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Human presence exerts sex-biased effects on the activity budgets of temple rhesus macaques in the Pashupatinath Area, Nepal

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Abstract Understanding how nonhuman primates adjust their behavior in human-dominated environments is essential for effective urban wildlife management. This study examined the daily activity budgets of urban rhesus macaques in the Pashupatinath Temple area of Kathmandu, Nepal, comparing groups exposed to high (HAP) and low anthropogenic pressure (LAP). Behavioral data were collected using focal animal sampling and scan sampling methods. Resting/sitting and allogrooming were the most frequently observed activities of the macaques in both study blocks. However, feeding/foraging differed significantly between the blocks, occurring more frequently in HAP than in LAP. Sex-based differences in behavior were noted between the groups for resting, grooming, movement, and aggression, but not for feeding. Notably, the increased presence of visitors was negatively associated with grooming behavior, particularly among females (Mann–Whitney U = 12464, $p < 0.05$). An increased number of visitors around the focal subjects in HAP was associated with a decrease in grooming behavior ($\rho = -0.2$, $p < 0.01$), which may reflect the combined influence of food provisioning and visitor disturbance (e.g. teasing, threatening behavior) observed at the site. Reduced grooming in areas with high human activity can weaken social bonds, heighten stress, and undermine group cohesion, reducing macaques' social stability and resilience. These findings highlighted nonhuman primate behavior in human-dominated environment, emphasizing the need for effective urban management strategies.

Keywords: focal animal sampling, grooming, human–primate interaction, urban macaques

1. Introduction

Urbanization and human disturbance have visibly altered the natural habitats of flora and fauna (Lowry et al., 2013; Thatcher et al., 2019; Maharjan et al., 2025). This anthropogenic impact on the environment poses numerous challenges for wildlife, including the loss of habitat and food availability. In response to these survival challenges, certain species have undergone behavioral adjustments to their surroundings, resulting in modified behavioral time budgets (Lowry et al., 2013; Kaburu et al., 2019; Thatcher et al., 2019). This behavioral flexibility is closely linked to advanced cognitive abilities, a trait particularly prominent in primates (Dunbar & Shultz, 2007). Over the past two decades, several studies have explored the adaptability of primates to human-altered environments and the related human–primate interactions (McLennan et al., 2017; Sengupta et al., 2025). For example, bonnet macaques (*Macaca radiata*) in human areas prefer foraging on human food and show social changes such as single-male groups (Sinha et al., 2005; Balasubramaniam et al., 2020). Barbary macaques (*M. sylvanus*) modify their behavior to find food and avoid predators like shepherd dogs (Waterman et al., 2019). Rhesus macaques (*M. mulatta*) are highly adaptable, thriving in urban parks and temples across South Asia (Ogawa et al., 2024). Studying these adaptations helps us understand their responses to human presence.

Affiliative behaviors, such as social grooming, play a crucial roles in the health and fitness of primates including elimination of ectoparasites, improved thermoregulation (Akinyi et al., 2013; Solanki et al., 2020), strengthening social bonds, augmenting mating prospects, offering support during conflicts, reinforcing overall group dynamics (Lehmann et al., 2007; Balasubramaniam et al., 2018) and mitigating stress (Jaman & Huffman, 2013). Social grooming, involving visual inspection, exploration, and manipulation of a partner's skin or hair using one's hands which stands out as the most prevalent form of social affiliation among primates, accounts for up to 20% of primates' daily time allocation (Jaman & Huffman, 2013; Kaburu

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et al., 2019; Solanki et al., 2020). Variations in grooming behavior among primates are influenced by factors such as an animal's social rank, proximity to others, level of disturbance, and climatic conditions such as temperature and humidity (Kaburu et al., 2019; Marty et al., 2019; Li et al., 2020; Caselli et al., 2021).

The balance between resting and foraging in primates is influenced by factors such as body mass discrepancies between adults and immature individuals (Jaman & Huffman, 2013). Distinct responses are observed among different age–sex classes, particularly concerning the exploitation of novel or limited food resources (Jaman & Huffman, 2013). Moreover, primate behavior and ecology exhibit adaptive variability in the context of food augmentation and are contingent on their utilization of anthropogenic food sources (Sha & Hanya 2013). Primate activity budgets are also subject to fluctuations based on seasonal variations, including temperature changes, rainfall patterns, fruiting seasons, and plant growth dynamics, relative to specific habitat types (Zhou et al., 2022). Additionally, the close proximity between humans and primates raises significant concerns, including the risks of pathogen transmission and potential retaliatory killing (Riley & Wade, 2016; Schurer et al., 2019). This dynamic can also lead to group instability and potentially impact the socialization of primates (Kaburu et al., 2019).

Human-altered landscapes create new pressures on primate behavior by increasing interactions and conflicts due to habitat loss (Air, 2015; Beisner et al., 2015; Kyes et al., 2018). Despite this, humans and nonhuman primates often share spaces, leading to varying degrees of interaction, from neutral to aggressive (Radhakrishna & Sinha, 2011; Sengupta et al., 2015). Human food provisioning can also cause physiological changes, increase stress, and lead to increased aggression within and between primate groups (Sugiyama, 2015; Yang et al., 2016). While research on primates' behavioral adaptations is growing, the effects of human presence on social behaviors such as grooming are less studied (Balasubramaniam et al., 2020). This study assessed the activity budgets and social behavior of temple rhesus macaques under different levels of anthropogenic pressure. Explicit comparison of high vs low visitor areas within one temple complex; integration of visitor counts with sex-specific activity budgets, serving as an extension of previous research. Furthermore, the study hypothesized that grooming decreases with visitor density, especially among females; feeding/foraging increases with increasing anthropogenic pressure (indexed by visitor density and food provisioning); and males show greater aggression and movement than females. The results provide insights into the different ways in which primates adapt to potential disturbances, which can inform their management and conservation efforts.

2. Materials and Methods

2.1. Study area: Pashupatinath Temple area

This study was conducted at Pashupatinath Temple (precisely located between 27°42'33" and 27°42'34" in northern latitude 85°20'43" to 85°21'02" in eastern longitude with elevations ranging from 1312–1344 m), which is one of the oldest Hindu temples in the Kathmandu Valley and a UNESCO World Heritage Site (since 1979). In the Kathmandu Valley, the average monsoon season (June–September) contributes the most rainfall, accounting for 78.79% (1333.25 mm) of the annual total, whereas the winter season (December–February) contributes 3.06% (51.84 mm), representing the total rainfall. The premonsoon period (March–May) contributes 13.53% (229.0 mm), and the postmonsoon period (October–November) contributes 4.62% (78.11 mm) (Bhattrai et al., 2025). The average annual mean temperature was 19.68°C as of 2017 (Thapa et al., 2021). The Pashupatinath area lies at the bank of the sacred Bagmati River and includes 518 temples and monuments (Wijesuriya & Forbes, 2021), forest patches and residential areas. In addition to several resident groups of rhesus macaques, the area supports spotted deer (*Axis axis*), barking deer (*Muntiacus vaginalis*), stray dogs (*Canis lupus familiaris*), cattle, and a variety of birds. Among all these species, the rhesus macaques are the major tourist attraction of this site. They are dispersed throughout the temple area and are sometimes considered to be nuisances to visitors.

2.2. Ethical considerations and permits

All research procedures involving rhesus macaques were conducted in accordance with established ethical guidelines for the study of nonhuman primates and complied with local and institutional regulations. Prior to data collection, necessary research permits were obtained from the Department of Forest and Soil Conservation, the Government of Nepal (Permission No- 262/080/081) and the Pashupati Area Development Trust. The observations were strictly noninvasive and involved only behavioral monitoring without any physical contact, capture, or manipulation of the animals. Researchers maintain a safe and respectful distance to minimize disturbance and avoid provisioning or interfering with macaques' natural activities. The study adhered to the ethical principles outlined by the International Primatological Society (IPS) Code of Best Practices for Field Primatology, ensuring the welfare of the animals and the integrity of the research.

2.3. Study blocks

Three primary groups of rhesus macaques are widely distributed across the temple area (Ogawa et al., 2024). The forest area consists of three main types of forest: *Schima-Pyrus*, Moist (*Myrsine-Persea*), and Mixed (*Quercus-Myrsine*) (Shrestha & Devkota, 2013). During preliminary field visits from 1–15 January 2021, the number of macaque groups and their home ranges were identified. The study site was then divided into two study blocks on the basis of the intensity of anthropogenic pressure

(i.e., visitor–macaque interaction/hour): 1) low anthropogenic pressure (LAP) and 2) high anthropogenic pressure (HAP) (see Table 1 for defining features of the study blocks), and Figure 1 for locations). The two blocks were separated by a segment of the Bagmati River passing through the middle of the study area. There was a bridge that connects both study blocks. Two groups of macaques, one from each block, were selected for behavioral sampling. The LAP group (G1) was found around the office of the Pashupati Area Development Trust and the main Pashupatinath Temple area, an area characterized by low anthropogenic pressure. The HAP group (G2) included the areas of the Mrigasthali, Biswaroop Forest and Guheswori Temple where interactions with visitors were frequent. Throughout our field observation period, the two study groups were found to have ranged within their respective blocks.

Table 1 Study blocks, level of disturbance, and study groups.

Block code	Disturbance intensity	Study group ID	Level of anthropogenic pressure	Number of visitor-macaque interactions/hour
LAP	Low anthropogenic pressure	G1, 45 individuals	The block experienced lower anthropogenic pressure and the likelihood of interactions between visitors and macaques was less. The presence of physical barriers (i.e., walls and fences) within the enclosed park prevented visitor access while also offering hiding spots for the monkeys.	33.27
HAP	High anthropogenic pressure	G2, 57 individuals	The block experienced high anthropogenic pressure during periods of high visitor influx, leading to frequent and direct interactions between visitors and macaques.	48.31

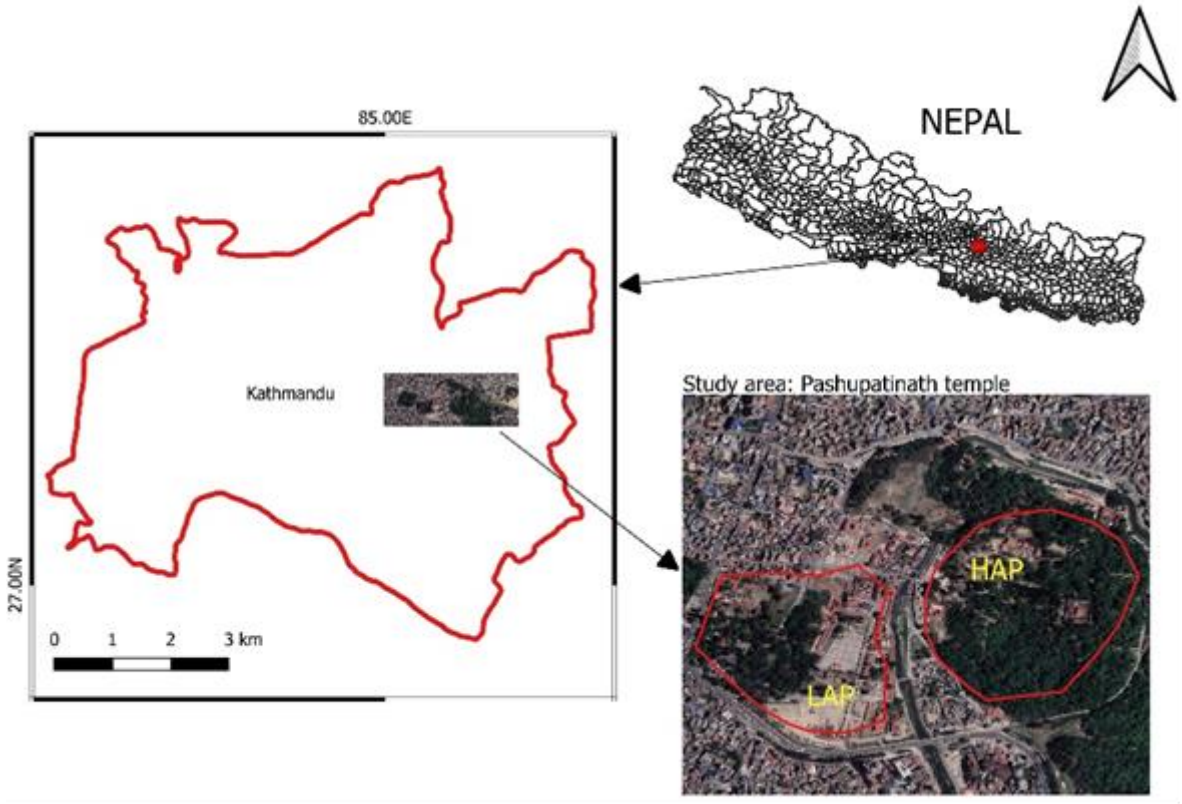

Figure 1 Map of the study area showing the two study blocks (LAP and HAP) where the behavioral observations were conducted.

2.4. Selection of focal animals

Group-G1 from the LAP block was composed of 45 individuals including 10 adult males, 16 adult females and 19 juveniles and infants with a sex ratio = 1:1.6. Six individuals (three adult males and three adult females) were selected and identified based on their natural marks, scars and facial features for behavioral sampling. Group G2, from the HAP block, was composed of 57 individuals, including 15 adult males, 22 adult females and 20 juveniles and infants, with a sex ratio = 1:1.47. Six individuals (three males and three females) were also selected from this group for behavioral sampling. In the event that a selected focal individual disappeared and was not detected for three consecutive days, another individual of the same sex and age was selected to replace the missing individual, and the observed individuals were replaced with individuals following the

same behavior protocol. Throughout the sampling period, focal individuals were selected randomly via a lucky-drawing method with name cards. Macaques were categorized into age classes on the basis of body size, observable sexual characteristics, and estimated age.

2.5. Behavioral data collection

Behavioral observations were conducted four days per week from 17 January to 16 September 2021. Observations were conducted in two shifts: morning (7:00 AM–12:00 PM) and afternoon (12:00 PM–5:00 PM) for both groups. A total of 170 hours (85 hours from LAP and 85 hours from HAP) of data were collected throughout the study period. Behavioral observations were conducted via the focal animal sampling method (20 minutes per focal) in combination with scan sampling at two-minute intervals (Altmann, 1974). During each scan, behavioral states and the number of visitors with visitor–monkey interactions (feeding/teasing/touching) within a 10 m radius of the focal individual were recorded, and the hourly rates of visitor–monkey interactions were subsequently calculated. The behaviors recorded are summarized in the ethogram in Table 2. Instances where the focal animal moved out of sight resulted in a temporary pause in data collection until the animal became visible again (Balasubramaniam et al., 2020). If the animal did not become visible again that day, the individual's data for that session were discarded from analysis. Under conditions of HAP, 146 behavioral bouts were recorded for females, and 154 were recorded for males. Similarly, for the LAP condition, 149 bouts were recorded for females, and 152 bouts were recorded for males.

Table 2 Ethograms of behaviors recorded during the observational period.

Behavior	Description
Moving	Traveling some distance by the macaque in response to any factors such as dogs, humans, and other members or group of macaques
Feeding/foraging	Animals either consuming or searching for natural food or anthropogenic food whether by sitting or moving also include begging and waiting for tourists to get provision food.
Allogrooming/Social grooming	It is the act of cleaning or manipulating the hair, by another member or to the other member of the observation group.
Sitting/resting	Laying down, looking around and sitting without any actions, sleeping, sleeping in sitting position.
Aggression	Fighting with same group or different group either male or female: with at least one of the following: facial expressions (Open mouth bared-teeth threat, lip smack, eyebrow lifting), bite, fight, scream, chase, vocal threat

Source: The major behavioral categories were taken from Dancer and Burn (2019) and amended on the basis of direct observations in the field.

2.6. Data analysis

The behavioral data collected from the two groups (G1 from the LAP and G2 from the HAP) were organized for an initial examination to assess assumptions related to a normal distribution and equal variance. Normality was assessed via the Shapiro test (Royston, 1982), whereas the equality of variances was analyzed via Bartlett's test (Bartlett, 1937). Since the data did not meet the criteria for a normal distribution, nonparametric Mann–Whitney tests (Bauer, 1972) were used.

We used generalized linear mixed-effects model (GLMM) to test for differences in time allocation among the five behavioral categories (e.g., aggression vs movement vs feeding/foraging vs resting/sitting vs allogrooming), pooling data across both study blocks. The time spent per bout in each behavior category was considered a response variable, whereas behavior categories were considered fixed effects and individual IDs were included as random effect. Additionally, post-hoc pairwise comparisons using Tukey adjustment revealed significant differences in duration among behavioral categories. Assumptions were checked using residual vs fitted plot. Residual plots showed no evidence of model misfit. GLMM was performed using "*lme4*" package and post-hoc pairwise comparisons were conducted using "*emmeans*" package (Bates et al., 2015, Length, 2025) in R (R Core Team, 2025).

Mann–Whitney tests were performed to identify potentially significant differences in behaviors exhibited by the macaques between the study blocks and by sex. Specifically, the grooming behavior exhibited by male and female macaques in both study blocks was analyzed separately. This analysis aimed to identify whether significant differences existed between females and males within and between the HAP and LAP study groups in terms of grooming behavior. Since the analyses involved nonparametric tests, the results are presented as the median ± median absolute deviation (MAD). Spearman rank correlation coefficient tests were performed to determine the degree of association between grooming and feeding/foraging behavior and the number of visitors within the 10 m radius of the focal subject (ρ and p values are reported). All the analyses were performed via R 4.5.0 (R Core Team, 2025). To create plots "*ggplot2*" package was used (Wickham, 2016). Data summarization and descriptive statistics (median ± MAD) were performed via the "*dplyr*" package (Wickham et al., 2025).

3. Results

3.1. Diurnal activity budget of rhesus macaques in the Pashupatinath Temple area

The overall combined activity budget of the temple rhesus macaques (both G1 and G2) revealed that resting/sitting accounted for the majority of their behavioral repertoire (40.98%). Grooming was next, making up 24.81% of their time budget, followed by moving (17.47%), feeding (15.87%) and engaging in aggression (0.87%) (Table S1 and Table S2 in supplementary material). The results of a generalized linear mixed effect model indicated a significant difference in the overall combined behaviors exhibited by the macaques between the two study blocks ($p < 0.001$) (Figure 2). Aggression as the reference category (mean duration = 1.36 ± 0.58 SE), all other behaviors exhibited significantly longer durations. Feeding/foraging lasted on average 3.73 units longer than aggression ($p < 0.001$), grooming 5.40 units longer ($p < 0.001$), moving 2.82 units longer ($p < 0.001$), and resting/sitting 7.43 units longer ($p < 0.001$). Resting/sitting showed the greatest duration among all behavioral categories. Subsequent via post-hoc pairwise comparisons using Tukey adjustment revealed significant differences in duration among behavioral categories. Only a pair of behaviors (moving and feeding/foraging) did not differ significantly (p adjusted > 0.05), whereas other pairs of behaviors differed significantly from each other (p adjusted < 0.001, Table S3 and Table S4 in supplementary material) (Figure 2).

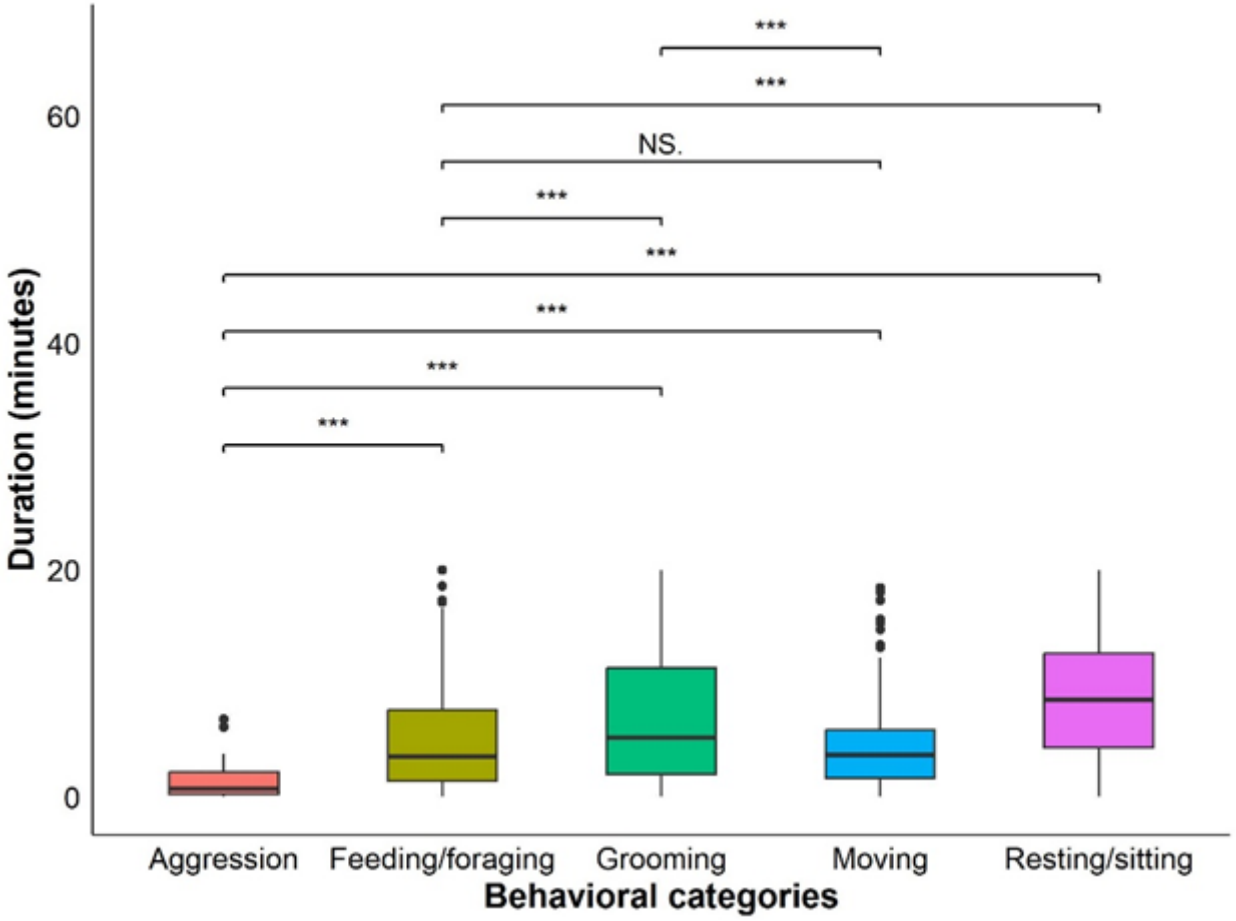

Figure 2 Overall combined activity budget of the rhesus macaques (groups G1 from LAP and G2 from HAP) in the Pashupatinath Temple area. *** represents significant differences between the behaviors. The bold horizontal lines within the boxes refer to the median and the vertical lines extending from the boxes represent the range of distribution within 50% of the IQR from the median. Grooming refers to allogrooming.

3.2. Activity budget in response to anthropogenic pressure

The macaques from G2 at HAP engaged in significantly more feeding/foraging behavior (median ± MAD = 4.26 ± 3.04 minutes, $p < 0.001$) than those from G1 at LAP (median ± MAD = 2.88 ± 2.16 minutes, $p < 0.001$) (Figure 3). Furthermore, macaques at high anthropogenic pressure (HAP) sites spent less time grooming and engaging in aggression than did those at low anthropogenic pressure (LAP) sites did, although these differences were not statistically significant (grooming: HAP median ± MAD = 5.08 ± 3.86 min; LAP = 5.46 ± 4.17 min; aggression: HAP = 0.65 ± 0.53 min; LAP = 0.87 ± 0.85 min). In contrast, the time spent moving and resting/sitting was slightly greater at the HAP sites, but these differences were also not significant (moving: HAP = 3.80 ± 2.00 min; LAP = 3.52 ± 2.38 min; resting/sitting: HAP = 8.68 ± 3.95 min; LAP = 8.18 ± 4.47 min).

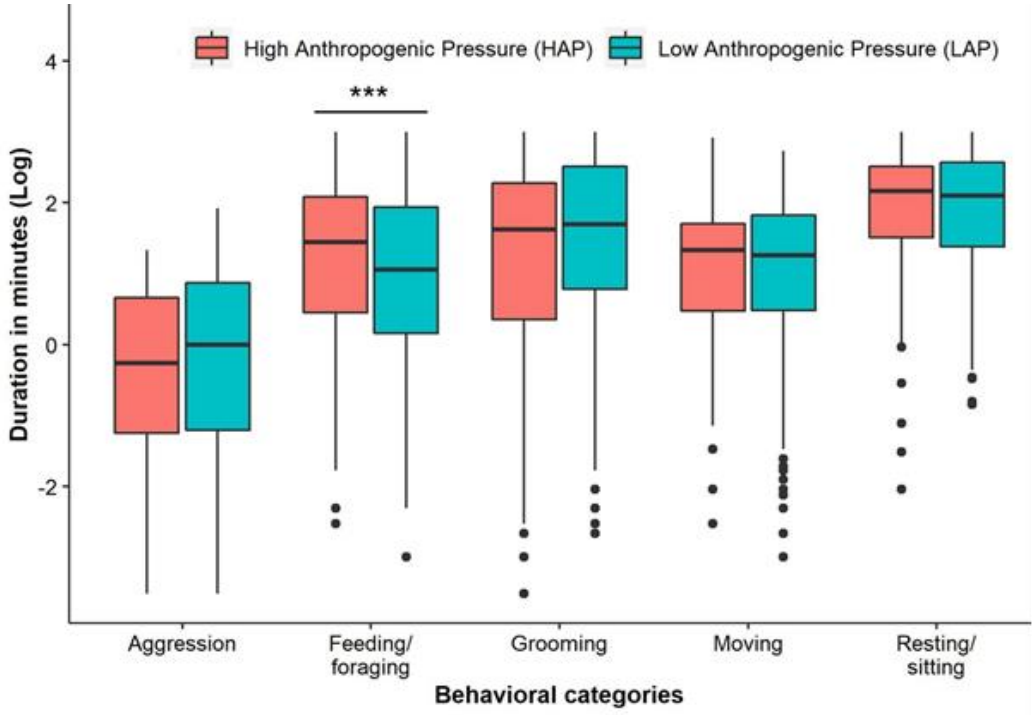

Figure 3 Activity budgets of rhesus macaques under different levels of anthropogenic pressure. *** represents significant differences of according to the Mann–Whitney test. The bold horizontal lines within the boxes refer to the median and the vertical lines extending from the boxes represent the range of distribution within 50% of the IQR from the median. Grooming refers to allogrooming.

Sex-based differences were observed in the activity budgets of the rhesus macaques (Figure 4). Males engaged in significantly more aggressive behavior (median ± MAD = 1.19 ± 0.99 minutes, $p < 0.001$) than females did (median ± MAD = 0.33 ± 0.3 minutes, $p < 0.001$) in each average observation bout of 20 minutes. Movement was also significantly greater among males (median ± MAD = 4.20 ± 2.08 minutes, $p < 0.001$) than females (median ± MAD = 3.16 ± 2.12 minutes, $p < 0.001$). Additionally, resting/sitting behavior was significantly more prevalent in males (median ± MAD = 9.89 ± 3.93 minutes) than in females (median ± MAD = 6.01 ± 3.88 minutes, $p < 0.001$). Conversely, grooming behavior was significantly greater in females (median ± MAD = 7.21 ± 4.85 minutes, $p < 0.001$) than in males (median ± MAD = 3.90 ± 3.22 minutes, $p < 0.001$).

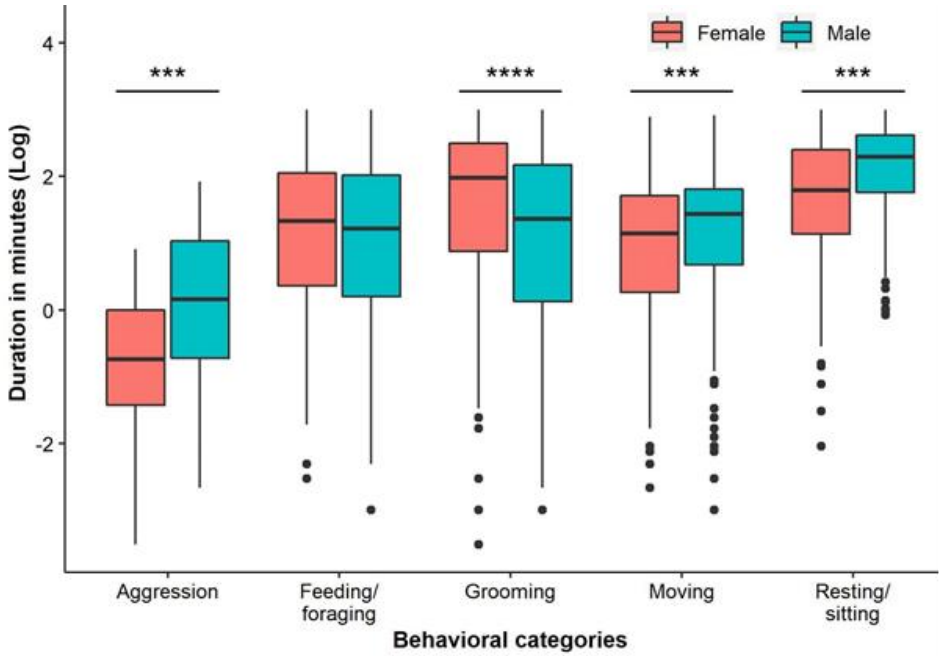

Figure 4 Activity budgets of the rhesus macaques on the basis of sex. *** represents significant differences according to the Mann–Whitney test. The bold horizontal lines within the boxes refer to the median. The vertical lines extending from the boxes represent the range of distribution within 50% of the IQR from the median. All analyses of sex differences refer to adult males and adult females. Grooming refers to allogrooming.

3.4. Grooming and feeding behavior under different levels of anthropogenic pressure

The overall combined grooming behavior exhibited by the macaques did not differ significantly between the two study blocks. However, it varied significantly when the sex of the macaques was considered. Comparative analysis of grooming behavior between female–female and male–male pairs from the LAP and HAP blocks via the Mann–Whitney test revealed that females demonstrated grooming behavior with different intensities ($U = 12464$, $p < 0.05$), whereas males did not exhibit such variation ($U = 11934$, $p > 0.7585$). The females from the LAP (median ± MAD = 7.25 ± 6.1 minutes, $p < 0.001$) invested more time in grooming than did the females from the HAP (median ± MAD = 5.04 ± 4.62 minutes, $p < 0.001$), suggesting that the greater number of visitors around the focal subjects in HAP reduced the amount of grooming but in less intensity ($\rho = -0.2$, $p < 0.001$; Figure 5A). The temple macaques showed a positive association between the time spent on feeding/foraging and the number of visitors ($\rho = 0.33$; $p < 0.01$, Figure 5B).

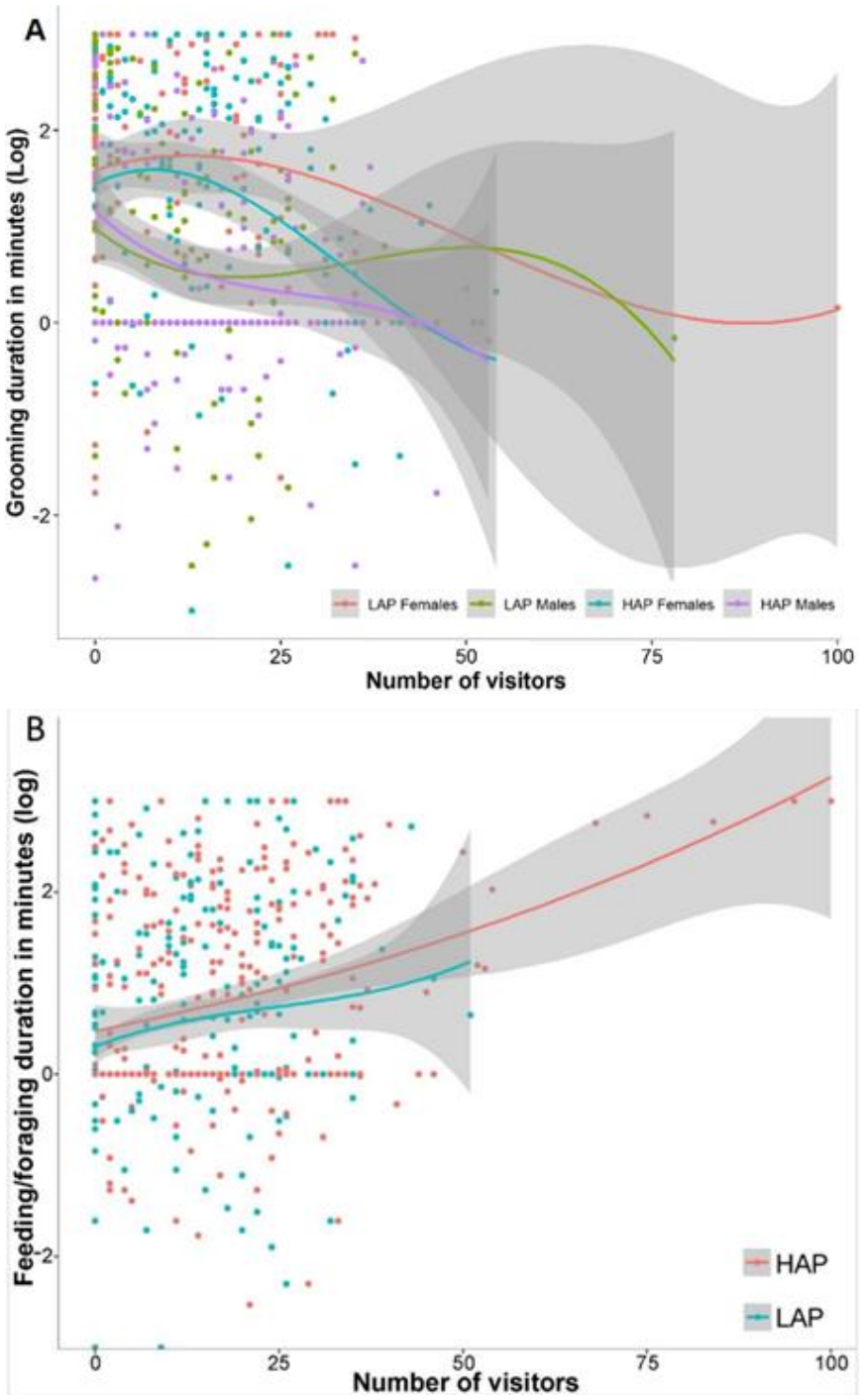

Figure 5 Effects of the number of visitors on feeding and grooming time allocation; A- Group and sex-based time budgets on the grooming behavior of rhesus macaques in response to the number of visitors; B- Group-based feeding/foraging behavior in response to the number of visitors. Correlation tests were run on pooled bouts across both groups and sexes. Grooming refers to the allogrooming.

4. Discussion

This study examined the behavioral activity of rhesus macaques living in the Pashupatinath Temple area of Kathmandu, Nepal, to understand how anthropogenic pressure affects their daily activity budgets. The findings provide valuable insights into the composition of their behavioral repertoire in relation to varying levels of human presence. Regardless of the number of visitors (LAP or HAP study block), resting and sitting were the most common activities observed, followed by grooming, feeding and foraging, moving, and aggression. The variations in the time budgets for these behaviors can be attributed to the fluctuating environment in which the macaques reside (Jaman & Huffman, 2008). When wild-feeding and semi-provisioned groups of Barbary macaques (*M. sylvanus*) were compared, the semi-provisioned groups spent more time resting than their wild-feeding counterparts did (El Alami et al., 2012). Adhikari et al. (2018) noted that semiprovisioned Assamese monkeys (*M. assamensis*) in Nepal invested less time in feeding and foraging. The limited natural habitat and available food provisioning for the rhesus macaques at Pashupatinath Temple may be the primary reason for their increased resting and sitting behavior.

Regular food provisioning occurs twice a day in the Pashupatinath Temple area where macaques are provided with boiled flour dough. Additionally, visitors provided fruits and high-calorie foods such as grams, bananas and maize. Owing to the intake of high calorie diets, macaques likely spend much of their time resting and engaging in social activities (Jaman & Huffman, 2013). Grooming and resting are often interconnected; as monkeys rest near one another, this proximity may encourage them to initiate new grooming sessions (Hikida, 2022; Shrestha et al., 2024) or post grooming sessions (Schino & Alessandrini, 2015). This could explain why grooming was the second most common activity, while feeding and foraging ranked third. All major and longer feeding/foraging episodes were recorded just after food provisioning. As such, provisioning provides macaques with the benefits of minimizing feeding/foraging time (Kaburu et al., 2019) and increasing social behavior (Balasubramaniam et al., 2020). The downside of provisioning, however, increases macaques' dependency on anthropogenic food (Sengupta and Radhakrishna, 2018; Kaburu et al., 2019) and the risk of disease transmission from humans to macaques (Sengupta et al., 2014). Aggressive behavior was observed primarily among rhesus macaques during these feeding sessions, a phenomenon also noted in other provisioned populations (Wu et al., 2025).

Our results revealed a notable difference in the feeding/foraging behavior of rhesus macaques in the two study blocks under different anthropogenic pressures. Compared with those in the HAP block, the macaques in the LAP block spent less time on feeding/foraging activities. This variance might be attributed to differences in food provisioning and visitor access restrictions between the two study blocks. In the LAP block, where visitor entry was restricted and food provisioning was less frequent, the macaques encountered fewer disturbances and had their own fixed feeding timeframe, potentially leading to lower engagement in feeding activities than in the HAP block did. Conversely, in the HAP block, where food provisioning occurred more frequently, the macaques readily engaged in feeding the provisioned food, likely because of the frequent availability of food. Notably, both groups of macaques also, fed on natural food sources, such as insects, leaves, and seeds, in addition to human-provided food. The feeding/foraging behavior of the macaques in both study blocks may also be influenced by factors such as the spatial distribution of food resources, social hierarchy, desirability of certain food items, propensity for begging and ability to opportunistically acquire food from visitors or residents (Sengupta & Radhakrishna, 2018). These multifaceted influences underscore the complexity of primate feeding behaviors in urban environments.

The macaques from both the LAP and HAP blocks allocated their time primarily to resting/sitting and grooming activities. Males spent more time resting/sitting, whereas females predominantly engaged in grooming activities in both groups. This grooming behavior among females is likely related to their social roles, as it involves self-grooming, grooming of other individuals, and caring for their offspring, which is essential for hygiene and social bonding (Solanki et al., 2020). In contrast, males often groomed females, particularly as a strategy to increase their mating opportunities (Cooper & Bernstein, 2008), while occasional grooming of infants was also observed. Notably, there was a variation in grooming time between females of LAP and HAP, potentially influenced by levels of anthropogenic activities but in less strength and might be heavily influenced by other latent variables such as presence of nearby dogs, dominant hierarchy, temperature, rainfall etc. The LAP block females may have had more opportunities for undisturbed grooming as visitor access to that area was more restricted. Conversely, HAP females may have faced greater interruptions during grooming due to visitor presence and provisioning. In the LAP block, the macaques used to go outside only to feed and then returned for other social activities. In the HAP group, there was Mrigasthali Deer Park where visitors were allowed to see the deer. Similarly, we observed that visitors sometimes provided food and teased the monkeys, which might explain the reduced grooming time of the HAP blocked females.

The study also revealed that aggressive encounters were predominantly observed in males and peaked during feeding. Similar sex-based variation in aggression has been observed in other primates (Sabbi et al., 2021; Mouginot et al., 2024). Male monkeys often engage in aggressive interactions, which are influenced by hierarchy and the availability of food resources at specific times of the day (Kaburu et al., 2019; Jaman & Huffman, 2013; Sharma et al., 2023). Our results also revealed that the macaque movement in HAP was greater than in LAP, which may be largely influenced by the presence of predators such as dogs and eagles, or neighboring macaque groups. The groups of rhesus macaques shared home ranges with neighboring groups but avoided proximity to reduce encounters, which can range from nonaggressive interactions to chases and fights. In general,

during aggressive encounters, male monkeys typically display higher levels of aggression than females do (Yang et al., 2024), possibly due to their dominant roles and the need to protect their feeding/foraging ranges (Cooper & Bernstein, 2008).

The results underscore a significant sex-based difference in grooming time between the macaques of the two study blocks. Notably, females in the LAP block engaged in substantially more grooming than those in the HAP block did. This contrast may be attributed to the limited human presence in the LAP block, where females could devote more time to social grooming. Human presence appeared to influence grooming behavior, with increased interactions between humans and macaques associated with shorter grooming sessions, which aligns with findings from several other studies on rhesus macaques (Kaburu et al., 2019; Balasubramaniam et al., 2020; Sharma et al., 2022). Notably, the reduced social activities in the HAP block group may represent an adaptive behavioral strategy in response to their anthropogenic environment (McLennan et al., 2017). Furthermore, the reduction in grooming activity during periods of high human presence is consistent with findings from a study of Bonnet macaques, which demonstrated a decrease in grooming behavior and partner diversity due to anthropogenic time constraints (Balasubramaniam et al., 2020). Consequently, reduced grooming behavior in areas with high anthropogenic pressure can negatively impact social bonds, as grooming serves as a vital social activity that reinforces alliances and group cohesion among macaques (Dunbar, 2024). When grooming diminishes, individuals may experience weakened social ties, leading to increased social tension and decreased cooperation within the group (Yates et al., 2022). Additionally, grooming has been associated with stress alleviation, as it promotes the release of endorphins and reduces cortisol levels; thus, less grooming could increase stress levels, impairing overall health and well-being (Yates et al., 2022; Beisner et al., 2023). Consequently, diminished social bonds and heightened stress may compromise group cohesion, increasing the vulnerability of macaques to external threats and reducing their collective resilience in environments with high levels of human disturbance (Kaisin et al., 2021). The marked reduction in grooming among macaques exposed to high levels of human activity suggests that anthropogenic disturbance disrupts key social behaviors essential for maintaining group cohesion and stress regulation. Such behavioral alterations likely reflect adaptive responses to human presence but may ultimately weaken social bonds, increase stress and reduce the overall resilience of macaque groups in human-disturbed environments.

This study has certain limitations; that might influence the findings of this study. The study did not explicitly control seasonal variation. Although the data were collected over approximately eight months, potential seasonal differences in resource availability, temperature, or visitor frequency were not statistically tested, which may have influenced behavioral patterns. Several unmeasured covariates, such as ambient temperature, rainfall, and time of day, could have affected behavioral responses but were not included in the analysis. These factors should be considered in future research to elucidate the effects of anthropogenic and ecological influences on the behavior of macaques. Furthermore, several factors including repeated measures within individuals and within study groups were not modeled explicitly, only two social groups of macaques were studied and reliance on visitor counts rather than direct quantification of provisioning/teasing, etc., should be taken into consideration when the results are interpreted.

5. Conclusion

The behavioral activity budgets of the temple rhesus macaques revealed that resting, grooming, and feeding were the dominant behavioral activities. The macaques in areas with greater anthropogenic disturbance invested longer durations of their diurnal time in feeding but shorter durations of grooming. Sex-based variations were evident, with males displaying more resting/sitting, aggressive and moving behavior, and females dedicating more time to grooming. Females in areas with lower anthropogenic pressure groomed more than females in areas with higher anthropogenic pressure did, indicating the negative influence of human disturbance on the social behavior of rhesus macaques. Our results suggest that high levels of human disturbance are associated with reduced grooming, particularly among females, which may have implications for social cohesion and resilience. Based on our findings and previous work on human–macaque interactions, we recommend to establishing visitor codes of conduct, which are supported by informative signage and texts, and limiting direct feeding could help maintain more natural behavioral patterns and support long-term coexistence.

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6. Declarations

6.1. Ethical considerations

Observations were strictly noninvasive, limited to behavioral monitoring without contact or disturbance. Researchers maintained a respectful distance and avoided provisioning. The study adhered to the International Primatological Society's Code of Best Practices for Field Primatology, ensuring animal welfare and research integrity.

6.2. Use of artificial intelligence (AI)

The authors declare that no generative artificial intelligence (AI) tools were used in the preparation, analysis, or writing of this manuscript.

6.3. Conflict of interest

The authors declare that they have no conflicts of interest.

6.4. Funding

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References

Adhikari, A., Khanal, L., & Chalise, M. K. (2018). Status and effects of food provisioning on ecology of Assamese monkey (*Macaca assamensis*) in Ramdi area of Palpa, Nepal. *Journal of Institute of Science and Technology, 22*(2), 183–190. https://doi.org/10.3126/jist.v22i2.19611

Air, A. (2015). *Crop raiding and conflict: Study of rhesus macaque–human conflict in Shivapuri-Nagarjun National Park, Kathmandu, Nepal* (Master's thesis, Norwegian University of Science and Technology).

Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J., & Alberts, S. C. (2013). Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour, 85*(3), 559–568. https://doi.org/10.1016/j.anbehav.2012.12.012

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3–4), 227–266. https://doi.org/10.1163/156853974x00534

Balasubramaniam, K. N., Beisner, B. A., Berman, C. M., De Marco, A., Duboscq, J., Koirala, S., … McCowan, B. (2018). The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure. *American Journal of Primatology, 80*(1), e22727. https://doi.org/10.1002/ajp.22727

Balasubramaniam, K. N., Marty, P. R., Arlet, M. E., Beisner, B. A., Kaburu, S. S. K., Bliss-Moreau, E., … McCowan, B. (2020). Impact of anthropogenic factors on affiliative behaviors among bonnet macaques. *American Journal of Physical Anthropology, 171*(4), 704–717. https://doi.org/10.1002/ajpa.24013

Bartlett, M. S. (1937). Properties of sufficiency and statistical tests. *Proceedings of the Royal Society A, 160*, 268–282. https://doi.org/10.1098/rspa.1937.0109

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bauer, D. F. (1972). Constructing confidence sets using rank statistics. *Journal of the American Statistical Association, 67*, 687–690. https://doi.org/10.1080/01621459.1972.10481279

Beisner, B. A., Hannibal, D. L., Vandeleest, J. J., & McCowan, B. (2023). Sociality, health, and welfare in nonhuman primates. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman primate welfare* (pp. 413–443). Springer. https://doi.org/10.1007/978-3-030-82708-3_18

Beisner, B. A., Heagerty, A., Seil, S. K., Balasubramaniam, K. N., Atwill, E. R., Gupta, B. K., … McCowan, B. (2015). Human–wildlife conflict: Proximate predictors of aggression between humans and rhesus macaques in India. *American Journal of Physical Anthropology, 156*(2), 286–294. https://doi.org/10.1002/ajpa.22649

Bhattrai, S., Bagale, D., & Shrestha, S. S. (2025). Rainfall variability in Kathmandu Valley, Nepal. *Scientific World, 18*(18), 116–127. https://doi.org/10.3126/sw.v18i18.78437

Caselli, M., Zanoli, A., Dagradi, C., Gallo, A., Yazezew, D., Tadesse, A., … Fashing, P. J. (2021). Wild geladas (*Theropithecus gelada*) in crops more than in pasture areas reduce aggression and affiliation. *Primates, 62*(4), 571–584. https://doi.org/10.1007/s10329-021-00916-8

Cooper, M. A., & Bernstein, I. S. (2008). Evaluating dominance styles in Assamese and rhesus macaques. *International Journal of Primatology, 29*(1), 225–243. https://doi.org/10.1007/s10764-008-9236-y

Dancer, A. M., & Burn, C. C. (2019). Visitor effects on zoo-housed Sulawesi crested macaque (*Macaca nigra*) behaviour: Can signs with "watching eyes" requesting quietness help? *Applied Animal Behaviour Science, 211*, 88–94. https://doi.org/10.1016/j.applanim.2018.12.005

Dunbar, R. I. M. (2024). Structural and cognitive mechanisms of group cohesion in primates. *Behavioral and Brain Sciences, 48*, e162. https://doi.org/10.1017/S0140525X2400030X

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science, 317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

El Alami, A., Van Lavieren, E., Rachida, A., & Chait, A. (2012). Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered Barbary macaque (*Macaca sylvanus*) in the central High Atlas Mountains, Morocco. *American Journal of Primatology, 74*(3), 210–216. https://doi.org/10.1002/ajp.21989

Hikida, K. (2022). Eyeblink rate as an indicator of concentration on grooming in Japanese macaques (*Macaca fuscata*). *American Journal of Primatology, 84*(7), e23392. https://doi.org/10.1002/ajp.23392

Jaman, M. F., & Huffman, M. A. (2008). Enclosure environment affects the activity budgets of captive Japanese macaques (*Macaca fuscata*). *American Journal of Primatology, 70*(12), 1133–1144. https://doi.org/10.1002/ajp.20612

Jaman, M. F., & Huffman, M. A. (2013). The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates, 54*(1), 49–59. https://doi.org/10.1007/s10329-012-0330-6

Kaburu, S. S. K., Beisner, B., Balasubramaniam, K. N., Marty, P. R., Bliss-Moreau, E., Mohan, L., … McCowan, B. (2019). Interactions with humans impose time constraints on urban-dwelling rhesus macaques (*Macaca mulatta*). *Behaviour, 156*(12), 1255–1282. https://doi.org/10.1163/1568539x-00003565

Kaburu, S. S. K., Marty, P. R., Beisner, B., Balasubramaniam, K. N., Bliss-Moreau, E., Kaur, K., … McCowan, B. (2019). Rates of human–macaque interactions affect grooming behavior among urban-dwelling rhesus macaques (*Macaca mulatta*). *American Journal of Physical Anthropology, 168*(1), 92–103. https://doi.org/10.1002/ajpa.23722

Kaisin, O., Fuzessy, L., Poncin, P., Brotcorne, F., & Culot, L. (2021). A meta-analysis of anthropogenic impacts on physiological stress in wild primates. *Conservation Biology, 35*(1), 101–114. https://doi.org/10.1111/cobi.13656

Kyes, P., Thamsenanupap, P., Tanee, T., Intralawan, A., & Kyes, R. C. (2018). Previously unreported population of rhesus macaques (*Macaca mulatta*) in Chiang Rai Province, Thailand: Preliminary observations. *Asian Primates Journal, 18*(1), 6–13.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour, 74*(6), 1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Lenth, R. V. (2025). *emmeans: Estimated marginal means, aka least-squares means* (R package version 1.11.2) [Computer software]. https://doi.org/10.32614/CRAN.package.emmeans

Li, Y., Huang, X., & Huang, Z. (2020). Behavioral adjustments and support use of Francois' langur in limestone habitat in Fusui, China: Implications for behavioral thermoregulation. *Ecology and Evolution, 10*(11), 4956–4967. https://doi.org/10.1002/ece3.6249

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews, 88*(3), 537–549. https://doi.org/10.1111/brv.12012

Maharjan, M., Ghimire, A., Subba, A., Pandey, N., Kyes, R. C., & Khanal, L. (2025). Anthropogenic noise and vegetation cover affect the vocalizations of resident Oriental magpie-robins in Kathmandu Valley, Nepal. *Journal of Animal Behaviour and Biometeorology, 13*(3), 2025027. https://doi.org/10.31893/jabb.2025027

Marty, P. R., Beisner, B., Kaburu, S. S. K., Balasubramaniam, K., Bliss-Moreau, E., Ruppert, N., … McCowan, B. (2019). Time constraints imposed by anthropogenic environments alter social behaviour in long-tailed macaques. *Animal Behaviour, 150*, 157–165. https://doi.org/10.1016/j.anbehav.2019.02.010

McLennan, M. R., Spagnoletti, N., & Hockings, K. J. (2017). The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *International Journal of Primatology, 38*(2), 105–121. https://doi.org/10.1007/s10764-017-9962-0

Mouginot, M., Wilson, M. L., Desai, N., & Sarbeck, M. (2024). Differences in expression of male aggression between wild bonobos and chimpanzees. *Current Biology, 34*(8), 1780–1785. https://doi.org/10.1016/j.cub.2024.02.071

Ogawa, H., Khatiwada, S., Paudel, P., Koirala, S., Khanal, L., & Chalise, M. K. (2024). Distribution and group composition of Assamese and rhesus macaques in northwestern Kathmandu Valley, Nepal. *Mammal Study, 49*(3), 185–193. https://doi.org/10.3106/ms2023-0061

R Core Team. (2025). *R: A language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org

Radhakrishna, S., & Sinha, A. (2011). Less than wild? Commensal primates and wildlife conservation. *Journal of Biosciences, 36*(5), 749–753. https://doi.org/10.1007/s12038-011-9145-7

Riley, E. P., & Wade, T. W. (2016). Adapting to Florida's riverine woodlands: The population status and feeding ecology of the Silver River rhesus macaques and their interface with humans. *Primates, 57*(2), 195–210. https://doi.org/10.1007/s10329-016-0517-3

Royston, P. (1982). An extension of Shapiro and Wilk's W test for normality to large samples. *Applied Statistics, 31*, 115–124. https://doi.org/10.2307/2347973

Sabbi, K. H., Thompson, M. E., Machanda, Z. P., Otali, E., Wrangham, R. W., & Muller, M. N. (2021). Sex differences in early experience and the development of aggression in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America, 118*(12), e2017144118. https://doi.org/10.1073/pnas.2017144118

Schino, G., & Alessandrini, A. (2015). Short-term costs and benefits of grooming in Japanese macaques. *Primates, 56*(3), 253–257. https://doi.org/10.1007/s10329-015-0468-0

Schurer, J., Ramirez, V., Kyes, P., Tanee, T., Patarapadungkit, N., Thamsenanupap, P., Trufan, S., … Chantima, W. (2019). Long-tailed macaques (*Macaca fascicularis*) in urban landscapes: Investigating gastrointestinal parasitism and barriers for healthy co-existence in northeast Thailand. *The American Journal of Tropical Medicine and Hygiene, 100*, 357–364. https://doi.org/10.4269/ajtmh.18-0241

Sengupta, A., & Radhakrishna, S. (2018). The hand that feeds the monkey: Mutual influence of humans and rhesus macaques (*Macaca mulatta*) in the context of provisioning. *International Journal of Primatology, 39*(5), 817–830. https://doi.org/10.1007/s10764-018-0014-1

Sengupta, A., Anand, S., & Radhakrishna, S. (2025). Behavioural flexibility in rhesus macaques (*Macaca mulatta*) in human-modified environments. *International Journal of Primatology, 46*, 932–954. https://doi.org/10.1007/s10764-025-00506-1

Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2014). Seed dispersal by rhesus macaques (*Macaca mulatta*) in northern India. *American Journal of Primatology, 76*(12), 1175–1184. https://doi.org/10.1002/ajp.22302

Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2015). Primates, provisioning and plants: Impacts of human cultural behaviours on primate ecological functions. *PLoS ONE, 10*(11), e0140961. https://doi.org/10.1371/journal.pone.0140961

Sha, J. C., & Hanya, G. (2013). Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology, 75*(6), 581–592. https://doi.org/10.1002/ajp.22137

Sharma, S., Khanal, L., Shrestha, S., Pandey, N., Bellanca, R. U., & Kyes, R. C. (2023). Zoo visitors as a source of enrichment to reduce abnormal behavior in captive rhesus macaques (*Macaca mulatta*) in the Central Zoo, Kathmandu, Nepal. *Journal of Animal Behaviour and Biometeorology, 11*(1), e2023005. https://doi.org/10.31893/jabb.23005

Sharma, S., Shrestha, S., Pandey, N., & Khanal, L. (2022). Determinants of grooming behavior in captive langurs under human disturbance: A case study from the Central Zoo, Kathmandu, Nepal. *Punjab University Journal of Zoology, 37*(2), 98–105. https://doi.org/10.17582/journal.pujz/2022.37.2.98.105

Shrestha, L. J., & Devkota, M. (2013). Forest types of Pashupati Sacred Grove, Kathmandu, Nepal. *Journal of Natural History Museum, 27*, 72–77. https://doi.org/10.3126/jnhm.v27i0.14155

Shrestha, S., Sharma, S., Kyes, R. C., & Khanal, L. (2024). Comparative analysis of mother–infant interactions between free-ranging and captive rhesus macaques in Kathmandu, Nepal. *Journal of Animal Behaviour and Biometeorology, 12*(2), e2024011. https://doi.org/10.31893/jabb.2024011

Sinha, A., Mukhopadhyay, K., Datta-Roy, A., & Ram, S. (2005). Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. *Current Science, 89*(7), 1166–1179.

Solanki, G. S., Lalremruati, P., & Lalchhuanawma, K. (2020). Grooming pattern in captive macaques: A comparative study. *Environmental Conservation Journal, 21*(3), 127–135. https://doi.org/10.36953/ecj.2020.21315

Sugiyama, Y. (2015). Influence of provisioning on primate behavior and primate studies. *Mammalia, 79*(3), 255–265. https://doi.org/10.1515/mammalia-2014-0028

Thapa, A., Silwal, A., Gautam, S. P., Nepal, C. K., Bhattarai, S., & Timsina, D. (2021). Surface air temperature trends in Kathmandu Valley for 2011–2017. *Bibechana, 18*(2), 95–104. https://doi.org/10.3126/bibechana.v18i2.29495

Thatcher, H. R., Downs, C. T., & Koyama, N. F. (2019). Anthropogenic influences on the time budgets of urban vervet monkeys. *Landscape and Urban Planning, 181*, 38–44. https://doi.org/10.1016/j.landurbplan.2018.09.014

Waterman, J. O., Campbell, L. A. D., Maréchal, L., Pilot, M., & Majolo, B. (2019). Effect of human activity on habitat selection in the endangered Barbary macaque. *Animal Conservation, 23*(4), 373–385. https://doi.org/10.1111/acv.12543

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2025). *dplyr: A grammar of data manipulation* (R package version 1.1.4) [Computer software]. https://dplyr.tidyverse.org

Wijesuriya, G., & Forbes, C. (2021). *Report on the joint World Heritage Centre/ICOMOS/ICCROM reactive monitoring mission to the World Heritage property of the Kathmandu Valley (Nepal, C 121bis), 16–21 October 2019*. UNESCO.

Wu, C. F., Xu, Z. H., Fan, Y. X., Chen, T., & Xie, P. Z. (2025). The influence of provisioning on the intergroup relationships of rhesus macaques in Hainan, China. *American Journal of Primatology, 87*, e23721. https://doi.org/10.1002/ajp.23721

Yang, B., Anderson, J. R., Han, M. Y., Meng, X. Y., Luo, J., Jia, K. S., … Li, J. (2024). Male aggressive behaviors as an indicator in primate tourism management assessment. *Global Ecology and Conservation, 50*, e02858. https://doi.org/10.1016/j.gecco.2024.e02858

Yang, L., Liu, S., Yu, P., Yu, H., & Hu, D. (2016). Relationships between food provisioning patterns, stress and reproductive parameters of *Rhinopithecus roxellana* (Milne-Edwards, 1870). *North-Western Journal of Zoology, 12*(1), 141–150.

Yates, K., Stanley, C. R., & Bettridge, C. M. (2022). The effects of allogrooming and social network position on behavioural indicators of stress in female lion-tailed macaques (*Macaca silenus*). *Behavioural Processes, 202*, 104740. https://doi.org/10.1016/j.beproc.2022.104740

Zhou, J., Li, W. B., Wang, X., & Li, J. H. (2022). Seasonal change in activity rhythms and time budgets of Tibetan macaques. *Biology, 11*(9), 1260. https://doi.org/10.3390/biology11091260