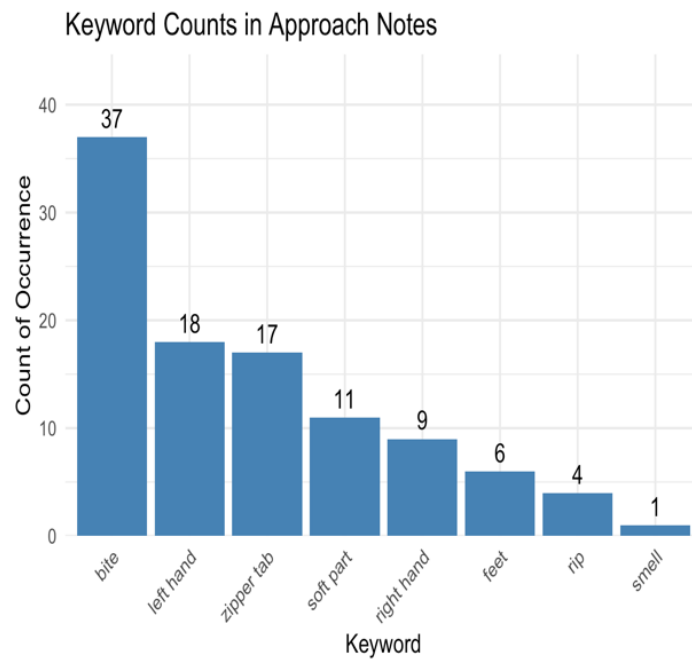


Figure 18. Histogram of keyword counts in approach notes

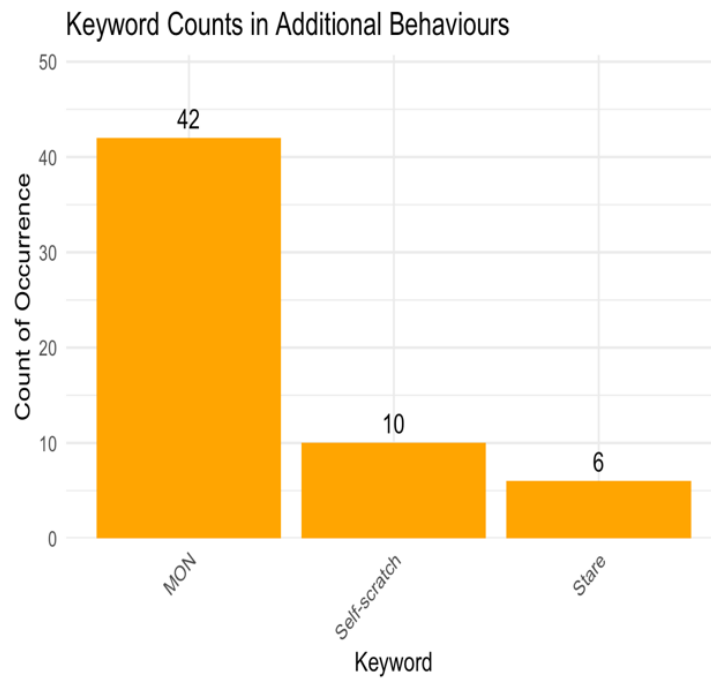


Figure 19. Histogram of Keywords counts in additional behaviours

positive effect ($\beta = 0.28$, $p = 0.037$), suggesting that stress-related behaviours increased in denser social settings, see figure 20. Because stress and conspecific presence were strongly linked and likely reflected similar aspects of arousal or vigilance, we only kept conspecific presence as a predictor in the main task models.

Latency to Solve the Task

We modelled latency to open the pencil case (in seconds) using a linear mixed-effects model among successful trials ($n = 27$). Fixed effects included group origin and standardised stress behaviours, with individual identity as a random intercept. Only stress significantly predicted latency ($\beta = 84.28$, $t = 2.13$, $p < 0.05$), such that more stressed individuals took longer to complete the task. Neither group origin nor conspecific presence were significant ($p > 0.1$). Latency varied descriptively between groups, with Royal Anglian Way showing the slowest average performance (322 seconds) and Prince Philip Arch the fastest (around 70 seconds), but these differences were not statistically robust, see figure 21 for the visualisation of the results. Residual diagnostics confirmed model validity (figure 22). These findings suggest that momentary emotional state as indexed by self-directed behaviours influenced task efficiency more than demographic or social context.

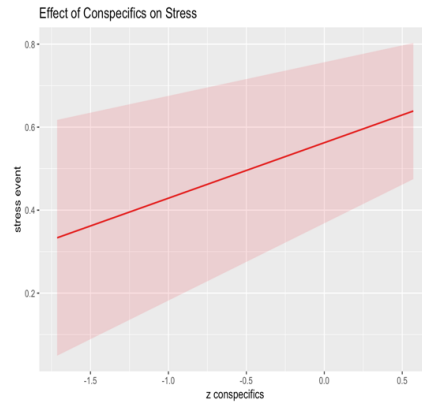


Figure 20. Plot of the effect of conspecific presence on stress-related behaviours, with regression line in red and confidence interval at 95% in red around the prediction

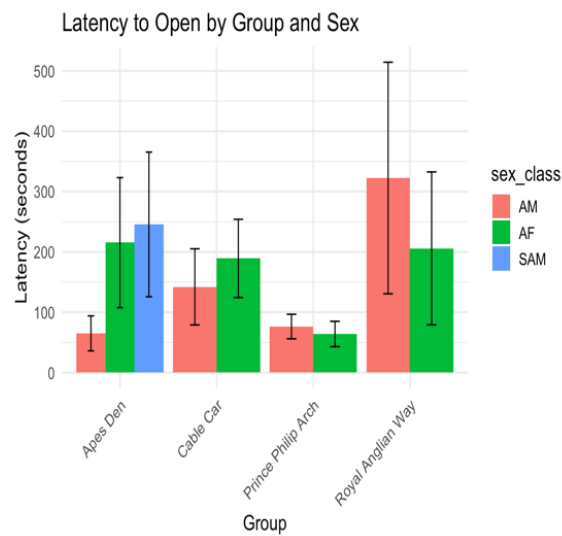


Figure 21. Histogram of the Latency (seconds) to open by group and sex

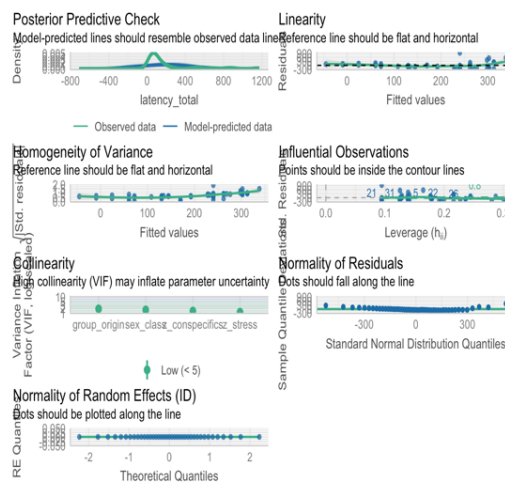


Figure 22. Model diagnostic plots for the latency linear mixed model (LMM), including checks for normality, linearity, collinearity, and influential observations

Task Success and Problem-Solving Performance

We then analysed task success as a binary outcome ($n = 48$), using a binomial GLMM with group origin and conspecific presence as fixed effects. Stress-related behaviours were excluded to prevent collinearity. The model revealed no significant predictors (all $p > 0.6$), and model comparison showed no improvement over the null model ($\Delta AIC = +8.9$, LRT $p = 0.91$). Sex class was retained in this model due to its marginal effect (LRT $p = 0.06$), which slightly improved model fit and was therefore considered informative. Although individuals from Prince Philip Arch and Cable Car appeared more likely to succeed, these patterns lacked statistical support. Predicted success probabilities showed overlapping confidence intervals, and ridge regression confirmed the absence of meaningful predictors ($p > 0.95$). Together, these results indicate that neither demographic nor contextual variables reliably predicted success in retrieving the food reward.

Use of the Zipper Tab as a Problem-Solving Strategy

Among individuals who succeeded in retrieving the food, we examined whether they used the intended strategy opening the zipper tab versus tearing the case. The model ($n = 27$) included group origin and conspecific presence as fixed effects, and individual identity as a random intercept. No effects were significant (all $p > 0.8$), and model comparison did not favour the full model ($\Delta AIC = +2.5$, LRT $p = 0.97$). Descriptively (figure 22), zipper use was most common at Prince Philip Arch and Cable Car, rare at Apes Den, and absent at Royal Anglian Way. Despite these trends, statistical analyses did not confirm group-level differences in strategy. Overall, variation in tool-use style may reflect situational or individual differences rather than systematic group effects.

IV. Discussion

This study examined how wild Barbary macaques navigate human presence across four sites that differ in structure, predictability, and intensity of anthropogenic exposure. The observational data provide insight into how local context shapes interaction patterns, especially in relation to food provisioning, social behaviour, and macaque-initiated contact. These findings reveal distinct ecological and social configurations, underlining the need to account for spatial variation when assessing behavioural adaptations in human-impacted environments.

Across the dataset, interaction rates were not evenly distributed between groups. While Cable Car showed the highest hourly rate of interactions, followed by Apes Den, Anglian Way, and Prince Philip's Arch, these differences were not statistically significant. This outcome suggests that raw frequency alone may not capture the subtle ways in which context structures interaction. When we move beyond overall rates to consider the nature and quality of these exchanges, more revealing patterns emerge. At Cable Car, the intensity of provisioning activity was particularly striking. Most food-related interactions there were driven by deliberate human actions, often facilitated by taxi drivers who prompted macaques to approach for photographs. This reflects findings by Maréchal et al. (2016), who noted that tourist behaviour is a major determinant of primate response, often outweighing demographic or ecological predictors. The prevalence of keywords such as “gave”, “bag”, and “car” at Cable Car supports the idea that these interactions are scripted, shaped by expectations and repeated scenarios where macaques learn to anticipate food access through human actions.

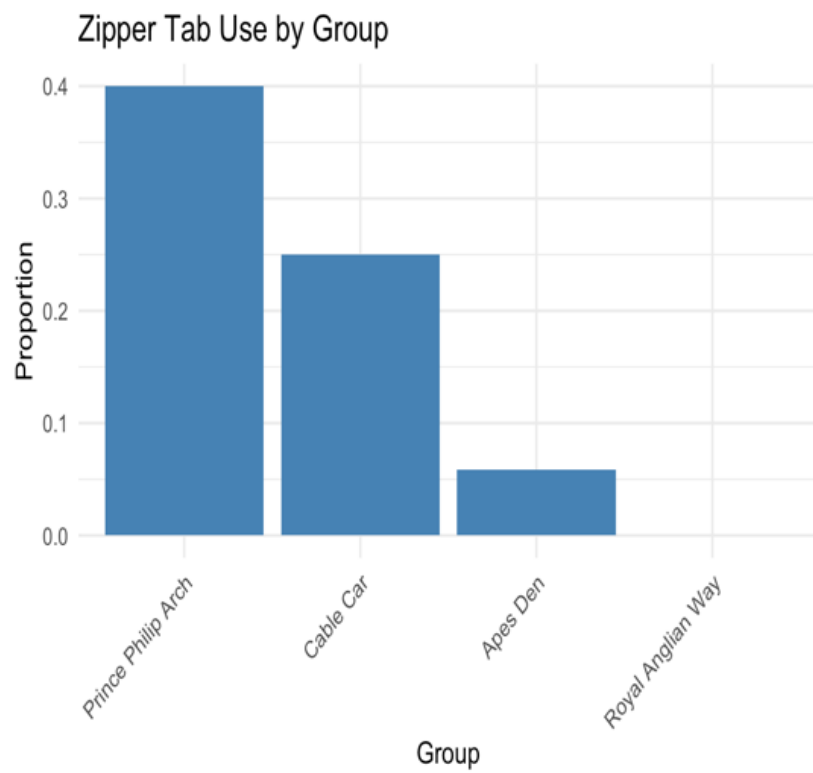


Figure 23. Histogram of the proportion of successful individuals using the zipper tab to open the pencil case, by group origin

By contrast, Apes Den revealed a paradoxical profile. Although the group experienced high tourist volumes and recorded long interaction durations, the proportion of food-related contact was the lowest across all groups. Tourists at this site tend to move quickly through the space without stopping for long periods or initiating feeding. Without structured provisioning, macaques seem less prone to engage actively, resulting in fewer transactional encounters but more observational or passive interactions. The implication is that site usage patterns, whether a space is a destination or a transit zone, have more influence on behaviour than visitor numbers alone. This nuance echoes broader findings in human-wildlife conflict research, where the shape of human activity, not just its intensity, often predicts behavioural change (Hill, 2002; Sha et al., 2009). In Royal Anglian Way, the dynamics were again distinct. Located near a restaurant, the site offered access to desirable food items such as ice cream, yet recorded only moderate levels of provisioning and pillaging. One likely explanation is the structured flow of tourists and the presence of staff maintaining vigilance. These constraints may reduce opportunities for macaques to exploit human food sources despite their availability. While provisioning occurred, it was less chaotic than at Cable Car and less opportunistic than at Prince Philip's Arch, suggesting that regulation can modulate the interaction tone. This reinforces the role of social context in mediating primate behaviour. It is not merely the availability of resources that matters, but how predictable, accessible, and socially permissible those resources are. Prince Philip's Arch represented the most opportunistic and conflict-prone setting. Despite lower overall tourist numbers, this site recorded the highest rates of pillaging and the highest percentage of macaque-initiated interactions. Here, the presence of taxi drivers who temporarily stop their vehicles to feed macaques from car windows contributes to a dynamic in which animals are reinforced for taking initiative. The lack of fixed stopping points, coupled with irregular tourist flow, creates an environment in which predictability is low but potential rewards are high. This matches patterns observed in other species, where unpredictability in resource distribution fosters proactive, exploratory, or risk-prone foraging strategies, traits often associated with neophilic tendencies. Behaviourally, macaques at Prince Philip's Arch may be responding to a cost-benefit structure that encourages boldness in the absence of routine provisioning.

Qualitative data, such as object types and interaction keywords, further highlighted these group-level differences. Cable Car had the most diverse and frequent object exchanges, including not just peanuts but a range of items such as biscuits, bananas, and even condiments. This diversity points to habitual provisioning and may reflect a form of cultural learning, where repeated exposure to specific human artefacts creates recognisable behavioural scripts. In comparison, Apes Den and Anglian Way had more modest item diversity, while Prince Philip's Arch showed an eclectic mix, blueberries, chocolate biscuits, and even flowers, supporting the idea that pillaging here is irregular and involve all kind of objects.

The statistical models reinforced these descriptive patterns. A negative binomial GLMM identified visitor density as the main predictor of interaction frequency, with macaque number showing no effect. This aligns with the idea that human behaviour, not ecological presence, drives contact dynamics. Model diagnostics confirmed the robustness of this effect, and predictions closely matched observed data. However, when it came to interaction duration, the

number of conspecifics, rather than people, emerged as a significant predictor. Longer interactions occurred when more macaques were present, possibly reflecting increased social facilitation or intraspecific competition. This shift in influence, from humans to conspecifics, depending on the behavioural metric examined, illustrates the multi-layered nature of social interactions in anthropogenic landscapes. Initiation dynamics offered additional insight. At

Prince Philip's Arch, nearly 70% of interactions were initiated by macaques, compared to below 40% in other groups. This high initiation rate is consistent with a context in which macaques must initiate more the interactions to secure resources. In contrast, at Cable Car, most interactions were human-initiated, highlighting the bidirectional nature of provisioning: in some sites, humans set the pace and invite contact, while in others, macaques must assertively seek it. A comparison of food-related initiations confirmed this pattern: humans were over twice as likely as macaques to initiate food-based interactions across all sites. This undermines simplistic narratives of "macaque aggressiveness" and points instead to human provisioning as a central driver of conflict-prone interactions. The spatial variation observed here reveals how fine-grained features of anthropogenic landscapes, from infrastructure to informal human routines, shape macaque behaviour. Locations like Cable Car, where feeding is encouraged, create expectations and routine; others, like Apes Den, support more passive observation. Prince Philip' Arch group location, with its transition between the restaurant where Royal Anglian Way group is and where Cable Car is and sporadic flux of people by foot and taxis, promotes bold, sometimes risky behaviour. These dynamics mirror findings by Hill (2002) and Maréchal et al. (2016), who noted that provisioning systems, more than primate traits alone, shape the trajectory of human-primate interaction.

Collectively, these results show that human-macaque interaction patterns are site-specific and shaped by the form and rhythm of human presence as much as its quantity. Provisioning behaviour, duration of stay, and structural features like photo stops or vehicle access routes all contribute to the behavioural ecology of these groups. Recognising this complexity is essential for both theoretical understanding and practical management. Efforts to mitigate conflict or support macaque welfare must therefore be grounded in a detailed understanding of local dynamics, not just general species-wide tendencies.

Having examined how ecological settings and human presence shaped macaque behaviour across the four sites, we now shift focus to the experimental component of the study. In this controlled setup, individual macaques were presented with a novel problem-solving task, offering a standardised lens through which to assess cognitive performance, emotional regulation, and strategy use. This phase provides an opportunity to evaluate whether the group-level differences observed in real-world human-macaque interactions translate into individual behavioural responses under controlled conditions. Interestingly, however, the patterns of exposure documented during the observational phase did not consistently predict performance in the experimental task. Macaques from high-exposure sites such as Cable Car and Prince Philip's Arch did not show markedly higher success rates than those from less exposed groups like Apes Den or Royal Anglian Way. This suggests that frequent exposure to humans, while shaping interaction dynamics in the field, may not directly enhance problem-solving abilities or emotional resilience in novel situations. While there were modest trends suggesting higher engagement and more use of complex strategies, such as manipulating the zipper tab, in Cable Car individuals, these differences did not reach statistical significance. This lack of a robust group effect could be due to several factors, including high intra-group variability, unbalanced sample sizes, or the influence of unmeasured traits like previous experience or neophobia.

Crucially, sex class also failed to emerge as a significant predictor of performance. Adult males, adult females, and subadult males all exhibited similar levels of engagement and task success. This is consistent with prior research showing limited sex-based cognitive differences in macaques (Fa, 1992; Maestripieri et al., 1992). In wild settings, where survival pressures and learning opportunities are similar for both sexes, sex may not represent a meaningful axis of cognitive differentiation, at least in the domain of extractive foraging tasks. One factor that did

show a consistent and robust association with performance was internal affective state. Self-directed behaviour such as scratching, long recognised as behavioural markers of stress and arousal in primates (Maestriperi et al., 1992; Troisi, 2002), was significantly associated with longer latencies to success. Individuals displaying more of this behaviour took longer to complete the task, suggesting that stress may impair not only the likelihood of engaging with a novel object, but also the cognitive efficiency required to solve it. This aligns closely with the classic Yerkes & Dodson law (Yerkes & Dodson, 1908), which describes a curvilinear relationship between arousal and performance, as well as more recent findings in macaques indicating that stress can impair executive functions (Kaburu et al., 2019).

Social context also played an important but complex, role. While the number of nearby conspecifics did not directly predict success or engagement, it was positively associated with stress-related behaviours, like staring at conspecifics to keep them away, monitoring around while doing the task or as said before, self-scratching. This suggests that individuals in socially dense settings may experience elevated emotional arousal or stress, possibly due to the need for social vigilance, rank-related concerns, or fear of interference. In highly social species like macaques, such concerns may lead to heightened tension that competes with cognitive resources during task performance. At the same time, social presence could also facilitate engagement through mechanisms like social facilitation or observational learning. This duality, where social context can both encourage and inhibit task focus, may help explain the absence of a clear directional effect on performance. It underscores the need for future studies to incorporate measures of relationship quality, proximity to specific group members, or dominance rank, which could moderate these effects.

The distinction between engagement and success is also critical. While 43 out of 48 individuals interacted with the pencil case, far fewer successfully retrieved the food reward, 27 out of 48. This disparity illustrates a key methodological challenge in studying wild cognition; differentiating between mere interest in a novel object and actual problem-solving capacity. It also emphasises the importance of selecting tasks that are not only ethologically relevant but also appropriately calibrated for the physical and cognitive capabilities of the target species. In this case, the zipped pencil case required specific motor skills, such as bimanual coordination or fine manipulation, that some individuals may not have possessed. Older individuals with missing teeth or reduced dexterity may have faced added constraints, not due to lack of insight but due to physical limitations. This highlights a recurring issue in field-based cognition research: separating cognitive capacity from motivational, physical, and affective influences.

Although binary success measures did not correlate significantly with group identity, sex, or conspecific presence, more continuous indicators proved more informative. Latency to success, a finer-grained behavioural outcome, captured subtle variation that was otherwise missed. Individuals who showed higher levels of stress-related behaviours took longer to retrieve the food reward, providing further evidence that emotional state directly modulates problem-solving efficiency. This reinforces one of the central insights of the study: that internal state, and not just external context, shapes cognitive outcomes. These results are consistent with work showing that even minor fluctuations in emotional state can impair working memory and task persistence in non-human primates (Maréchal et al., 2011; Kaburu et al., 2019). Manipulative strategies also showed interesting variation. While relatively few individuals used the zipper tab, a cognitively demanding method, it was most commonly observed among members of the Cable Car group. These individuals are regularly exposed to tourist artefacts such as backpacks, cameras, or zippers, and may have generalised prior experience to the experimental task. Although this behaviour was too infrequent to model statistically, its occurrence highlights the

potential for environmental exposure to shape exploratory behaviour or even functional learning. This is in line with previous work suggesting that urban-dwelling macaques may develop locally adapted behaviours when confronted with novel affordances or anthropogenic challenges (Hockings et al., 2015; Sueur et al., 2011).

Alternatively, individuals who used the zipper may have simply been more neophilic (tendency to be attracted to or interested in novel stimuli, experiences, or environments) or dominant, traits that often co-vary with problem-solving in social mammals (Reader & Laland, 2002). Unfortunately, the limited number of trials and the absence of repeated measures prevent a reliable separation between learned strategy, temperament, and opportunism. Collecting repeated measures across different contexts, including object manipulation tasks with varying complexity, would help identify whether such strategic variation reflects stable traits or context-specific choices.

Interestingly, the overall rarity of task success does not necessarily imply cognitive limitations. Instead, it may point to a mismatch between the task and the motivational ecology of wild macaques. Unlike captive settings, where animals have few alternative food sources and may be more incentivised to engage with enrichment items, wild individuals in Gibraltar face abundant provisioning from macaque management and visitors of the reserve or pillaging opportunities. As a result, a novel zipped object, even if food-rewarding, may simply not warrant sustained effort. Some individuals may have perceived the task as too risky, difficult, or irrelevant compared to other strategies like eating from the feeding platforms, monitoring tourists or foraging from the reserve.

This possibility is supported by field observations and earlier research showing that wild macaques are highly sensitive to foraging cost–benefit ratios (Fuentes et al., 2007). In Gibraltar, food provisioning and human artefacts are common, which may reduce both neophilia and persistence when encountering unfamiliar objects. The case used in the task, although standardised across trials, may have lacked the affordances or cues typically associated with edible items in the monkeys’ experience. Despite these challenges, the task yielded valuable behavioural variation, particularly in latency and engagement. These dimensions may offer more reliable windows into wild cognition than binary success, which is often overinterpreted or mismatched with real-world behaviour. For instance, latency captures motivation, planning, and persistence, while engagement reflects curiosity or exploratory drive. Both measures revealed meaningful associations with emotional state, supporting the view that cognitive performance is a dynamic outcome influenced by multiple internal and external pressures.

The implications of these findings go beyond the scope of individual cognition and touch on broader themes in behavioural ecology and conservation. In particular, this study highlights the need to interpret problem-solving behaviour not as a static trait or skill, but as a context-dependent phenomenon, modulated by ecological exposure, emotional arousal, and social pressures. This aligns with recent calls in cognitive ecology to move beyond traditional frameworks that treat cognition as a fixed ability and instead view it as emerging from interactions between the organism and its environment (Sih & Del Giudice, 2012). From a management perspective, this insight has direct consequences. In settings like Gibraltar, where macaques frequently encounter tourists, vehicles, and urban structures, their behavioural responses are often interpreted as signs of intelligence or deviance. Groups that interact frequently with humans may be seen as more “clever” or “problematic”, but this may simply reflect differential habituation, reduced fear responses, or learned opportunism. Conversely, groups that avoid human artefacts or fail to engage with experimental tasks may be incorrectly

perceived as less capable, when in fact they may be more cautious, neophobic, or socially inhibited (Maréchal et al., 2016).

Recognising this variation is crucial to avoid anthropocentric biases and to design more ethical and effective wildlife management strategies. Misinterpreting exploratory or avoidance behaviours as fixed traits could lead to misguided decisions, such as targeting specific individuals for relocation or reinforcing stereotypes about certain groups being more prone to “conflict”. Instead, integrating emotional, social, and ecological variables into assessments of animal behaviour allows for more nuanced interpretations and interventions.

Methodologically, the study also points to areas of improvement for future research. While the combination of observational and experimental data proved valuable, it also revealed the limitations of one-off cognitive tests in wild contexts. Cognitive traits are dynamic and sensitive to multiple situational factors; thus, repeated measures over time are essential to differentiate stable traits from ephemeral states. Longitudinal tracking could identify whether individuals improve with experience or whether their problem-solving abilities change with age, rank, or exposure to anthropogenic cues (Johnson-Ulrich et al., 2020).

Moreover, incorporating physiological measures, such as cortisol levels, would greatly enhance our understanding of the relationship between stress and cognition. Behavioural proxies like self-directed behaviours are useful but indirect; validating them with hormonal data would strengthen claims about affective state and performance. While such data are more difficult to obtain in wild populations, especially in a setting like Gibraltar, they represent a valuable frontier for future field-based cognitive research.

V. Conclusion

This study advances our understanding of how wild Barbary macaques navigate cognitive challenges in a context of varying anthropogenic pressures. By combining field behavioural observation with a standardised problem-solving task, we showed that individual responses emerge from the interplay between ecological exposure, internal affective states, and social dynamics. While demographic variables such as group origin and sex offered limited explanatory power; emotional regulation, particularly stress, as inferred from stress-related behaviours, proved a consistent modulator of task engagement and efficiency. Contextual factors like tourist density, provisioning practices, and artefact familiarity also shaped the likelihood and quality of object interaction, reinforcing that cognition in the wild cannot be disentangled from environment and experience. Importantly, frequent exposure to human activity did not automatically translate into superior performance in the task, suggesting that learning opportunities, motivation, and emotional state jointly constrain problem-solving outcomes. These findings highlight the behavioural plasticity of Barbary macaques in human-modified environments, as well as the role of emotional state and social context in shaping their responses. Rather than displaying uniform strategies, individuals and groups differ in how they approach human artefacts and manage cognitive challenges. This study contributes to our understanding of primate adaptability in anthropogenic landscapes and underscores the need to account for emotional and ecological variables in conservation and wildlife management strategies.

Contribution

Eliott Mestrallet and Dr Sylvain Lemoine conceived this internship project; Eliott Mestrallet collected the data and conducted the statistical analyses; Dr Sylvain Lemoine supervised and contributed to the statistical analyses; Eliott Mestrallet wrote this master thesis, Dr Sylvain Lemoine supervised it.

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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VII. R Packages (Software) Used and packages

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Used package: cowplot

Title: Behavioural Adaptations and Tourist-Macaque Interactions: A Comparative Study of Social Learning in Gibraltar's Barbary Macaques

Keywords: primatology, wildlife tourism, tourist-macaque interactions, adaptation

Abstract: In Gibraltar's Upper Rock Nature Reserve, Barbary macaques (*Macaca sylvanus*) are daily exposed to high levels of human presence, particularly through tourism. This study investigates how macaques from four social groups navigate such anthropogenic pressure, combining systematic observational data with a controlled problem-solving task. Behavioural observations were collected using a structured location sampling protocol, revealing group-level differences in interaction rates, food-related behaviours, and pillaging tendencies. Groups situated near high-density tourist areas showed more frequent and prolonged interactions, especially when food was involved.

An experimental task using a transparent pencil case filled with peanuts allowed for individual-level assessment of cognitive engagement. Results showed considerable variability in task interaction and success, which could not be explained by group origin or sex. Instead, behavioural indicators of stress, emerged as reliable predictors of problem-solving efficiency, with higher stress associated with longer latencies to success.

These findings highlight the behavioural plasticity of Barbary macaques in human-modified environments, as well as the role of emotional state and social context in shaping their responses. Rather than displaying uniform strategies, individuals and groups differ in how they approach human artefacts and manage cognitive challenges. This study contributes to our understanding of primate adaptability in anthropogenic landscapes and underscores the need to account for emotional and ecological variables in conservation and wildlife management strategies.