Can urbanization accentuate hand use in the foraging activites primates?

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ABSTRACT How a species differentially uses its appendages is determined by anatomy and physiology at a proximate level and by phylogeny and ecology at an ultimate level. Primates are often distinguished by their prehensile capabilities and manual dexterity characterized by complex skeletomuscular architecture, interconnected sensory systems and congruous cognitive mechanisms. However, species-specific predispositions and task-specific requirements can lead to differential use of anatomical manipulators. Theoretical explanations for intraspecific variation in the use of mouth and hands by nonhuman animals is non-existent. In context to the intense pressures of urbanization on natural habitats, we examined if hand and mouth use differed across the rural-urban gradient in tasks at the extreme ends of the complexity spectrum, food retrieval (simple) and food processing (complex and hierarchical) under experimental conditions in bonnet macaques (*Macaca radiata*) and more generally, under naturalistic conditions in an additional two primate species (Japanese monkey,*Macaca fuscata* ; vervet monkey, *Chlorocebus pygerythrus*). The use of hands in both tasks increased with urbanization and the converse was true for the use of mouth under experimental conditions. Even under naturalistic settings, all examined species of urban primates showed a bias in hand use during food acquisition. Thus, it appears that the adaptive pressures of urbanization, like the manual constraints of extracting packaged food and perhaps the need for visual-haptic exploration of novel objects accentuates hand use in even simple tasks among synanthropic groups of nonhuman primates. Additional research is needed to determine specific factors of urbanization influencing the trend observed and to ascertain similar patterns in other primates occupying forest-urban niches.

KEYWORDS hand use, packaged food, urbanization, synanthropic species

INTRODUCTION

The ecological conditions under which prehension and their concomitant anatomical, physiological and neurobiological correlates have evolved in tetrapods have been under intense investigation since the beginning of the 20th century (Fragaszy & Crast, 2016; Pouydebat & Bardo, 2019; Sustaita et al., 2013). Within the literature on prehension in anthropoids, manual grasping (reach and retrieval) and manipulation have received the most attention due to their direct implication on intelligence, cognitive development (DeLoache, 2000; von Hofsten & Rosander, 2018) and encephalization (Gibson, 1986) and the indirect implications on the evolution of our own species (e.g. Iriki & Taoka, 2012; Johnson-Frey, 2004; Ramayya et al., 2010). Though a general consensus exists on the complex selective pressures leading to the evolution of grasping, like arboreal locomotion (jump, grasp-leaping) and feeding on precarious substrates (Fragaszy & Crast, 2016), few studies have highlighted the need for greater attention to ecological factors in addition to other factors (morphological, cognitive and physiological) that 'first promoted hand use or advanced the diversity of prehensile capabilities' (Pouydebat & Bardo, 2019; e.g. Peckre et al., 2016; Toussaint et al., 2013). Additionally, almost all studies on grasp, grip, reach, retrieval and acquisition in anthropoids have focused on describing phylogenetic similarities/dissimilarities within an ecological context to build an evolutionary model of limbic specialization and skilled dexterous movements. Surprisingly, selective forces on food acquisition operating across heterogeneous populations of a species have never been investigated.

Considering unabated habitat modification and rampant urbanization throughout the ranges of different primates (Estrada et al., 2017; Mittermeier et al., 2006), we were interested in studying the adaptive pressures of urbanization on food retrieval and food processing in primate groups distributed across the urban-forest gradient. The pressures of urban survival in synanthropic groups of primates have led to dietary expansion (Corrêa et al., 2018; Thatcher et al., 2020), foraging on packaged processed food (Kaplan et al., 2011; Katlam et al., 2018) and complex foraging skills (e.g., Brotcorne et al., 2017; Mangalam & Singh, 2013) among other facilitatory transformations like object neophilia (Forss et al., 2015), explorative tendencies and innovative ability (Dhananjaya et al., 2021; Huffman & Quiatt, 1986). Since manipulative abilities and dexterity presumably coevolved with foraging on embedded/encased food (Gibson, 1986; Melin et al., 2014; Parker & Gibson, 1977; Van Schaik et al., 1999), we reasoned that the demands of extractive foraging from packaged artificial food in an urban environment would accentuate the use of hands relative to non-urbanized groups under foraging contexts. Concomitantly, we selected two behavioral actions differing in their manipulative complexities and demands, namely food acquisition (FA) and food processing/extraction (FP) to evaluate the effects of urbanization and dietary dependence on food items that are commonly packaged. Food acquisition entailed the action of collecting food that is typically accomplished either with the mouth or with the hand in anthropoid species (Schwenk, 2000), whereas food processing/extraction is a relatively complex behavior composed of hierarchical sequence of mental, perceptual and motor elements varying in degree of oral-manual dexterity (Russon, 1998; Stokes & Byrne, 2001; Trébouet et al., 2018). Plucking a fruit from a plant is an example of food retrieval while deshelling and depeeling a peanut are examples of food extraction and food processing, respectively (Dhananjaya et al., 2021). Firstly, we offered a food retrieval and a food extraction/processing task to three social groups of bonnet macaques (*Macaca radiata*) differing in urbanization within a standardized experimental condition. Secondly, we developed a framework for evaluating naturalistic instances of food retrieval and food processing from foraging and

feeding videos of additional primate species followed by characterizing urbanization of their habitat and encounter with packaged food. We anticipated higher hand use among more urbanized groups and groups with higher probability of encounter with packaged food during food retrieval and food processing.

MATERIALS AND METHODS

Experimental condition

We selected three groups of bonnet macaques from a set of 24 groups located around the city of Mysore, India (Erinjery et al., 2015) based on their exposure to anthropogenic packaged food (Bull temple group-High, Foot hill group-Moderate, T. Betahalli group-Low). Based on home range, habitats of the 3 groups could be also classified along the urban dimension based on built up area in the following manner: Bull temple group-Urban (>50% built-up area), Foot hill group-Semi urban (10-50% built up area) and T. Betahalli group-Rural/Natural (>10% built up area). All the groups have been under intermittent monitoring for over 25 years and hence their feeding ecology and access to sources of artificial enclosed food was adequately known (see Dhananjaya et al. (2021) for details on study groups). We offered an extractable food item, peanut (native form with intact shell) on terrestrial substratum to isolated and passive macaques and recorded their use of hand/mouth to acquire peanut and to process peanut (see Dhananjaya et al. (2021) for detailed experimental design). The experiment was conducted in three phases involving a single group in each phase and behavioral responses were recorded using camcorders (Sony DCR-SX21, Sony DCR-DVD 650 and Sony HDR-CX405).

Video analyses of naturalistic food acquisition and food extraction/processing of primate species

Hill (2018) compiled a list of 113 primate species that forage on cultivars and we have enlisted at least 16 primate species that are known to subsist around urban landscapes. We mined videos of 3 primate species from video databases/archives such that they spanned the urban-forest gradient alongside the possibility of acquiring packaged artificial food. Videos obtained covered foraging and feeding by primates in as many microhabitats of each species as possible and included their natural habitats (e.g., temperate evergreen forest, savanna), altered habitats (e.g., botanical garden, nature-park, linear structures through forests) and anthropogenic habitats (e.g., farmland, tourist spots, residential areas). Based on availability of videos and all relevant information, we included the following cercopithecid species in the analyses: bonnet macaque (*Macaca radiata*), Japanese macaque (*Macaca fuscata*) and vervet monkey (*Chlorocebus pygerythrus*). Several widespread primate species (e.g., rhesus macaque, long-tailed macaque) could not be included in the analyses due to inadequate video records or habitat representation(s).

We identified the year of video recording/uploading and the geographical location of the primate group(s) based on the metadata of video. Among videos containing foraging and feeding incidences, we shortlisted instances in which food items met the conditions described in Table 1. The conditions for food inclusion were based on delimiting the overlap of mouth use and hand use for FA and the overlap of mouth use, hand use and hand-mouth use for FP. Most conditions elucidated in Table 1 were based on research literature on grasp, food acquisition, reach-for-food and reach-for-grasp in primates (e.g. Peckre et al., 2019; Pouydebat & Bardo, 2019; Sustaita et al., 2013). The remaining conditions were determined based on the

logical evaluation of an equal likelihood of hand/mouth use in FA and FP with regard to species-food pairs. Several covariates including variables for habitat (urbanization, packaged food), individual characteristics (age), foraging style and characteristics of food (attachment, embeddedness) were considered. The description and inclusion/exclusion criteria of each covariate are provided in Table 2. The covariates and their scopes described in Table 2 were also drawn from published materials (e.g. foraging style: Le Gros Clark, 1959; Szalay et al., 1987; Van Horn, 1972; age: Colell et al., 1995; food size/shape: Peckre et al., 2019; Reghem et al., 2011; food consistency: Peckre et al., 2019; material texture: Yokoi et al., 2018; prey mobility: Peckre, Lowie, et al., 2019; Toussaint et al., 2013; foraging substrate: Fabre et al., 2017; Peckre, Lowie, et al., 2019; Toussaint et al., 2013). Two researchers (TD and SD) naïve of the habitat and 'encounter with packaged food' characterization of the groups in the videos coded a random set of videos to (1) standardize the coding framework mentioned in Table 2 and to (2) evaluate inter-coder consistency in identifying hand/mouth use for FA and FP, age, foraging style, food embeddedness and food attachment, i.e., attachment of the fruit to the plant. To characterize the degree of exposure to packaged anthropogenic food, we obtained information from either researchers familiar with the groups, videographers, published/unpublished research, residents of the region and/or from the narration in the videos.

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`Table.docx` available at https://authorea.com/users/440139/articles/540910-can-urbanization-accentuate-hand-use-in-the-foraging-activites-primates

Statistical methods

Comparison in oral and manual FA and oral, manual and oral-manual FP across extent of encountering packaged food under experimental conditions were done using the test of multiple proportion. For similar comparisons in the non-experimental scenario, we either applied multilevel binary logistic regression or permutation test depending on fulfillment of statistical criteria. Test of multiple proportions was carried out in Statistics Toolkit (StatsToDo, 2020), binomial logistic regression and permutation test were done in RStudio *v.1.4.1717*(RStudio Team, 2021) and effect size index (Cohen's d) was computed in an online effect size calculator (Wilson, 2001) based on Lipsey and Wilson (2000).

While analyzing data from naturalistic settings (non-experimental condition) for FA and FP, we treated each species separately. Due to near complete separation of hand and mouth use in FA along encounter with packaged food and urbanization in all species except vervet monkey, multilevel regression generated singularities and therefore, a permutation-based chi-square test was applied with *chiperm()*function in the *GmAMisc* package (Alberti, 2021). Hypotheses testing in vervet monkeys (1) modeled the distribution of FA as negative binomial using *glmmTMB()* function in the *glmmTMB* package (Brooks et al., 2017), (2) performed model diagnostics using*testDispersion()* and *simulationOutput()* functions in the*DHARMa* (Hartig, 2021) package and (3) selected optimal model based on Burnham and Anderson (2002).

RESULTS

Experimentation on bonnet macaques with peanuts and examination of naturalistic foraging/feeding behavior in bonnet macaques, Japanese macaques and vervet monkeys revealed a high expression of hand use among urban groups (i.e., synanthropic groups) to acquire food which inevitably, also have a high encounter

rate of packaged artificial food. Conversely, mouth use is relatively more prevalent among groups that are hardly exposed to packaged food and subsist under natural conditions. Despite the predominant combinatorial use of hand-mouth during extractive foraging of non-hard food items by primates, relative prevalence of hand use is maintained while deskinning a peanut under experimental condition but only in the urban group. Similar to the trend of mouth use observed in FA, even during peanut processing the rural group used their mouth more frequently relative to other groups.

Hand and mouth use during food acquisition and food processing under the experimental condition

All macaques acquired peanut either with their hand or mouth. We recorded 861 instances of FA by 76 individuals distributed across urban (N=160), semi-urban (N=553) and rural (N=148) groups. The use of hand during FA was comparable between urban and semi-urban groups, both of which were higher than the rural group (*FA by hand* ; Urban(P=160/160) = Semi-urban(P=551/553) > Rural(P_L=141/148); χ^2=23.61, df=2, p<0.0001; Cohen's $d_{\text{Moderate-Low}}$=0.426) (Fig. 1).

Extraction of nut from the shell was largely accomplished by the use of mouth and hand(s) and did not vary across the experimental groups. As a result, we focused our attention to deskinning of the extracted nut. Although, the occurrence of skin removal varied across groups (see Dhananjaya et al., 2021), monkeys removed the skin of peanuts either by using their hands, by using the tongue against mouth palate or by nibbling with their teeth while supporting the peanut with either, a single hand or both hands. From the perspective of organ use, the primary agents of peeling were the hands, the mouth and both, hand and mouth (hand-mouth). A cumulative record of 763 instances of peanut extraction was recorded, of which 197 were from the urban group, 396 were from the semi-urban group and 170 were from the rural group. Peels of peanuts were removed by exclusively using hand(s), exclusively within the mouth or a combination of hand and mouth. Use of hands to remove peel of peanut was the most widespread in the urban group, followed by the semi-urban and the least in the rural group (*FP by hand:*High(P_H=92/197) > Moderate(P_M=5/395) > Low(P_L=0/170), whereas use of mouth to deskin peanut followed the reverse order (*FP by mouth:*Urban(P_H=31/197) < Semi-urban(P_M=230/395) < Rural(P_L=132/170); χ^2=154.28, df=2, p<0.0001; Cohen's$d_{\text{High-Moderate}}$=0.471). However, use of hand and mouth for FP was comparable between the urban and semi-urban groups and was the least in the rural group (*FP by hand-mouth:*Urban(P_H=74/197) = Semi-urban(P_M=160/395) > Rural(P_L=38/170); χ^2=17.32, df=2, p<0.001; Cohen's $d_{\text{High-Low}}$=0.498, Cohen's $d_{\text{Moderate-Low}}$=0.497) (Fig. 1).

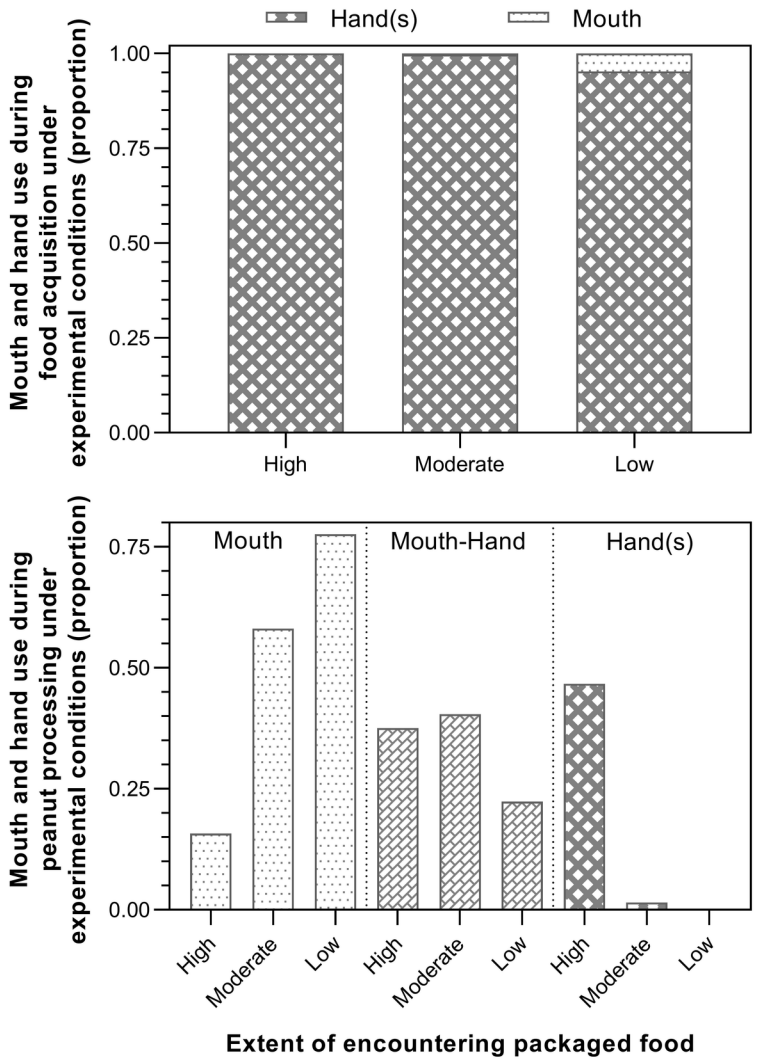

Figure 1: **Figure 1** Results of food acquisition and food processing task under experimental conditions. Proportionate use of hand and mouth during food acquisition across a gradient of encounter with packaged food is shown at the top and proportionate use of hand, mouth and hand-mouth during food processing across the same gradient is depicted below. a caption

Hand and mouth use during food acquisition under naturalistic conditions

We characterized encounter with packaged food and urbanization for 25 videos of bonnet macaque (BM), 5 videos of Japanese macaque (JM) and 10 videos of vervet monkey (VM) which resulted in 174, 282 and 130 instances of FA and FP, respectively. As a result of paucity of video records, all categories of encountering packaged food and urbanization were not adequately obtained for all taxa. Classification of food items considered in the analyses and their relative representation is shown in Figure S1. In addition, comparison

of hand/mouth use in FA between urbanization conditions with regard to individual food type show higher hand use in more urbanized groups than less urbanized groups (BM: fruit; JM-leaf and seed; Fig. S1), except for processed food in BM where hand use was equivalent between moderately urbanized and highly urbanized groups.

Inter-rater agreement based on a two-way random effects model (ICC(2,2), see Koo & Li, 2016) was over 0.86 (N=50) for each variable (age, foraging, attached, embedded and anatomical manipulator). We found near identical pattern of hand use during FA in every primate species we analyzed, i.e., higher hand use on higher encounter with packaged food and higher degree of urbanization. The dataset in bonnet macaques (BM) was devoid of any record of mouth use in the High categories of encounter with packaged food and urbanization and had the following trend in mouth use across both these variables, encounter with packaged food - High (P=0/75) < Moderate (P=18/73) and degree of urbanization - High (P=0/46) < Moderate (P=18/98) (Fig. 2). The illustration of Pearson's standardized residuals for bonnet monkeys in Figure 2 affirms the hand/mouth bias across High and Moderate categories in encounter of packaged food and urbanization. Assessment of FA in the Japanese monkey (JM) and vervet monkey (VM) showed a similar trend across encounter of packaged food (JM: High (P=0/93) < Moderate (P=15/51) < Low (P=73/127), Cohen's$d_{\text{Moderate-Low}}$=0.508; VM: High (P=4/49) < Low (P_L=11/33), Cohen's$d_{\text{High-Low}}$=0.527) and urbanization (JM: Moderate (P=15/144) < Low (P=73/127); VM: Moderate (P=4/50) < Low (P_L=11/33)) (Fig. S2 and Fig. 2). The alternate statistical approach, which modeled FA in the vervet monkey as a negative binomial distribution within a binary logistic regression did not find any influence of age, foraging style, food attachment and food embeddedness but extent of encounter with packaged food (Log likelihood(N=82)=-34.9; FA: Mouth (*ref.*); Encounter with packaged food: High (*ref.*); β_{Low}=-1.727±0.639SE, p=0.007; Table S1). The probability of FA using hands by vervet monkeys of the low encounter category decreased by a factor of 0.18 relative to vervet monkeys in the high encounter category (Table S1). Because the covariates of FA, extent of encounter with packaged foods and urbanization were correlated (Contingency coefficient=0.71), only one of the variables was used in the model.

Processing of embedded food typically involved peeling fruits/flowers/nuts and removing inedible portions of fruits/leaves, while extraction involved tearing garbage bags using hands, mouth or both (hand-mouth) in tandem. The use of hand during hand-mouth assisted extraction/processing also included situations where the hand has a passive role of supporting food as well as ones where the hand is actively involved in orienting/manipulating food (e.g., grabbing by hand while tearing with mouth) while in the mouth. Due to low sample sizes (N_{BM}=20, N_{JM}=11, N_{VM}=47) and insubstantial statistical representation across encounter with packaged food and urbanization, we could not analyze hand/mouth use during food extraction by any species.

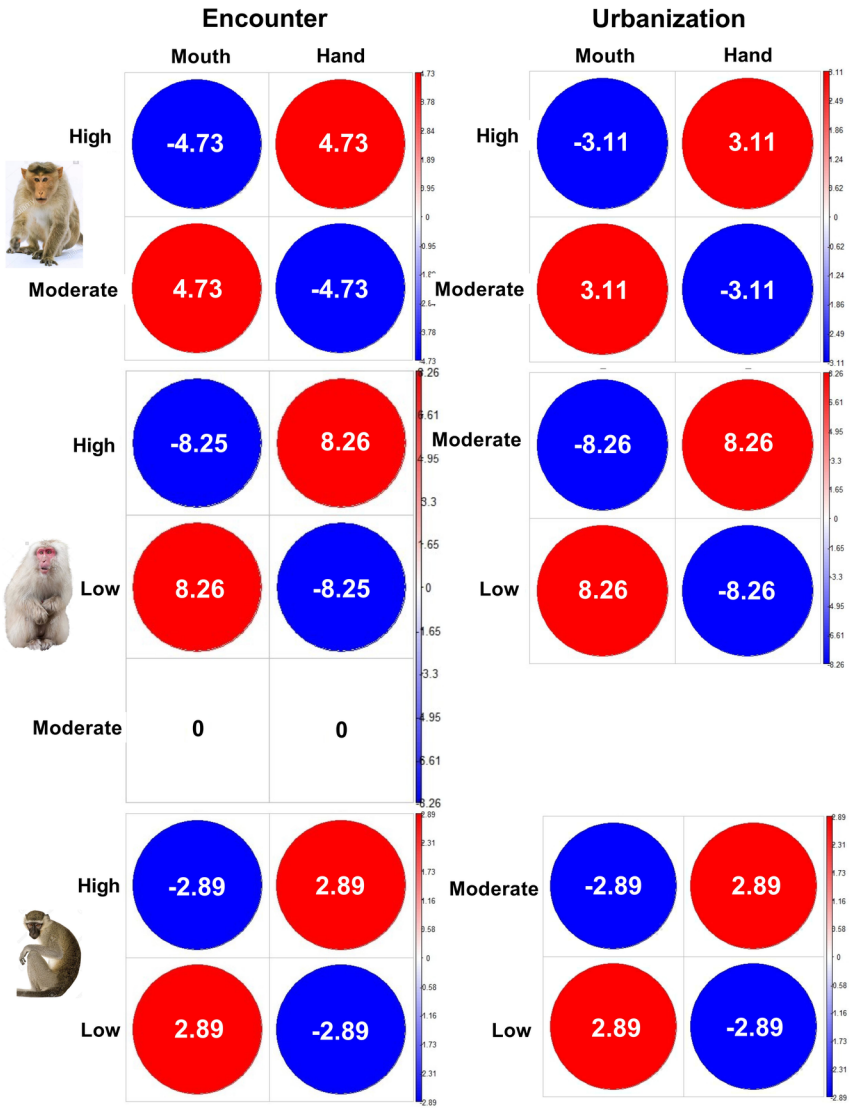

Figure 2: **Figure 2** Output of the permutation tests comparing hand/mouth use during naturalistic food acquisition is shown for bonnet macaque, Japanese macaque and vervet monkey across the gradient of urbanization and 'encounter with packaged food'.

DISCUSSION

Selective pressures modulating intraspecific differentiation in foraging associated hand/mouth use have never been reported in higher mammals. We demonstrated manual bias in food acquisition and in food processing across gradients of urbanization and exposure to packaged food through experimentation in a macaque species and retrieved an identical result on the evaluation of naturalistic foraging in additional cercopithecid species.

Hand and mouth use during food acquisition and food processing under experimental condition

The design of the experiment controlled for probable confounding (food size/shape/texture, food attachment, food embeddedness) and direct variables (foraging style) that are known to affect differential use of hand and mouth during FA and their combination during FP at the species level. Conducting the experiment across a gradient of urbanization and alternately, dietary dependence on packaged food allowed independent examination of these two factors. The dietary dependence of the urban group on packaged foods as well as their tendency of tactile exploration, manipulation of artificial objects in their habitat and other undescribed adaptive constraints of urbanization possibly accentuates the use of hand over mouth during FA and FP beyond task-specific motor requirements. We speculate that the relative overrepresentation of hand use is because most objects encountered by the urban group are optimally designed for manual handling by humans (see Goodman-Deane et al., 2016; Rowson & Yoxall, 2011) and hence, are perhaps more efficient for even macaques to control/maneuver/manipulate with hand rather than the mouth. Remarkably, extractive foraging from packaged food influences the most fundamental aspect of manual action pattern and exploration, i.e., food acquisition to be biased towards hand use.

Hand and mouth use during food acquisition under naturalistic conditions

Analyses beyond a controlled setting and across species in similar ecological condition allowed much broader and critical examination of the strength of urbanization and encounter with packaged food on hand/mouth use during FA. Though we could include only 3 primate species in our preliminary analyses, we obtained identical trends of hand/mouth use in FA across every cercopithecid species along the gradient of urbanization and encounter with packaged food. The trend in hand use remained conserved even when analyses were carried out at the level of food types. The results obtained on hand use in vervet monkeys offered a numerical estimate of the effect of urbanization and dependence on packaged food, which lends credence to the near-universal impact of urbanization on cercopithecid foraging and perhaps on other urban species with phylogenetic and/or anatomical similarities.

Analogous to our previous proposition on the role of artificial object exploration on hand use biases in FA and FP, recent neurobiological studies (e.g. Fleming et al., 2015; Goda et al., 2014, 2016; Hiramatsu et al., 2011; Pasupathy et al., 2019) on perception of material properties of objects have found the role of long-term visual and haptic (crossmodal) experience with objects 'for neural representation of non-visual object properties', which is essential for object categorization (Hiramatsu & Fujita, 2015). Object categorization is believed to be an essential adaptive behavioral feature of urban animals since it allows animals to 'adjust their response to novel items in their environment" (Barrett et al., 2019). We reasoned that since urban primates are perpetually exposed to novel objects/foods and haptic experience is critical for developing object familiarity and consolidating object categorization, they are biased towards hand use during food acquisition as a result of frequent manual exploration/manipulation. However, our study is limited by a number of factors, like inadequate statistical representation of food types across an urban gradient, unavailability of data from all habitat types and foraging evaluation of just 3 cercopithecid species. We intend the article to prompt research efforts towards verifying and validating trends observed in the study along with bridging the gaps mentioned above. Of great interests are also determinations of additional proximate factors within urbanization that seem to be driving concerted adaptive pressures on urban foraging behaviors.

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CONFLICT OF INTEREST

The authors declare no conflict of interests

AUTHOR CONTRIBUTIONS

Tejeshwar Dhananjaya: Conceptualization; formal analysis, methodology; data collection; project administration, statistical analyses; writing original draft; review & editing. **Sayantan Das:** Conceptualization; formal analysis; funding acquisition; methodology; data curation; data collection; statistical analyses; visualization, writing original draft; review & editing. **Monica Harpalani**: Data curation; formal analysis; methodology; review & editing. **Michael A. Huffman:** data characterization; review & editing. **Mewa Singh:** funding acquisition, project administration, supervision; writing original draft; review & editing.

DATA AVAILABILITY STATEMENT

The raw data used in the research leading to this article are available as supplementary material.

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SUPPORTING INFORMATION

Supplemental information includes supplemental tables and supplemental figures. Raw data files have been submitted to Mendeley Data and are awaiting approval.

Hosted file

Supplemental Information.docx available at https://authorea.com/users/440139/articles/540910-can-urbanization-accentuate-hand-use-in-the-foraging-activites-primates