Primates in the urban mosaic: terminology, flexibility and management

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Abstract

Continuous human expansion is affecting landscape composition, in particular through urbanisation. Wildlife persistence in the urban mosaic is generally negatively affected; however, many primate species show behavioural plasticity and thrive in the urban mosaic. Urban primates often show selective behaviours in the urban mosaic, e.g. responses to anthropogenic food resources. However, as the urban mosaic becomes more prominent and important for biodiversity, conservation and management, clearer definitions and terminology used to describe the urban mosaic are needed. Therefore, we use this chapter to review current definitions and suggest using the term 'mosaic' to discuss urban landscape ecology moving forward. Throughout our review, we consider the complexity of the urban mosaic and emphasise the value of considering quantified anthropogenic disturbance and species-specific knowledge in urban primate ecology. We suggest that management focus on the multiple facets of the urban mosaic, both human and primate derived, and discuss the benefits for biodiversity, conservation and human-primate coexistence.

Key words: Urbanisation, mosaic, matrix, management, human-primate coexistence, fitness

1 Introduction

Almost all wildlife live in an environment that is subject to some level of anthropogenic disturbance (Soulsbury and White 2015). The effects of this disturbance vary dramatically with the nature of the environmental change (McKinney 2008). Research on wildlife living in the urban mosaic is increasing (Perry et al. 2020), yet research on non-human primates (hereafter primates) in the urban mosaic is complex because of the multi-dimensional and heterogenous nature of urban areas. The viability of biodiversity in an urban environment is influenced by multiple aspects such as the environment's ecological structure (Mackenstedt et al. 2015), species-specific physiological and behavioural adaptations (Humle and Hill 2016) and human-primate relationships (Naughton-Treves et al. 1998). In this chapter, we will first consider terminology used to discuss the urban mosaic and then review research on primate ecological and behavioural flexibility in an urban environment. Finally, we will consider the application of this knowledge for management and conservation.

2 The urban mosaic

Global environmental change, caused by human land use requirements, often has detrimental impacts on ecosystems (e.g. Lambin et al. 2000). The growth of human populations, resulting in anthropogenic changes to landscapes and urban sprawl, is now considered a key driver of environmental change (Grimm et al. 2008). Urbanisation creates a unique landscape ecology through increasing human populations, anthropogenic topography and habitat fragmentation (Werner, 2011). These urban landscapes vary dramatically from large cities to small settlements; therefore, the ecological effects are difficult to measure quantitatively (Bennett and Gratton 2012).

Increases in human populations have resulted in changes to the natural ecosystem's function and biodiversity (Bonier et al. 2007). Although effects are species-specific, certain primate species have shown behavioural flexibility to ecological changes and thrive in these conditions (McLennan et al., 2017). Desirable characteristics linked to the urban environment, such as increased resources and a reduction in predation, provide an attractive habitat (Bateman and Fleming 2012; de Andrade et al. 2020); hence some species often favour the urban environment to its rural counterpart (Kaplan and Rogers 2013). Generally, urban primates persist in these areas because of their omnivorous foraging behaviour (Lowry et al. 2013). By optimising their foraging strategies, exploiting human resources (Thatcher et al. 2020), altering ranging patterns for food access or changing foraging activity to avoid increased aggression from humans (Thatcher et al. 2019a,b) and using the city as a refuge (Waite et al. 2007), many primates are able to thrive in the urban mosaic.

Although the urban mosaic has many positive aspects, there are also many negative consequences (Bicca-Marques 2016; Perry et al. 2020). Primates in the urban mosaic face challenges of habitat destruction and fragmentation resulting in poor habitat quality and connectivity (Bicca-Marques 2016), as well as challenges associated with anthropogenic topography, human-wildlife interactions, pollution and food restrictions (Gordo et al. 2013). These challenges can bring an increased risk of stress (Giraudeau et al. 2014) and increased chances of death and/or injury related to the human-primate interface (O'Riain and Hoffman 2012), power lines (Lokschin et al. 2007; Lindshield 2016; Pereira et al. 2020) and dog predation (see this volume). Furthermore, studies on endangered primate populations have shown the genetic risks of increased fragmentation (e.g. banded leaf monkey, *Presbytis femoralis femoralis*, Ang et al. 2012; pied tamarin, *Saguinus bicolor*, Farias et al. 2015). This research stresses the importance of considering the urban sprawl for genetic conservation of endangered species.

2.1 Defining the Urban mosaic

It is commonly acknowledged that landscapes are spatially heterogeneous areas comprised of a mosaic of patches that differ in spatial patterns and ecological processes (Wu 2013; Forman and Gordon 1986). Urban patch mosaics form key attributes for wildlife providing anthropogenic resources (Johnson and Munshi-South 2017) and green space (de Andrade et al. 2020; Downs et al. 2021). Although the term urban mosaic is becoming more widely used within urban ecology (e.g. Corrêa et al. 2018) it is still not clearly defined, likely because of global variation in these landscapes (see: Werner 2011). Here, we will consider the two most commonly accepted definitions of Werner (2011) and Marzluff et al (2001) and define the urban mosaic as: '*a habitat made up of areas of building density, residential human-density, anthropogenic disturbance, green areas and linear anthropogenic structures'*.

In conducting this review we found multiple discrete phrases for urban landscapes within the primate literature, including: 'urban', 'peri-urban', 'semi-urban', 'urban-city/forest/farm/rural/semi-rural/tourist', 'human disturbance', 'anthropogenic' and 'tourist'. All these studies used the word 'urban' at some point to describe their study either within the abstract, introduction, or methods, yet their study sites varied dramatically. Most studies only described the study site, with few studies defining landscapes and anthropogenic terminology (e.g. Scheun et al. 2019; Chowdhury et al. 2020). We, therefore, suggest that studies should more clearly describe the matrix within their study site, providing a clear ecological description of the habitat composition (Werner, 2010) and considering landscape scales (See: Marzluff et al. 2001, pp. 11, Table 1) to clearly define the habitat type. Understanding this matrix of connected habitats and species requirements in the urban mosaic is important for ecosystem services and biodiversity conservation (Zungu et al. 2020a, b; Downs et al. 2021). We acknowledge the value of these diverse and discrete terms within the developing urban mosaic, nevertheless, within this chapter we will focus primarily on research conducted in 'urban' habitats as clearly defined in the study's methodology and/or following our definition. More detailed analysis of the above subcategories can be seen in the respective chapters throughout this book.

2.2 Quantifying anthropogenic disturbance

With increasing urban expansion, interest in the human-primate interface is growing, evidenced by recent ethnoprimatology studies (McKinney and Dore 2018). Currently, most research that focuses on the anthropogenic interface classifies disturbance by habitat type (see section 2.1), and data are often compared interchangeably without consideration of the varying ecological pressures within these landscapes (McKinney, 2015). Additionally, as the urban mosaic varies globally, so does the nature of the human-primate interface (Beisner et al. 2015). For example, economic loss to communities (Dickman 2012) differs from the economic and cultural benefits of tourism (Zhao 2005). In response, McKinney (2015) suggested a generalised classification system allowing researchers to clearly report four major variables within their study site including landscape, nonhuman primate interface, diet and predation risk. Although McKinney's descriptive system is a valuable initiative, it is not necessarily applicable to accelerating urban landscapes, for example, with respect to the value of opportunistic foraging for urban primates. McKinney's classification has only been used in one urban study so far (Thatcher et al. 2018; Table 1), although with modifications the premise of this system could be used more widely across the urban mosaic.

Nevertheless, some studies do provide a quantified estimate of field site variables (Table 1). For example, research has attempted to quantify anthropogenic topography by calculating the density of key urban mosaic features (e.g. buildings and green-space) (Santos et al. 2014; Thatcher et al. 2018; de Andrade et al. 2020). Additionally, some studies have considered the effect of noise pollution in the urban environment, measuring noise amplitude (Duarte et al. 2011; de Andrade et al. 2020).

Measuring interactions and associations within the human-primate interface is one of the most common measures of anthropogenic disturbance (Table 1). Multiple studies have used behaviour sampling to record all human-primate interactions, the initiator and context, providing a detailed account of interactions (e.g. Beisner et al. 2015; Suzin et al. 2017). Additionally, studies have highlighted the importance of considering the nature of human-primate interactions in the urban mosaic, both positive and agonistic/negative, providing an understanding of the drivers of urban primate behaviour (Suzin et al., 2017; Thatcher et al., 2019a, b; Thatcher et al., 2020). What is noteworthy, is that although studies have considered both human and primate orientated interactions (Table 1), to our knowledge no study has simultaneously considered both positive and negative interactions from both the human and primate perspectives, an important consideration to fully understand the multiple facets of the human-primate interface.

As the importance of studying the urban mosaic becomes a more prominent issue (Perry et al. 2020), clearer definitions and understanding within this landscape are needed to allow comparisons of research and support management plans for biodiversity and conservation. Although Table 1 highlights the current array of quantified anthropogenic pressures measured in urban studies, the methods and techniques within these studies are still variable, and as the human-primate interface varies with both anthropogenic and ecological pressures, these quantified measures need to be supported with an ecological description of urban mosaic characteristics.

Table 1. *Different measurements of quantified anthropogenic disturbance for primates in the urban mosaic. Each shows a brief description of the method and the associated study*

Measure of urbanisation	Definition	Study
McKinney's classification	Code landscape variables including: diet, human-nonhuman primate interface and predation level (See McKinney, 2015)	Thatcher et al. 2018
Land cover	Anthropogenic topography	Santos et al. 2014; Thatcher et al. 2018; de Andrade et al. 2020
	Tourism rate	Ilham et al. 2017
	Human proximity (distance)	
	Human population (per km^2)	Thatcher et al. 2018
Human presence	Human traffic scans (humans, bikes, motorcycle, bus, truck, cars)	Beisner et al. 2015
Noise disturbance	Noise amplitude	Duarte et al. 2011; de Andrade et al. 2020
	Human-primate conflict (injury or death)	Pragatheesh 2011; O'Riain and Hoffman 2012
	Human-primate interaction from local human community perspective (questionnaire)	Rodrigues and Martinez 2014; Teixeira et al. 2015; Patterson et al. 2017; Olaleru and Ogunfuwa 2020
Human-primate interface	Human-primate interactions (behavioural observations)	Chauhan and Pirta 2010; Beisner et al. 2015a; Suzin et al. 2017; Kaburu et al. 2018, 2019; Marty et al. 2019a, b; Thatcher, 2019; Thatcher et al. 2019a, b, 2020
	Human-monitoring (behavioural observations)	Kaburu et al. 2018, 2019; Marty et al. 2019a, b
	Provisioning, rate and food type	Kaplan et al. 2011; Suzin et al. 2017; Ilham et al. 2018; Thatcher et al. 2020
Human impact index	Human activity score	Fourie et al. 2015

3 Behavioural flexibility

To successfully thrive in an urban mosaic, animals must display behavioural flexibility to adapt to changing environmental pressures (Wright et al. 2010). Species that display a high degree of behavioural flexibility can adjust to a range of conditions and thrive in the urban mosaic (Healy and Nijman 2014). Therefore, research has focused on this plasticity in the urban environment to understand fitness implications (Sol et al. 2013) and how this knowledge can be used for management plans (Sol et al., 2002; McLennan et al., 2017).

As time is a bounded resource, its allocation and use reflect ecological pressures (Dunbar et al., 2009). Time budgets have been applied to primates in the urban mosaic to demonstrate trade-offs in behaviour (McLennan et al., 2017). For example, urban properties such as high-value food generally decrease foraging time (Hoffman and O'Riain 2011; Jaman and Huffman 2013; Back et al. 2019), often corresponding with reduced movement (Jaman and Huffman, 2013) and associated with an increase in social interactions and resting (Jaman and Huffman 2013; Ilham et al. 2018; Scheun et al. 2019). Additionally, studies on primates in the urban mosaic have shown that urban primates can flexibly adjust their activity seasonally (Jaman and Huffman, 2013; Thatcher et al., 2019a).

3.1 Foraging

Generalist species who display foraging flexibility and dietary plasticity can typically adjust more readily to anthropogenic changes than specialist species, therefore, foraging/dietary plasticity is highlighted as a key attribute to thrive in the urban mosaic (Lowry et al. 2013). Research on primates in the urban mosaic highlights a preference for high-calorie anthropogenic food resources (Hoffman & O'Riain, 2012a; Dasgupta et al., 2020). Foraging patterns in urban primates show that both natural and human foods are important to their diet, but dependence on either resource can differ between species, and even within species (Ilham et al., 2017; Thatcher et al., 2020). More so, urban primates have been shown to modify the proportion of anthropogenic and natural food dependent upon food availability, largely influenced by provisioning and natural food availability (long-tailed macaques, *Macaca fascicularis*, Ilham et al. 2017; gray langurs *Semnopithecus entellus*, Dasgupta et al. 2020; vervet monkeys, *Chlorocebus pygerythrus*, Thatcher et al., 2020).

Research highlights that human-food within a primate's diet can have varied fitness effects across anthropogenic landscapes; studies show this high-value food can increase individual fitness and reproductive success in agro-ecosystems because of higher nutritional content (Warren et al. 2011) and increase intergroup competition (Sinha and Mukhopadhyay 2013) and subsequently increasing anxiety and social tension (Maréchal et al. 2011) in areas of high tourism. Although these examples come from studies across anthropogenic landscapes, the consequences most likely hold true within the urban landscape as urban primates show a high degree of foraging flexibility and increased human-primate proximity (Thatcher et al. 2019a,b, 2020). Additionally, urban research has previously suggested that this increased foraging opportunities in the urban mosaic can lead to increased group size (Patterson et al., 2018). Therefore, an enhanced understanding of urban primates dependence on anthropogenic food, and the potential fitness implications, is necessary to implement and sustain management plans (Thatcher et al. 2020).

3.2 Ranging

Primate studies in the urban mosaic generally show that increased anthropogenic effects reduce home range size, primarily because of increased urban resources (Hoffman and O'Riain 2011; Hoffman and O'Riain 2012b; Klegarth et al. 2017). Research in the urban mosaic has also shown that urban primates express shorter daily path lengths (Corrêa et al. 2018; Thatcher et al. 2019b). Generally this is highlighted to be an adaptive strategy, with a preference for habitats with greater food resources associated with reducing the energy and need to travel for food (Hoffman and O'Riain 2012a; Patterson et al. 2019). Further research has shown that such habitat selection can be an adaptive strategy to avoid areas of high noise pollution and human disturbance (Duarte et al. 2011).

Conversely, research on urban vervet monkeys that quantified human-primate interactions reported the opposite, that home ranges increased with anthropogenic disturbance (Thatcher et al. 2019b). This differing result is likely due to the quantified measures of the human-primate interface in Thatcher et al's research (2019b) suggesting that this study population show an avoidance strategy to avoid human-directed aggression or that they ranged further to forage at more predictable sources of high value human food. Although clear interpretations of the costs and benefits of this strategy cannot be derived from the findings, it nonetheless suggests a complex attraction-avoidance scale within the urban mosaic. Although current research on primates in the urban mosaic is limited and does not show consistent patterns, it does imply that primates show spatial feeding strategies dependent upon anthropogenic pressures, highlighting fitness consequences and the value of species-specific studies.

3.3 Sociality

Social flexibility of wildlife has been shown to be plastic to change (review: Smil, 1993) and is an important behavioural trait that persists in the urban mosaic (Skandrani et al. 2017). Increased anthropogenic food availability can allow more time for socialising (Jaman & Huffman, 2013; Thatcher et al., 2019). Kaburu et al. (2019) found that rhesus macaques who interacted more frequently with humans spent significantly less time resting and grooming, suggesting unpredictable human behaviour is a time constraint. Furthermore, Thatcher et al. (2019) categorised human interactions as either positive (food) or negative (conflict) and found that human interactions influenced time-budget behaviour, suggesting a complex relationship between the costs and benefits of urban living. These studies therefore highlight the benefits of urban living, with more time for socialising (Jaman & Huffman, 2013; Kaburu et al. 2019; Thatcher et al., 2019) likely because of provisioning and increased dispersed feeding opportunities (Back et al. 2019; Scheun et al. 2019).

There are of course costs to social living in the urban mosaic, for example greater anthropogenic food availability has been shown to increase competition and aggressive behaviours (Sinha and Mukhopadhyay 2013). Furthermore, research on the human-primate interface shows the complexity of social dynamics between humans and primates; trends generally highlight that human-actions and resources cause primate reactions (e.g. aggression) (Chauhan and Pirta 2010; Beisner et al. 2015) and that human interactions are exacerbated by primate reactions (Chauhan and Pirta 2010) and economic loss/damage (Beisner et al. 2015). A wealth of research on inter-individual differences in primate social behaviour has been conducted on macaques in the urban mosaic. Research has shown that bonnet macaques, *Macaca radiata*, (Balasubramaniam et al., 2020), rhesus macaques (Kaburu et al., 2019) and long-tailed macaques (Marty et al. 2019b) that spend more time monitoring human activity, reduce their grooming effort. Furthermore, research has shown that long-tailed macaques spend less time grooming when human presence increases (Ilham et al. 2018). This research therefore highlights the importance of studying the more complex individual social dynamics within the urban mosaic, an area of research that is continually developing.

4 Urban health

Urbanisation is commonly linked to more complex and disturbed habitats increasing human-wildlife interactions, all of which have been suggested to increase the intensity and diversity of parasites (Soto-Calderón et al. 2016; Thatcher et al. 2018). However, the effects of urbanisation on parasite load are not always consistent, and other studies have found that a more anthropogenic environment can lead to a reduction in the intensity and diversity of parasites (Lane et al. 2011) or no difference in parasite prevalence (Adrus et al. 2018). Although parasite diversity trends are mixed throughout the anthropogenic landscape, studies on parasite diversity and intensity are important for human-health and wellbeing (Díaz et al. 2006). Primates in the urban mosaic are often found in proximity to humans, and this increases opportunities for zoonosis (Singh and Gajadhar 2014; Sapkota et al. 2020). Although studies have suggested the potential for transmission between urban primates and humans, data are still preliminary and currently inconclusive (Aitken et al. 2016; Debenham et al. 2017).

Parasite load and urbanisation have been linked to further primate health concerns. For example, White-footed tamarins, *Saguinus leucopus*, living in the urban mosaic were found to be overweight, and have a higher body mass and cholesterol level than rural tamarins (Soto-Calderón et al. 2016). Additionally, urban populations of the African lesser bushbaby (*Galago moholi*) have a greater body mass index and females have higher faecal glucocorticoid than their rural counterparts (Scheun et al., 2015). Overall, these studies highlight the risks of increased time and dependence on anthropogenic resources and potential negative health impacts of the urban mosaic, suggesting species may show flexibility and habituate to humans' presence, but not necessarily to the conflict and stress associated with the urban mosaic.

5 Managing the urban mosaic

Understanding an animal's phenotypic and behavioural flexibility in response to urban challenges provides an educated rationale to form species-specific management techniques for human-wildlife coexistence and conservation management (Lowry et al. 2013). Acquiring further knowledge on the impact of urbanisation on wildlife populations is a priority to be able to implement appropriate management (Redpath et al. 2013). Due to their intelligence and sociality, primates pose a complex challenge to execute effective management plans (Woodroffe et al. 2005).

Knowledge of behavioural flexibility can be beneficial for species management. Research has shown Black-tufted marmosets (*Callithrix penicillata*) in the urban mosaic avoid high noise areas, even if the area has high food availability, showing noise has potential benefits as aversive management (Duarte et al. 2011). Additionally research on chacmas baboon (*Papio ursinus*) has been applied for the benefit of species management in the urban mosaic (Hoffman & O'Riain 2011). For example, Kaplan et al (2011) studied the effectiveness of a food station in deterring chacmas baboons away from urban spaces, showing the need of a combined approach. Additionally, O'Riain and Hoffman (2012) modelled characteristics of chacma baboons spatial ecology to predict potential human-baboon conflict and show the benefit of applying this knowledge to make informed management suggestions. Overall, this research across the urban mosaic highlights the value of behavioural studies for management and the consideration of urban mosaic features.

Research generally highlights that foraging flexibility and anthropogenic food play a key role in wildlife success and should be the focus of management (Bicca-Marques 2016; Thatcher et al. 2019b, 2020). In Box 1, we present a case study that highlights the role of anthropogenic food and human-wildlife interactions to create a complex attraction-avoidance scale that should be considered for human-wildlife management. Acknowledgement and incorporation of the human-primate interface in research and the positive and negative consequences of this interface, both for primates and humans, is beneficial to make informed management strategies for primate welfare and biodiversity conservation (Setchell et al. 2017; Dore et al. 2018). Understanding the dynamics and frequencies of human-wildlife interactions is necessary to feed forward into appropriate management (Beisner et al. 2015). Although primatology is moving away from the term human-wildlife conflict and focusing on coexistence (McKinney and Dore 2018), it is important that we consider both positive (e.g. anthropogenic resources) and negative (e.g. human-directed aggression) aspects of the human-primate interface (Thatcher et al. 2019a, b).

Additionally, it is just as important to consider human perceptions and roles within urban species management. In particular, an ethnographic perspective is essential when designing strategies to ensure they are truly inclusive, advocating a decolonial approach to research in the urban mosaic (Ehlers Smith et al. 2021) and wider anthropogenic landscapes (Setchell et al. 2017; Waters and Setchell 2018; Waters et al. 2019). Diverse multi-cultural beliefs, views and philosophies may be embedded within local human-wildlife relationships and these need to be fully considered in order to develop effective management strategies, for example shepherd's perception of Barbary macaques in the anthropogenic landscape (Waters and Setchell 2018). Therefore, consultation with local communities and indigenous populations must be a priority during the conceptualisation of any plan in the urban mosaic.

Community science studies have highlighted human concern for urban primates, emphasising the value of incorporating a human dimension within urban ecology and management (Patterson et al. 2017; Suzin et al. 2017). Although human-focused behaviour change can be more challenging to implement in the urban mosaic (Bicca-Marques 2016), education is considered a key action in managing the human-primate relationship and research has shown a public willingness to engage in these measures (Sha et al. 2009). Furthermore, the presence of urban wildlife is also beneficial at a public level because often humans in the urban mosaic only encounter urban wildlife (Lunney and Burgin 2004), and it has been shown that exposure to wildlife at an early age can encourage support for conservation (Soga and Gaston 2016), even making humans more tolerant of exploitive wildlife (Hosaka et al. 2017). Recent research has also highlighted the mental health benefits of the human-primate interface, suggesting positive consequences for human well-being (Barua et al. 2021).

As urbanisation is only predicted to increase with the growing human population, a developed understanding of species-specific primate reactions to urban drivers is needed (Lowry et al. 2013). Species that can thrive and tolerate anthropogenic drivers are currently 'winners' in this developing mosaic (Perry et al. 2020). However, as the urban mosaic becomes more dominant, knowledge of flexible behavioural ecology will be necessary to predict and manage species adaptations to the changing landscape to benefit human-wildlife coexistence and biodiversity conservation. We suggest the best way to facilitate this moving forward is clearer measurements and definitions of urbanisation where possible.

Box 1. *A case study showing that positive and negative human-interactions create a complex attraction-avoidance scale for urban vervet monkeys that should be considered for management.*

Urban ecosystems present complex challenges for the human-primate interface. Thatcher et al.'s analyses considers time budget behaviours (Thatcher et al. 2019b), ranging behaviours (Thatcher et al. 2019a) and foraging flexibility (Thatcher et al. 2020). In these studies, Thatcher et al. measured rates of human-wildlife interaction, considering both positive (e.g. food) and negative (e.g. aggression) urban drivers from a vervet monkey perspective. Results highlighted that vervet monkey behaviour is influenced by human-wildlife interactions, suggesting that urban vervet monkeys express behavioural flexibility. In this case study, we summarise key findings, highlighting the application of this approach for managing the human-primate interface.

Vervet monkeys in an urban mosaic take shorter (Thatcher et al. 2019b) and more direct journeys (Thatcher et al. 2019a) if they have increased access to human-food. However, if the rate of positive human-interactions decrease and negative human-interactions increase, these routes become longer and less direct. Results further highlight that vervet monkeys' movement is highly dependent on the value of available food resources, as vervet monkeys are less likely to move in response to human aggression when anthropogenic-food is available. Therefore, managing access to this anthropogenic-food can directly affect vervet monkey movement patterns.

The interaction of positive and negative human-interactions was also significant for foraging, indicating that if vervet monkeys have access to high-value anthropogenic food, then, despite human-aggression, their time spent foraging would increase (Thatcher et al. 2019b). Again, this result has important consequences for management showing the key role of human-food, but the ineffective deterrent of human-aggression. However, more recent in-depth analysis showed that foraging depended upon availability of resources (human-derived food and horticultural plants) (Thatcher et al. 2020). Thus, vervet monkeys show strong seasonal foraging, but that negative human-interactions can reduce foraging rate of specific food resources. These results (Thatcher et al. 2019a; 2020) highlight the foraging flexibility of urban vervet monkeys, but also highlight some conflicting results that could possibly be because Thatcher et al.'s (2019a) study population depends solely on human-derived resources (horticultural garden plants and human-derived food), emphasising the need for refined foraging terminology within the urban landscape.

Overall, Thatcher et al.'s studies highlight the key role of human-food and that increased human aggression does not necessarily reduce the 'unwanted' behaviour of vervet monkeys. Therefore, management strategies should aim to reduce opportunities for human-food consumption that may support human-wildlife conflict through education and local management programmes.

Overall, findings emphasise vervet monkey behaviourally flexibility. Demonstrating how vervet monkeys respond to the urban landscape by altering their behaviour under periods of positive human-interactions to benefit from the potentially high calorific food. The interplay between positive and negative aspects of the urban environment creates a complex attraction-avoidance scale, and both aspects must be considered to fully understand behavioural adaptations under anthropogenic pressures for species management.

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