Activity budget, diet and foraging behaviours of urban dwelling Rhesus macaques in northern India.

1 ABSTRACT

Due to rapid urbanisation, many animals are forced to exploit anthropogenic environments. However, they come with many benefits, such as more predictable food and higher-calorie food sources. There are many associated costs as well, including human-wildlife conflict, making urban areas a challenging place to survive in. Rhesus macaque (*macaca mulatta*), are one such species that thrive in urban settings across south and east Asia, in the widest geographic range of all non-human primates. This is accredited to their behavioural and diet flexibility allowing them to forage across a large variety of anthropogenic and natural food sources. Therefore, this study quantified which specific food items were foraged upon most frequently by Rhesus macaques in an urban city, Shimla, in India, and documented their daily activity budget to investigate impacts of urbanisation. Our study finds they spend a large proportion of the day resting, 51% with an additional 6.9% grooming. This is thought to be due to food being readily available, and of high calorie content, with macaques consuming 61% anthropogenic food. Grain (14.9%), ice cream (10.8%), and bread (10.7%), all made up significant proportions of adult and juvenile macaques' diet, with high percentages of anthropogenic fruit (10.8%). Leaves, grasses and other natural plants consisted of just 35.4% of their diet. Male macaques are especially at risk from this high sugar high calorie diet, consuming 75.4% anthropogenic food. This has wide implications in wildlife management strategies as removing the availability of food and decreasing provisioning for monkeys in cities is key to reducing human-wildlife conflicts, as well as monitoring the health of free ranging urban macaque groups.

2 INTRODUCTION

Rapid urbanisation, habitat modification, and agricultural expansion directly impacts animal behavioural ecology (Dhananjaya *et al*., 2022) and drives many species to marginal habitats if they do not show behavioural flexibility. Behavioural flexibility allows animals to quickly modify their behaviour due to variation in the consequences or contexts of their actions (Amici *et al.*, 2018). This ability critically affects the survival and fitness of individuals in complex, dynamic environments, such as urban settings (McLennan, Spagnoletti and Hockings, 2017; Amici *et al*., 2018; Marty *et al.*, 2019). Generalist wildlife species often thrive in urban contexts; however, this causes problems for wildlife management due to heightened human-wildlife interactions (Thatcher, Downs and Koyama, 2019). Species that are specialists in habitat or diet are more vulnerable to the effects of habitat modifications due to their limited ability to adjust their behaviour (Maibeche *et al*., 2015). Therefore, understanding primate behaviour in urban settings is important in guiding human-wildlife cohabitation urban management plans and conservation (Bicca-Marques, 2017).

Primates adapt to urban environments in varying ways, including modifying foraging behaviour and their activity patterns (Thatcher, Downs and Koyama, 2019). In primates, anthropogenic environments can significantly increase an individual's fitness due to access to anthropogenic food resources as they are frequently higher in calories, and many sources have predictable locations and timing of access, increasing foraging efficiency (Cooper *et al*., 2022). Anthropogenic food sources are also more reliable food options as they are less likely to be influenced by seasonal fluctuations than natural and semi-natural foods such as fruit trees (Thatcher, Downs and Koyama, 2019). The importance of anthropogenic food in the diet of urban living primates has thus increased, leading to macaque-human conflict which usually occurs when humans carry food or food cues (Sha *et al*., 2009). Anthropogenic food is more prevalent in some primate diets, indicating a preference for anthropogenic foods (Marty *et al.*, 2019).

In primates, males and high-ranking individuals in both sexes have higher percentages of anthropogenic food in their diets than lower-ranking individuals (Marty *et al.*, 2019). In macaques, individuals who incur lower costs related to life history (males) and resource access (high ranking), but also higher costs regarding advantages of being in the core of their group, are most likely to take risks in human-primate interactions (Balasubramaniam *et al*., 2020). This unequal access to anthropogenic food is thought to also increase within-group competition (Marty *et al*., 2019).

Rhesus macaques (Macaca mulatta) show great ecological variation as they live in a wide range of environments and are generalist omnivores with highly flexible and varied diets (Cooper *et al.*, 2022). Recently, rhesus macaques have adapted to intense and rapid environmental disturbance caused by urbanisation and agricultural expansion. Whilst many other primate populations have shrunk in response to these processes, with an overall decline in primate species worldwide, with 75% of primate species declining, and ~60% threatened with extinction (Estrada *et al*., 2017), rhesus macaques have thrived and changed their diets (Cooper *et al*., 2022). The urban success of these species provides an excellent opportunity to study their behavioural flexibility in response to cohabitation with humans, as well as the impacts of the urban environments and anthropogenic foods on physiology, health, and ecological functions (Cooper *et al*., 2022). Anthropogenic environments offer excellent conditions to observe the behaviour of primates to rapidly changing environments and are well-suited to study the flexibility of food acquisition and processing among primates as a result of the availability of diverse food items with variable characteristics (Dhananjaya *et al*., 2022).

Thus far, studies tend to distinguish between anthropogenic, semi-anthropogenic, and non-anthropogenic food sources. However, considering the variation in anthropogenic resources, this terminology may not be sufficient to describe urban populations (Thatcher, Downs and Koyama, 2019). Different foods have different values to humans and primates, for example, crops are likely to be controlled more than resources from leisure areas such as parks (Thatcher, Downs and Koyama, 2019).

Rhesus macaques are prevalent in northern India and are often involved in conflicts with humans over food, such as damaging property in search of food, as well as crop depreciation (Saraswat, Sinha and Radhakrishna, 2015). However, macaque management in India is difficult due to the cultural significance of the species. The rhesus macaque is seen as a living representation of Hanuman, the Hindu deity, and thus cultural beliefs about the species sanctity often influence discussion regarding wildlife management (Saraswat, Sinha and Radhakrishna, 2015; Anand, Binoy and Radhakrishna, 2018). Many people are reluctant to harm the macaques but are also greatly affected by crop depreciation. Significant income is lost by rhesus macaque foraging, and aggressive contact is a concern, especially in urban areas (Beisner

et al., 2015; Saraswat, Sinha and Radhakrishna, 2015). This conflict often stems from food-related issues, for example, much human conflict stems from damage to crops, or stealing food resources, whereas macaque aggression is often influenced by intimidating behaviour by humans (Beisner *et al*., 2015). Thus, understanding the macaques dietary index and preferences may also bring clarity to human-macaque conflict and thereby be useful in wildlife management schemes.

Many techniques have been applied to primate management in urban environments, focusing on either managing the environment, the primates, or the people (Bicca-Marques, 2017). Education is the most effective and long-term strategy, however, this is difficult to implement, so strategies often aim to reduce the amount of waste in areas accessible to primates (Bicca-Marques, 2017). The analysis of the exact food sources rhesus macaques eat should help inform these initiatives, and aid in reducing human-macaque conflict.

Therefore, this study aims to identify the activity budget of urban dwelling Rhesus macaques in the city centre of Shimla in northern India where there is a strong anthropogenic influence on the primates' day to day life. This will be separated into sex and age of the macaque, and throughout the span of the day to identify differences in macaque behaviour. This study will also classify the exact food items foraged upon by the macaques to quantify the percentage of natural versus anthropogenic food in their diet. This will be used to calculate a diet diversity and to determine differences in feeding patterns throughout the day and between different ages and sex patterns in rhesus macaques. Food sources will also be identified more precisely, when possible, grouped into more detailed food categories such as 'fruit', 'vegetables', and 'bread'. This should allow more nuanced analysis of the rhesus macaques preferences and degree of reliance on anthropogenic food. This will additionally provide further information on the nutritional value of the anthropogenic food the macaques eat.

3 METHODS

3.1 STUDY SITE AND METHODOLOGY

The study was carried out in Shimla (31.1052°N, 77.1724°E), a city in the northern province of Himachal Pradesh in India, with data collected between 1st July and 2nd August 2024. Behavioural observations were taken along Mall Road, Pedestal Road, the Ridge to US Club and Kari Bari Road, which encompass most of the pedestrianised areas of Shimla city centre. These areas are characterised high densities of people, surrounded by many commercial shops and food vendors. This and the frequent green spaces with tall trees throughout the city create the perfect environment to attract many Rhesus macaques (Figure 1).

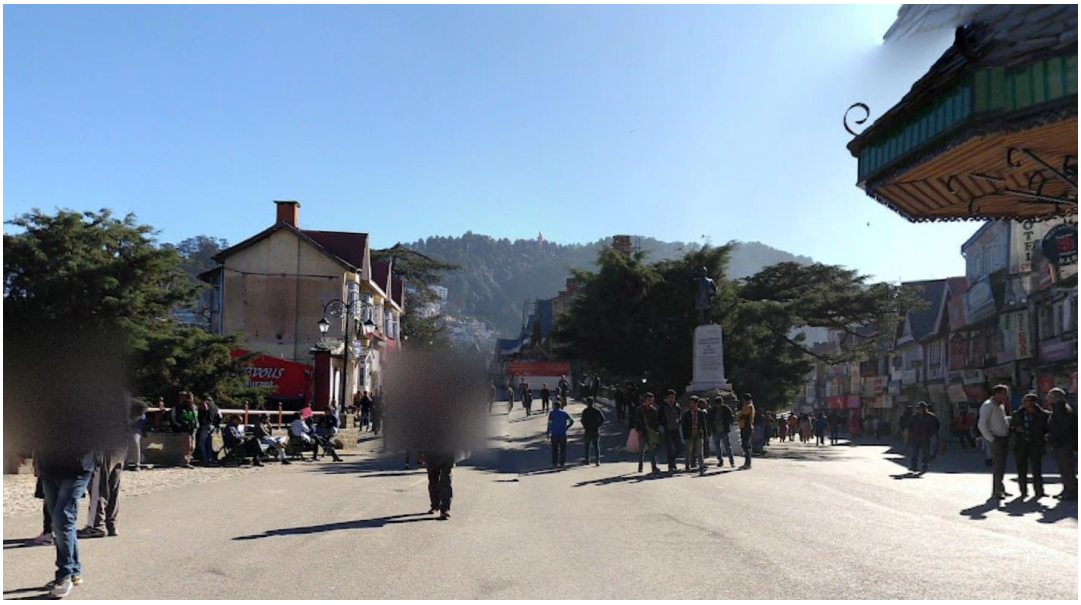

Figure 1. Mall road in Shimla: the central road spanning the length of the city is lined with shops and restaurants which attracts many tourists and macaques. There are many trees in the city centre providing a refuge for Rhesus macaques.

Observational focal samples of 10-minutes were conducted, recording the behaviour using the below ethogram (Table 1) each minute. Individuals' full activity budget was recorded. A focal sample was considered aborted if an individual went out of sight for more than 2 minutes in each sample. Relatively short focal periods were used as macaques were often skittish due to the high human density, as they can easily hide behind or on buildings, which avoided underrepresenting bolder individuals. Any food items the macaque forages or feeds on were recorded as well as the location of the macaque on the minute. Before each 10-minute focal sampling session, the individuals' age category and sex were also recorded. Age was broken down into infant, juvenile and adult, with sub-adult being classed as adult as they are nearly indistinguishable from adults (Beisner et al., 2012). Male macaques are typically bigger than females and are characterised by larger canines and testes. Macaques also have different perinea colourations (Beisner *et al*., 2012). Data was collected from 9:00 to 19:00 allowing a daily activity budget to be recorded.

Table 1. The ethogram used to identify the Rhesus macaque behaviour, as described in (Poti *et al.*, 2015; Whitehouse *et al*., 2017; Wright *et al*., 2018).

Behaviour	*Description*
Aggression	Showing hostility to either a conspecific or a human, through chasing, lunging, vocalisation, or biting.
Feeding	Macaque must currently be eating a food source, either anthropogenic or natural.
Foraging	Actively searching for a food source by grabbing leaves, branches from trees or looking through bins.
Drinking	Drinking water or other liquids from a tank, floor or bottle.
Grooming	Social grooming: licking, rubbing or stroking the fur of another macaque. Self-grooming is classed as resting.
Locomotion	Movement from one location to another by pedal, climbing or jumping movement.
Play	Either social, object or locomotor play, which can involve chasing, fighting, holding objects or tree shaking; most common in juveniles and infants.
Rest	Macaque is motionless, either lying or sitting and not feeding or interacting with a conspecific.
Out of sight	Macaque is fully or mostly not visible such that the behaviour cannot be determined.

The type of food a macaque was observed eating is divided into either anthropogenic or non-anthropogenic food sources. Anthropogenic food resources are defined as anything produced by humans, ranging from processed foods like bread or crisps to anthropogenic fruit or grain. Natural food resources are defined as food items that the macaque would feed on without the presence of anthropogenic influence, such as invertebrates or locally occurring fruit (Thatcher, Downs and Koyama, 2020). These food resources were then further broken down into specific categories, as previous studies have not analysed the dietary diversity of rhesus macaques in an anthropogenic setting. Anthropogenic food was categorised into processed and non-processed food. Processed food is defined as any food that has been modified from its raw agricultural form (Poti *et al.*, 2015). Plants were identified using Plantnet (plantnet.org, 2024) taking a minimum of 3 photos of the leaves and bark and using species range data to ensure accuracy.

3.2 DATA ANALYSES

A total of 94.5 hours of observations were recorded across 567 different focal samples. Data from focal samples in each hour were averaged to calculate the hourly activity budget and the proportion of anthropogenic food in each hour. Activity budgets for age and sex classes were calculated using the total average percentage of time displaying in each behaviour. Each instantaneous sample of foraging was considered an independent sample when calculating food proportions. Unless otherwise stated in the

analyses, feeding behaviour encompassed all types of food acquisition behaviours as described in Table 1: feeding, foraging and drinking.

Statistical analyses were conducted in R Studio (R Core Team, 2024), using packages tidyverse and ggplot2. A one-way analysis of variance test was used to analyse hourly activity budget, and a TukeyHSD test to identify where the differences lay. A t-test was used to calculate differences in hourly proportion of anthropogenic food. Diet diversity was analysed using a Shannon Wiener Diversity Index. Proportion of individual food items were calculated as a percentage of total food items for each sex or age class.

3.3 ETHICS

All experimental procedures have been approved by Durham University Animal Welfare Ethical Review Board and follow the International Primatological Society Code of Best Practices For Field Primatology (Riley *et al.*, 2014). Protocols were designed in accordance with the Himachal Pradesh Forestry Department and complied with all Indian laws.

3.4 DATA AVAILABILITY

The datasets generated and analysed during the study are available from the authors upon reasonable request.

4 RESULTS

4.1 ACTIVITY BUDGET

A total of 567 focal samples were conducted, with 288 focal samples on adult female macaques (50.8%), 83 adult males samples (14.6%), 118 juveniles (20.8%) and 78 infants (13.8%), roughly equivalent to the adult sex ratios expected among macaque groups (Fooden, 2000). Urban dwelling rhesus macaque spend an average of 51.0% (±5.7) of the day resting, 20.2% (±3.9) foraging, 16.5% (±3.3) in locomotion, 6.9% (±2.6) grooming, 4.8% (±2.9) playing and 0.8% (±0.6) on other behaviours. Macaques spend significantly more time on certain behaviours than others ($F_{(5, 52)} = 253$, $p < 0.001$). Rhesus macaques spent significantly more time resting than any other behaviour (TukeyHSD, $p < 0.01$ for all behaviours). There is no difference in the amount of time macaques spend feeding and locomoting ($p = 0.21$), but they spend more time on either of these behaviours than grooming, playing or on other behaviours ($p < 0.01$). There is no significant difference between time spent playing or grooming ($p = 0.77$).

Macaques significantly vary their behaviour throughout the day (Figure 2). There is an increase in resting and grooming behaviour at 14:00 and 13:00 respectively, reaching a maximal of 60.7% and 10.4%. This coincides with a large decrease in the percentage of feeding and locomotion behaviours at 14:00, at a minimal of 13.1% and 11.5%. Play behaviour similarly varies throughout the day, although this is manifested by a sustained increase in the afternoon after 14:00 and reaching a peak of 9.0% in the evening at 17:00. This is especially significant as Figure 2 shows behaviours from all macaques, with infants and juveniles, the only age class observed playing, making up just 34.6% of samples.

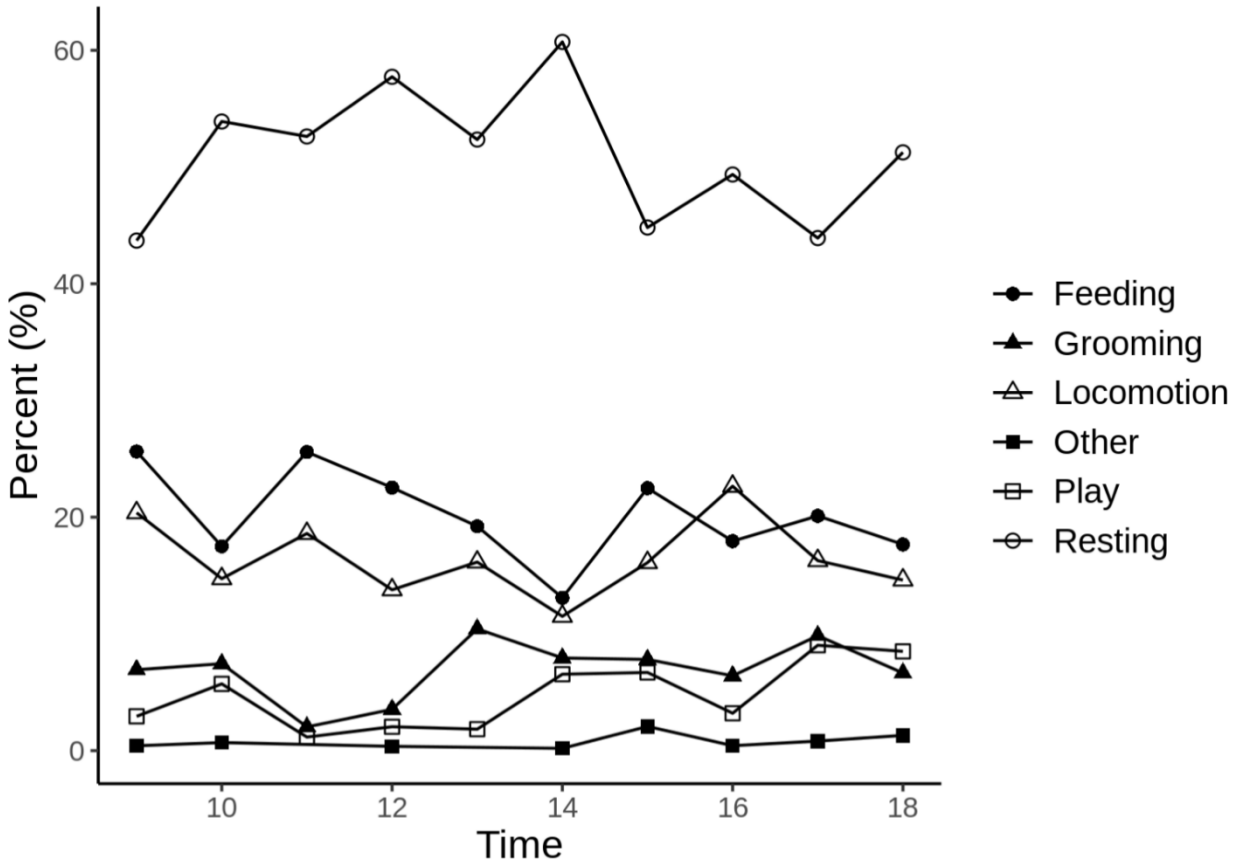

Figure 2. The diurnal activity budget of Rhesus macaques from 9:00 to 19:00 in Shimla city centre.

Sex- and age-specific roles play a great part in shaping the activity budget of Rhesus macaques. The sex and age of the macaque significantly impacts how much time is spent on each behaviour (Chi-squared test with Yates correction, $\chi^2 = 1041$, df = 15, $p < 0.001$) (Figure 3). Adult females spent the most time resting at 58.6%, closely followed by adult males at 51.9%, with immature macaques spending much less time resting at just 33.5% for juveniles and 46.1% for infants. The majority of grooming behaviours were observed in females, spending 11.8% of their time grooming. Females most often groomed other females, only sometimes grooming juveniles and infants. There were only eight instances of a male grooming a conspecific, constituting 2.7% of males' activity budget, all of which were directed towards females. There are little differences in amount of time feeding in females and infants at 17.7% and 17.3% respectively. Juveniles spent more time feeding at 22.5%, but males spent by far the most amount of time feeding at 26.1%. This does not, however, correlate to amount of time locomoting, which one might assume is linked, as finding food sources, especially anthropogenic ones, requires movement between buildings, walls and trees. Infants and juveniles spent the most time locomoting, at 23.8% and 22.6%, while males spent slightly less at 17.7%, and females who spend the most amount of time resting and grooming, unsurprisingly spent just 11% moving. Play was only observed in infants and juveniles, who spend a large proportion of their time (12.4% and 17.5% respectively), playing.

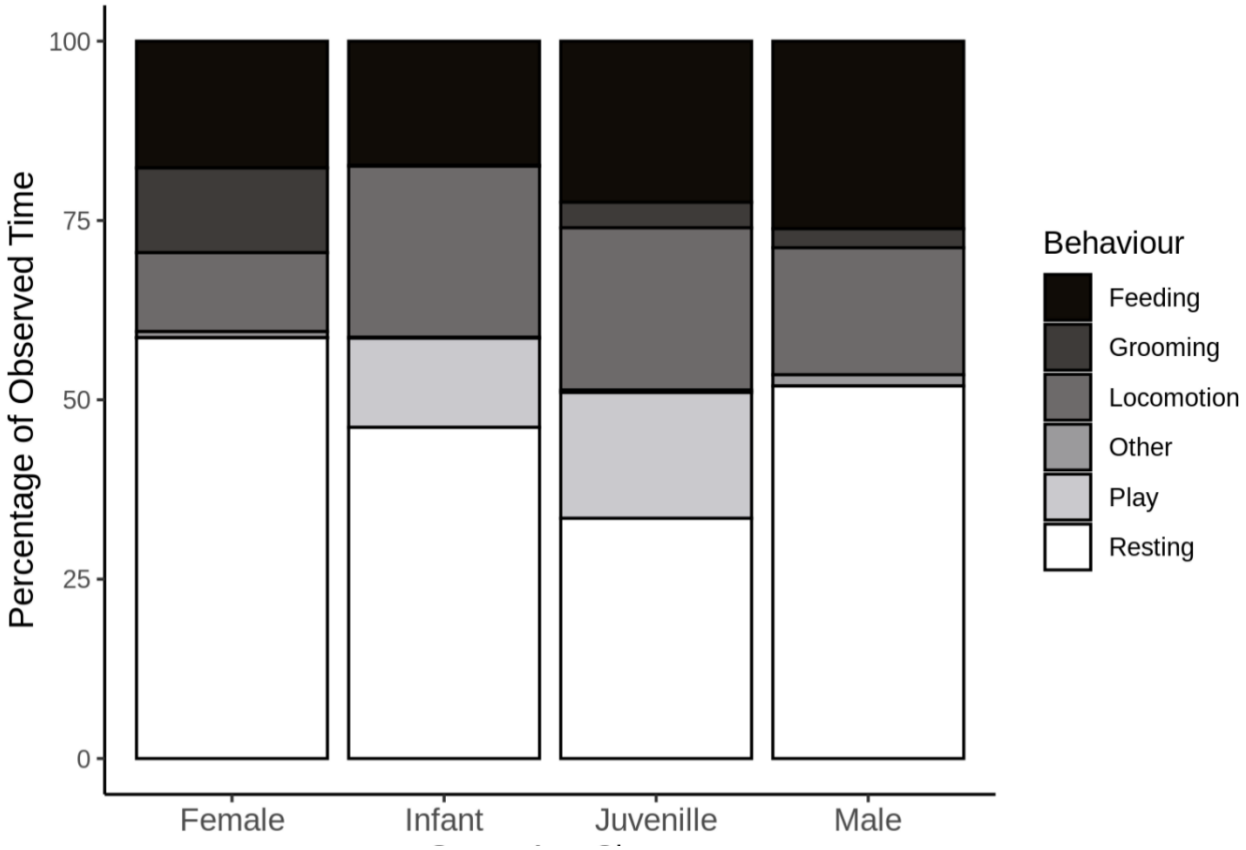

Figure 3. The activity budget of adult female, adult male, juvenile and infant Rhesus macaques. Shows average percentage of observed time spent on each behaviour from 9:00 to 19:00.

4.2 DIET AND FOOD SOURCES

A total of 48 food items were foraged upon by Rhesus macaques, 36 of these items anthropogenic, and 12 natural. 61.0% of the food sources Rhesus macaques feed upon are anthropogenic, compared to just 39.0% from natural food sources. The proportion of anthropogenic and natural food sources fed upon by macaques varied throughout the day evident by an increase in anthropogenic food sources foraged upon on at midday (11:00 to 13:00) and late afternoon (16:00 to 17:00) (Figure 4). Urban rhesus macaques feed upon anthropogenic food sources significantly more than natural food sources ($t = -4.84$, $df = 18$, $p < 0.001$), when comparing adult male, adult female and juvenile macaques. Infant macaques were excluded from this analysis because of their consistent high reliance on their mother's milk.

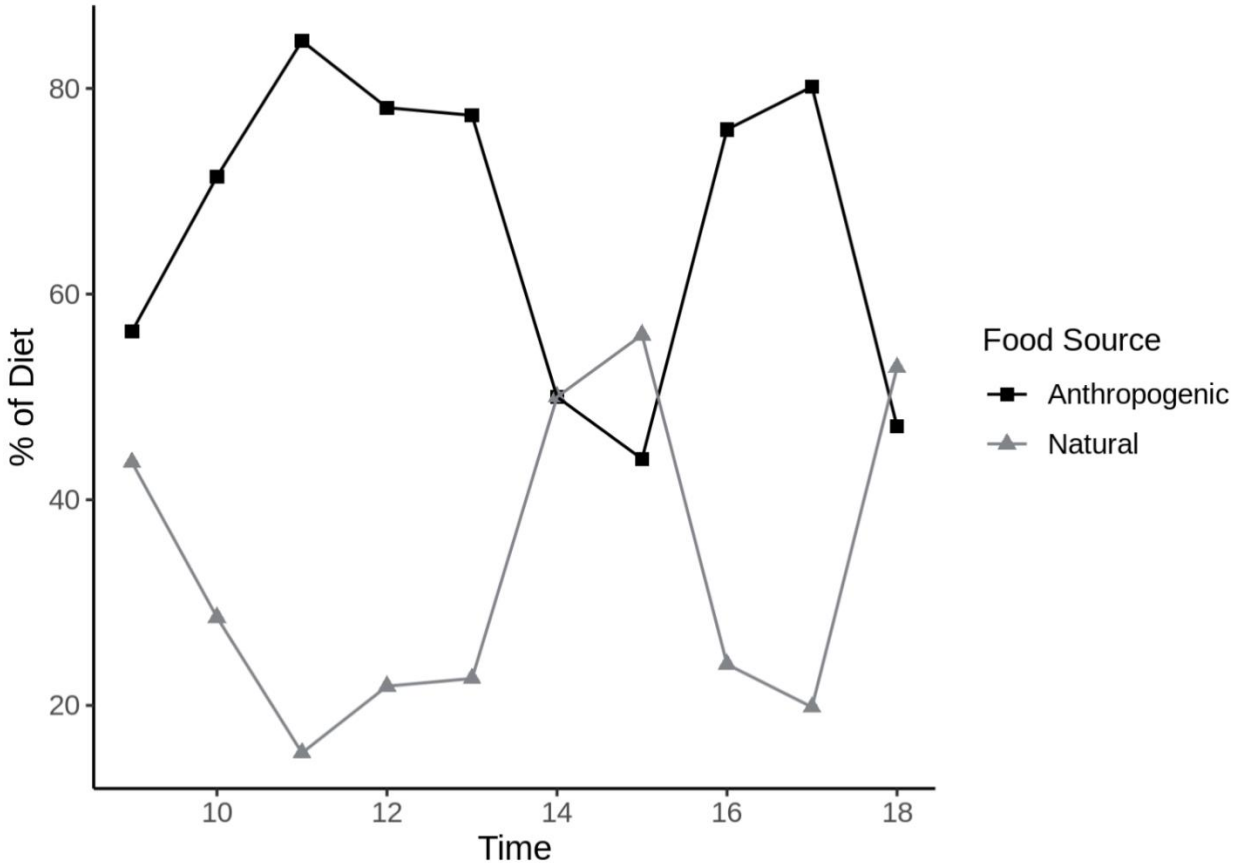

Figure 4. Percentage of anthropogenic and natural food sources urban Rhesus macaques feed on from 9:00 to 19:00, in adult male, adult female and juvenile individuals combined.

Plants were the only natural food sources observed by Rhesus macaques to feed upon, except for infants suckling on their mothers. Leaves and grass made up 35.4% of macaques diet, across a total of 11 plant species. The main species foraged upon are as follows (in adult females, adult males and juveniles): Cypress (*Hesperocyparis lusitanica*, 25.9%), Deodar cedar (*Cedrus deodara*, 22.2%), Spanish boxwood (*Buxus balearica*, 11.1%), Indian horse-chestnut (*Aesculus indica*, 7.4%), Triputree (*Tipuana tipu*, 7.4%) and Monkey pod tree (*Samanea saman*, 3.7%).

Age and sex specific factors have little impact on diet diversity (Shannon-Weiner Index), except for infants which subsist on 80% from their mother's milk having a far lower diversity (Table 2). These factors did, however, largely influence the specific food items within a diet. Males had by far the highest percentage of anthropogenic and processed food sources at 75.4% and 55.9% respectively than any other class, characterised by highly sugary food items, notably ice cream consisting 22% of their diets, as well as a large proportion of anthropogenic fruit (12%) and grain (11%). Although females and juveniles had a 'healthier' diet, characterised by just over 50% anthropogenic food sources and less processed food sources than males, ice cream, anthropogenic fruit and grain still made up a significant proportion of their diet. Infants' diet, expectedly, is characterised by suckling accounting for 81% of feeding occurrences. Infants often practiced feeding upon other items, but were usually unsuccessful, except with grain with was frequently successfully foraged upon.

There were no observations of a macaque foraging upon other natural food sources such as fruit, flowers, invertebrates, roots or bark. Fruit and vegetables were consumed, but they all originated from an anthropogenic source. “Other” food sources include highly sugary and processed food items: crisps (2.2% of total food items), sugar balls (2.1%), biscuits (1.5%), nuts (0.7%), dumplings (0.6%), and popcorn (0.2%). A total of 36 anthropogenic food items were foraged on. We observed 92 occurrences of macaques feeding on fruit, and although anthropogenic fruit makes up an average of 10.8% of Rhesus macaques diet, just three fruits were observed being fed upon: 41.3% apples 41.3% mango, and 17.4% banana, and vegetables were almost exclusively comprised of corn on the cob. We additionally observed 25 instances of a macaque drinking or feeding upon a sugary drink, predominantly 52% fruit juice, 24% cola, 16% lemonade and one occurrence of mountain dew and milk. The macaques were also observed drinking from bottled water by piercing the bottle and drinking the spilt water from the floor, although this has been excluded from the analysis.

Table 2. A summary of urban Rhesus macaque diet showing the proportion of anthropogenic and processed food in their diets, and the exact food items that are commonly foraged upon.

		Female	**Male**	**Juvenile**	**Infant**
Shannon’s Diet Diversity Index		2.19 (n = 13)	2.2 (n = 12)	2.03 (n = 13)	0.65 (n = 5)
% Anthropogenic food		58.2	75.4	56.6	15.5
Percentage of anthropogenic food that is processed		39.1	55.9	33.5	14.3
Food Item	**Food Type**				
Leaves	N	24	21	34	-
Grass	N	15	4	5	1
Mother’s Milk	N	-	-	5	81
Grain	A	14	11	14	14
Ice Cream	A	7	22	8	-
Fruit	A	9	12	14	-
Bread	A	11	10	9	2
Vegetable	A	7	6	1	-
Sugary Drink	A	1	2	7	2
Other	A	12	12	3	-

4.3 FOOD ACQUISITION AND AGGRESSION

Although not quantified in this study, the majority of anthropogenic food sources were acquired through stealing from or provisioning by a human. Therefore, urban Rhesus macaque foraging results in

a high rate of human interactions, as 61% of their food sources are anthropogenic. This results in a high occurrence of macaque-human conflict within Shimla city centre, especially in food items which were stolen. Foods valuable to people were often the items stolen: ice cream, bread, fruit and vegetables. Some anthropogenic food items were provisioned and includes all the grain and som bread. Most anthropogenic food acquisition was through stealing or snatching behaviours, often aggressive. Only some anthropogenic foods were foraged for, with macaques frequenting bins as a source of fruit, rubbish and other anthropogenic food sources.

Feeding behaviour encompasses all feeding, foraging and drinking related behaviours. Subdividing feeding results in 86% of the time feeding, 9% foraging and 5% drinking. Water was most frequently drunk, typically from water butts on roofs, but occasionally from the floor following rainfall.

Figure 5. The diet of the urban Rhesus macaque contains a high percentage of anthropogenic food sources. Rhesus macaques feeding on stolen food items: (A) ice cream, (B) bag of bananas, (C) roti, (D) foraging in a bin, (E) ice lolly, (F) licking spilt fizzy drinks.

5 DISCUSSION

This study employed a comparative approach to examine the activity budget of urban-dwelling rhesus macaques to determine the influence of the urban environment on the rhesus macaques' behaviour and dietary habits when compared to previously studied wild populations. The findings contribute to the

understanding of the species' behavioural flexibility and may help inform wildlife management plans in urban areas.

5.1 ACTIVITY BUDGET

The observed macaques allocated the majority of their time resting (51%), followed by foraging (20.2%) and locomotion (16.5%). These results align with Jaman and Huffman (2013) who reported resting comprised 46% of the activity budget of urban dwelling-rhesus macaques in Bangladesh, with feeding the next highest at 22.4%.

Comparatively, non-provisioned rural populations of rhesus macaque exhibit significantly less time resting, such as 36.8% (Jaman and Huffman, 2013) and 42.1% (Tang *et al.*, 2017). Similar results across other rural macaque species also demonstrate lower proportions of time spent resting (Hanya, 2004; El Alami *et al.*, 2012; Hambali, Ismail and Md-Zain, 2012; Li *et al.*, 2020; Zhou *et al.*, 2022). This disparity suggests that the urban environments, abundant in high-calorie reliable food sources, allow macaques to satisfy their individual energetic needs quickly, allowing more time for non-essential activities such as increased resting. This highlights the significant role anthropogenic food, and the urban environment play in the urban macaques' activity budgets.

Interestingly, observations of grooming and locomotion were reversals of what was observed in Jaman and Huffman's (2013) study. They found the amount of time spent grooming (16.5%) was higher than locomotion (10.8%), compared to our results which revealed 6.9% and 16.5% of the activity budgets respectively. This may reflect differences in the spatial distribution of anthropogenic food sources when compared to Jaman and Huffman's (2013) study site. Studies have shown that both long-tailed macaques (Hambali, Ismail and Md-Zain, 2012) and urban capuchins (Back, Suzin and Aguiar, 2019) exhibit increased locomotion when anthropogenic food sources are available but scattered compared to natural food sources. This is because the primates show a preference for human food and thus spend more time searching for it. This preference can be seen in the Shimla macaques we observed, who demonstrated a clear preference for anthropogenic foods which made up 61% of their diets, despite natural food resources being reliably scattered across the city centre in various green spaces such as parks. This preference, coupled with the hilly terrain of Shimla, meant anthropogenic food sources were more spread out compared to Jaman and Huffman's (2013) study which occurred in a relatively flat landscape. This necessitated greater time spent locomoting to acquire anthropogenic food. Additionally, the reduced time allocated to grooming may reflect heightened vigilance due to human interaction, as Kaburu *et al.,* (2019) observed shorter grooming bouts due to frequent human interaction. This heightened vigilance in macaques is evidence by the macaques' preference for resting locations in elevated or secluded areas such as roofs and trees to avoid human interaction.

Although feeding behaviour was at its lowest in the early afternoon which coincides with increases in resting and grooming, it did not vary greatly throughout the day (from 17.5% to 25.6%), indicating that urban macaques have a more stable daily activity budget than rural macaques who are influenced by thermoregulation (Zhou *et al.*, 2022), and thus base their activity budgets around maximizing foraging

efficiency by ingesting more food at lower temperatures when the requirement for thermoregulation is greater. Urban macaques appear less affected by natural seasonal and daily variations, likely due to their consistent access to urban resources.

5.2 SEX-AGE CLASS DIFFERENCES

Age and sex differences were evident in activity budgets. Females devoted the lowest proportion of their daily activity budget locomoting, at only 11%, almost half compared to males at 17.7%. This was due to the higher proportion of time they spent resting and grooming, 58.6% and 11.8% compared to males at 51.9% and 2.7% respectively. This is consistent with Kaburu *et al*., (2019) who also found females maintained higher levels of grooming than males in urban environments. Kaburu *et al.,* (2019) suggest that this is due to female rhesus macaques being the core of the social group and female-female grooming key to maintaining the stability of the social group. These behaviours reflect the matrilineal, highly despotic, and intolerant group structure (Mielke *et al.*, 2021), with a high bias towards kin relationships. In this social structure, maintaining strong social bonds in the steep dominance hierarchy is important as they are highly influential on individual life history, health and fitness (Cooper *et al.*, 2022). Furthermore, nonkin bonds also impact fitness and are vital in the social relationships of female rhesus macaques (Mielke *et al.*, 2021). These social bonds are most often maintained through grooming and thus, the high investment in time spent grooming for females compared to males reflects the importance of social bonds. The timing of the study, shortly after the birthing season, likely accentuated this trend, as many adult females were caring for an infant, meaning maintaining social bonds with female kin who might be able to help would be important to reduce mothers' stress. Moreover, females across macaque species are attracted to infants and tend to groom mothers to access them (Gumert, 2007; Jiang *et al.*, 2018). This can be seen through the lens of the biological market theory, specifically, the infant market, where increased grooming increases the probability of handling infants (Tiddi, Aureli and Schino, 2010; Jiang *et al.*, 2018).

Males, conversely, were rarely observed grooming (2.7%) consistent with the fundamental differences behind the motivation for social bonds, which is linked to reproductive success (Schülke *et al.*, 2010). Another possible reason for this may be that high-ranking males are dominant over females and subordinate males so don’t need to dedicate as much time (Jaman and Huffman, 2013). This difference between time spent grooming in males and females is what we expect to see in both non-urban populations, highlighting the importance of social bonds to maintain group structure in rapidly changing urban environments.

Males spent the most time of any age-sex class feeding at 26.1% of their daily activity budget. This was also observed by Jaman and Huffman (2013) where urban males spent more time feeding than females, unlike their rural counterparts. This is likely due to the tendency of males to take risks by interacting with humans to access high-calorie anthropogenic foods, as the benefit of obtaining anthropogenic food impacts their competitive ability and reproductive success (Balasubramaniam *et al.*, 2020). This contrasts with females whose competitive ability is reliant on kinship and social bonds, whilst male fitness is dependent on physical features such as body size (Balasubramaniam *et al.*, 2020). Such differences exemplify how urban environments distinctly influence male and female activity patterns.

Whilst the increased calories in anthropogenic food allow females to spend less time feeding to prioritise social bonding and rest, males capitalize on the higher calorie food and instead increase time feeding.

Juveniles and infants allocated significant portions of their activity budgets to play (12.4% and 17.5% respectively), highlighting its developmental importance. This is notably higher than Jaman and Huffman (2013) findings, where immature macaques spent around 10% of their time playing. This increase in play may reflect the high-calorie anthropogenic diets of the Shimla macaques, allowing them to divert more of their energy to play behaviours.

5.3 DIET PREFERENCES

Overall, 61% of food sources were anthropogenic, indicating a preference for readily available and calorie-dense anthropogenic food such as grain and human snacks which was regularly provisioned. This matches the expectations set out at the start of the study that the food would be higher in calories and predictably accessed. This increases the value of the anthropogenic food sources to the macaques; thus the macaques are more incentivised to seek out these food sources.

Anthropogenic food consumption peaked in the morning and afternoon, possibly due to the risks associated with human interactions, such as aggression. The city was much busier in the early afternoon and coupled with the temperature rise, the macaques primarily rested around from 14:00 to 16:00. The macaques tended to rest further away from the main road, and thus there were more natural resources available, resulting in a decrease in anthropogenic food eaten. However, these foraging peaks may be the results of natural processes as a similar pattern of foraging in the morning and afternoon with a midday rest was also observed in unprovisioned Tibetan macaques (Zhou *et al.*, 2022). The authors explained this was due to the importance of thermoregulation as well as digestion time when eating fibrous foods. In the urban context however, it is more likely to be due to the risks of interacting with humans, as the fibre in the urban macaques' diet was greatly reduced compared to that of a rural macaque.

The macaques exploited a high diversity of anthropogenic food sources, with little difference between age-sex classes (Shannon's Diversity Index was 2.19 in females, 2.2 in males, and 2.03 in juveniles). Infants exclusively drank their mother's milk and thus had the lowest Shannon's diversity index score (0.65). The macaques exploited a large number of anthropogenic food sources compared to natural food sources, 36 and 12 respectively. The number of anthropogenic food sources is similar to other studies where macaques subsisted on 32 items of anthropogenic food (Ram, 2020), however macaques in our study subsisted on far fewer plant species than other studies. Estimates range from 52 (Zhou *et al*., 2024) to 104 (Ram, 2020) species of plants in Rhesus macaques diet compared to our estimate of 11 plant species. This is partially thought to be due to the altitude of Shimla at 2,276 m, as higher altitude is correlated lower plant diversity. Studies of Rhesus macaques found groups foraged on 102 species of plant at 225m elevation compared to just 35 species at 2360m, (Poti *et al*., 2015; Ram, 2020; Li *et al*., 2022), although this is still far higher than our study in Shimla. Another reason for low plant species richness is the observational procedure we adopted, as only high human density areas were sampled where there is little plant diversity, and focal samples were conducted some some distance from the

surrounding deodar forest, which the macaques likely also exploit for additional plant food sources. The macaques true diet diversity and nutritional intake are likely higher than estimated in our study.

Male macaques ate the highest percentage of anthropogenic food, totalling 75.4% of their diet. They also ate the most processed food, at 55.9%. This anthropogenic food was higher in calories than natural food, with ice cream making up over a fifth of their diet, with an adult male macaque spending on average 31 minutes feeding on ice cream each day. Whilst they also ate a lot of anthropogenic fruit, the nutritional value of these is very different from wild fruit as they have been bred for palatability and sweetness, making the anthropogenic fruit higher in sugar and energy, but lower in fibre and nutrients than non-anthropogenic fruit (Cabana, Jasmi and Maguire, 2018). The average of 10.8% anthropogenic fruit in their diet is still far lower than the ~70% of natural fruit that makes up some Rhesus macaque diets (Sengupta and Radhakrishna, 2016) but likely fills the same role in their diet. The overconsumption of anthropogenic, high-calorie foods has negative impacts on the macaque's health as it has been found that high fat/sugar and low fibre diets contribute to high incidences of obesity in primates (Duarte *et al.*, 2015) as well as other diseases such as gastrointestinal and dental diseases as well as contributing to diabetes (Cabana, Jasmi and Maguire, 2018). Females, whilst consuming slightly less anthropogenic food (50%), were similarly increasing their consumption of this high in sugar and low in fibre diet, exposing them to the same risks. Furthermore, there were 35 instances of macaques drinking a sugary drink such as fruit juice or cola, furthering the risk associated with a high sugar diet. Juveniles had a primarily anthropogenic diet and often ate similar food to the adult macaques around them, especially their mothers, reflected in their anthropogenic intake being 56.6% which is more similar to the average female (58.2%) than the male (75.4%). It has been found that maternal nutrition and environment impact the quality and composition (Hinde and Milligan, 2011), so the inappropriate anthropogenic diet the female macaques are consuming may also harm their offsprings heath.

Natural food consumption was minimal (39.0%), limited to leaves and grass, despite other natural resources being available in the city centre such as flowers, roots, invertebrates and bark. This stark preference for anthropogenic food underscores the significant behavioural and dietary shifts associated with the urban-dwelling macaques. This has the potential to significantly impact the urban macaques' health.

The need for wildlife management interventions to mitigate the negative impacts of urbanisation on these urban macaque populations is therefore urgent. Future research should focus on the health of Rhesus macaques and investigating the long term impacts of a high sugar high calorie diet, possible only through studies spanning multiple years. This could be achieved through looking at macaque oral health, as this is biuniquely correlated with a healthy balanced diet, through investigating macaque weight changes year on year, or looking at mating success of macaques in a highly urbanised environment. A possible solution to improve macaque health is by mitigating human-macaque conflict, with wildlife management strategies such as education, hazing, or macaque sterilisation programs all possible. Large success could be achieved through reducing the availability and accessibility of commonly foraged upon anthropogenic food sources by macaques as outlined by this study. This provides less incentives for macaques to utilise in urban areas as the diverse and calorie rich food sources which are plentifully available are the biggest incentive that drive macaques into urban environments. Education surrounding

provisioning of macaques is also crucial here to impede macaque acquisition of anthropogenic food sources and should be a focus of future research. This would not only reduce human-wildlife conflict, but also improve the health of the macaques. This study therefore provides insight into why Rhesus macaques not only survive, but thrive in urban environments, and are one of the few success stories of the Anthropocene.

6 REFERENCES

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