Anthropogenic influences on the behavioural ecology of urban vervet monkeys

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Abstract

An animal's behaviour is dependent upon its ability to adapt to environmental changes and available resources; consequently, generalist omnivorous species thrive in the continually developing urban landscape and preferentially choose the urban setting over its rural counterpart. Our understanding of wildlife's flexibility to anthropogenic change is developing; however, our knowledge of flexibility to the urban landscape is limited, particularly for primate species. Understanding an animal's ability to adapt behaviourally to urban challenges is necessary to provide guidance for human-wildlife management plans. This thesis focuses broadly on the behavioural ecology of the adaptive, generalist vervet monkey (*Chlorocebus pygerythrus)*. We use an integrative approach to assess the behavioural ecology of urban vervet monkeys under quantified anthropogenic pressures, assessing both positive (human-food) and negative (human-aggression) consequences of urban living. We use the previously neglected interaction between positive and negative human influences to assess ranging patterns and time budgets, showing a complex attraction-avoidance scale within the urban landscape. We also used social network analysis to show the importance of human-food consumption on vervet monkey social structure, both at the group and individual level. Finally, we suggest the use of a simple parasite protocol to monitor host-parasite responses to urbanisation. Overall, we provide primary evidence on the behavioural ecology and strategies of urban vervet monkeys, creating a foundation for future research on urban primates. We highlight trends in our findings, crucially the central value of human-food to vervet monkey's behavioural flexibility. We apply this knowledge to suggest management recommendations, that future strategies should focus primarily on education to prevent opportunities for vervet monkeys to consume human-food, for the benefit of primate-human cohabitation.

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Contents

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List of tables

List of figures

Chapter 1

General introduction

Almost all wildlife today live in habitats that are altered to some degree by human activity, due to growing human populations and land-use changes (Tilman et al., 2017). An animal's behaviour is dependent upon the environment and resources within it (Diquelou et al., 2015). Understanding how an animal persists in an anthropogenically disturbed environment is essential to provide guidance for human-wildlife cohabitation and conservation management (Dickman, 2010; Hockings et al., 2015; Nowak and Lee, 2013). Most literature on human–wildlife interactions, focuses on either positive or negative aspects of human–wildlife interactions (Angelici, 2016; McLennan et al., 2017; Seoraj-Pillai and Pillay, 2016; Woodroffe et al., 2005). In this thesis, I assess the anthropogenic flexibility of the vervet monkey (*Chlorocebus pygerythrus*), a generalist non-human primate (hereafter known as primate), previously shown to thrive in an anthropogenically disturbed environment (Patterson et al., 2018). In order to do this, I assess multiple aspects of vervet monkey behavioural ecology, using ranging patterns (Chapter 3), time budget analysis (Chapter 4), social network analysis (Chapter 5) and finally parasite load (Chapter 6).

1.1 Human-wildlife interactions

Human–wildlife interactions and their impact vary dramatically, they are often represented on a gradient of positive-neutral-negative (Nyhus, 2016). Nevertheless, there are further layers to these interactions including intensity (minor to severe), frequency (rare to common) and distribution (localised or ubiquitous) (See: (Nyhus, 2016). Human-wildlife interactions can be interpreted from different directions, such as the animal's perspective or the human's perspective (Soulsbury and White, 2015). For example, the value of human engagement with wildlife (Mascia et al., 2003) and increased zoonotic transmission (Hegglin et al 2015; Soto-Calderón et al., 2016; Soulsbury and White, 2015). With such potential for increased disease transmission, it is commonly acknowledged that an understanding of human-wildlife interactions is necessary, both for human well-being and ecological biodiversity conservation (Díaz et al., 2006; Soulsbury and White, 2015).

From an animal's perspective, the fitness consequences of human-wildlife cohabitation can be beneficial and/or detrimental depending on an animal's adaptability (Ditchkoff et al., 2006; McKinney, 2008) and can vary in intensity and frequency (Soulsbury and White, 2015). For example, research has shown that urban scrub-jays, *Aphelocoma coerulescens*, are more efficient foragers than their rural counterparts due to human-food consumption and that this foraging efficiency has further benefits for reproductive success (Fleischer et al., 2003). However, other research has shown the fitness costs of foraging in an urban landscape, for example foraging on human-food and road kill had detrimental effects on racoons, *Procyon lotor*, increasing disease transmission and decreasing population demography (Prange et al., 2004).

The term 'human-wildlife conflict' is commonly used to classify negative interactions between humans and wildlife (Graham et al., 2005). However, there is no common term used to classify positive human-wildlife interactions, reflecting a bias in current research (Peterson et al., 2010). Both negative and positive human-wildlife interactions are generally seen more frequently in adaptive, dietary generalist species living in dense populations (Charles and Linklater, 2013). Even though human-wildlife interactions occur in a variety of habitats, interactions are most frequent in sub-urban landscapes where animals are able to prosper from advantages of human associations, as well as patches of natural habitat (Goulart et al., 2010; Lukasik and Alexander, 2011;

Merkle et al., 2011). Consequently, urban expansion has caused a recent surge in negative human-wildlife relationships in urban areas (Davison et al., 2011; Kistler et al., 2013).

1.2 Behavioural flexibility

In order to successfully prosper in an urban environment animals must display behavioural flexibility to adapt to changing environmental pressures (Wright et al., 2010). Species that display a high degree of behavioural flexibility are able to adjust to a range of conditions and, as a result, are often considered ‘pests’ (Healy and Nijman, 2014). Research has therefore focused on this plasticity in the urban environment to understand fitness implications (Sol et al., 2013) and how this improved knowledge can be used for management plans (McLennan et al., 2017; Sol et al., 2002).

Continuous urban expansion is affecting landscape composition and subsequently wildlife that reside within the urban landscape (McKinney, 2008). 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 morphological/anatomical adaptations (hands, cheek pouches, locomotor abilities), advanced cognition (see Humle and Hill, 2016 table 14.1), as well as human-primate relationships (e.g. socio-economic, cultural, religious) (Naughton-Treves et al., 1998). Desirable characteristics linked to the urban environment, such as increased resources, provide an attractive habitat for adaptable species (Bateman and Fleming, 2012), hence species often favour the urban environment over its rural counterpart (Kaplan and Rogers, 2013). Consequently, the urban environment is now acknowledged as an important ecosystem (McKinney, 2008).

The terms ‘urban adapter’ and ‘urban exploiter’ are often interlinked and used to refer to a species which has adapted to the urban landscape (Fischer et al., 2015).

Generally, adaptive mammalian species often succeed due to their omnivorous foraging nature (Lowry et al., 2013; Widdows and Downs, 2018). Flexible omnivorous foraging strategies are fundamental to the survival and success of urban species (Lowry et al., 2013). Often dietary generalists prosper by optimising their foraging strategies, for example, by exploiting human resources (Murray and St. Clair, 2015), altering ranging patterns for food access (Widdows and Downs, 2018) or changing foraging activity to avoid increased aggression from humans (Riley et al., 2003). Cercopithecoids are the most succesful extant primates to adapt to human-cohabitation (Lambert, 2005). Cercopithecines are unique in that they possess cheek pouches, likely an adaptive quality in the urban landscape, allowing them to retreat to a safe place to consume human-derived food (Humle and Hill, 2016; Lambert, 2005).

1.3 Anthropogenic disturbance and primates

Expanding anthropogenic disturbance, has led to a surge in research on primates living in anthropogenic landscapes (Humle and Hill, 2016), so much so that the term ethnoprimatology is now acknowledged as a key area of primate research (Dore et al., 2018; Fuentes, 2012; Fuentes and Hockings, 2010). Ethnoprimatology focuses on the interface between humans and primates, encompassing multiple facets of their coexistence. Ethnoprimatology studies include, but are not limited to, social, economic, cultural and political aspects (Fuentes and Hockings, 2010; Hill, 2015; Hsu et al., 2009; McKinney, 2014). 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 necessary to make educated management strategies for primate welfare and biodiversity conservation (Dore et al., 2018; McKinney and Dore, 2018; Setchell et al., 2017).

Global environmental change, caused by human land use requirements, often has detrimental impacts on ecosystems such as altering land, water and food availability (Lambin et al., 2000). The unprecedented growth of human populations, resulting in anthropogenic changes to landscapes, is now considered a key driver of environmental change (Grimm et al., 2008; Wigginton et al., 2016). In today's climate, it is nearly impossible to encounter a primate population without some level of human influence (McKinney, 2015). Anthropogenic influences on primate ecology include, but are not limited to, habitat loss (Estrada and Coates-Estrada, 1996), tourism (Brennan et al., 1985; Fuentes et al., 2007; McKinney, 2014) and modified landscapes (Fuentes and Hockings, 2010). Data from field research are often compared interchangeably without consideration of the varying ecological pressures within these landscapes (McKinney, 2015). To combat this, McKinney (2015) suggested a generalised classification system for anthropogenic influences. McKinney's system uses four variables (landscape, human–nonhuman primate interface, diet and predation risk) to classify primate groups. Following McKinney's flow chart system for each variable, researchers will in turn create a four-letter code that is intended to represent their field site. A clearer classification of the scale and rate of anthropogenic disturbance can facilitate cross-site comparisons and the implementation of specific conservation management plans (Bennett and Gratton, 2012; Bradley and Altizer, 2007; Shochat et al., 2007).

As research into primate ecology continues to develop, it is important to consider anthropogenic disturbance not only at multiple scales but also in multiple species (McLennan et al., 2017). Currently, most research on anthropogenically disturbed primates has been conducted on select species including chimpanzees (*Pan spp.*), macaques (*Macaca spp.*) and baboons (*Papio spp.*) (McLennan et al., 2017). McLennan et al. (2017) recently reviewed research on primates living in anthropogenic landscapes; they reported that only 15% of current research was conducted in urban settings, such as towns and cities, highlighting a need for further research into urban populations. This figure of 15% included tourism-based research as well as urban dwelling primates with no tourism, hence the figure for urban dwelling primate research is much less than 15%. Largely speaking, tourism is often linked to a positive cultural and socio-economic outlook from humans towards primates (Fuentes et al., 2007), whereas primates living in urban areas generally have no financial benefit to the local community and are seen as a ‘pest’ species, reflecting negative human opinion (Brennan et al., 1985).

Most literature on urban primates is focussed on specific generalist primates such as: macaques (Debenham et al., 2017; Ilham et al., 2017; Jaman and Huffman, 2013; Klegarth et al., 2017; Maibeche et al., 2015), capuchins (*Cebidae*) (Aguiar et al., 2014; Duarte et al., 2011; Suzin et al., 2017), marmosets (*Callithrix*) (Goulart et al., 2010; Rodrigues and Martinez, 2014; Santos et al., 2014; Teixeira et al., 2015) and tamarins (*Callitrichidae*) (Aitken et al., 2016; Gordo et al., 2013). Furthermore, few of these studies consider the broader behavioural ecology and flexibility of these urban species. Intense behavioural studies necessary to assess the behavioural flexibility of urban species are often difficult to conduct due to the urban setting itself. Increased human populations often come with increased anthropogenic topography, as well as high traffic and crime rates, making fieldwork more complex.

Research into primate behavioural flexibility to anthropogenic change has demonstrated that many primates have successfully adapted to the pressures of human-nonhuman primate cohabitation (McLennan et al 2017). Among primates, research has shown a degree of preferences for anthropogenic features, particularly a behavioural preference for increased human derived food resources (Bryson-Morrison et al., 2017; Bryson-Morrison et al., 2016; Hoffman and O’Riain, 2012a; Saj et al., 1999; Sha and Hanya, 2013). Research into primate ranging patterns, generally highlight that greater anthropogenic disturbance reduces home range size (Altmann and Muruth, 1988; Hoffman and O’Riain, 2011, 2012b; McKinney, 2011; Riley, 2008). Supportive to this research into time budgets have also shown a decrease in movement and foraging behaviour when primates have access to high value food resources (Hoffman and O'Riain, 2011; Jaman and Huffman, 2013; Saj et al., 1999; Sha and Hanya, 2013; Wong and Candolin, 2015), this decrease in movement and foraging is often associated with an increase in social interactions (Jaman and Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). Furthermore, even though sociality is considered to be an important aspect of plasticity in the urban environment due to the beneficial fitness consequences (Sol et al., 2013), there are few studies on sociality in urban populations. Social structure has been shown to be affected by anthropogenic pressures using novel social network techniques in bottlenose dolphins (*Tursiops truncates*) (Pace et al., 2011) and spotted hyenas (*Crocuta crocuta*) (Belton et al., 2018), but so far, social network analysis has not been applied to study anthropogenic pressures on primates. Overall, most studies on anthropogenic primate behavioural flexibility are based on comparisons of disturbed and undisturbed populations or assumed disturbance rather than directly measured anthropogenic influences. An increase in research using a quantifiable and comparable measure of anthropogenic disturbance to assess behavioural flexibility is necessary.

1.3 Management implications

Human-wildlife interactions pose one of the greatest threats to the survival and success of many species (Dickman, 2010); establishing successful management, by reducing negative human-wildlife interactions, is therefore a priority (Redpath et al., 2013). Understanding an animals' ability to adapt to urban challenges can provide an educated rationale to form species-specific management techniques (Lowry et al., 2013). Previous research has shown that without sufficient scientific information, management plans cannot be monitored for progress and it is therefore hard to interpret their success (Fuentes, 2011). A successful example of research-led management is the well-established Cape Town Baboon Project, which assesses human-wildlife cohabitation. The Cape Town Baboon Project team used established research on baboon preferences for alien vegetation (Hoffman and O'Riain, 2011), to manipulate food accessibility and create artificial food patches to temporarily control populations (Kaplan et al., 2011). This project highlights the importance of using research to establish suitable management plans. Therefore, in order to reduce negative interactions between humans and wildlife, research should focus efforts for biological wellbeing rather than considering primates as pests (Sha et al., 2009).

1.4 Vervet monkeys

Increased urbanisation has meant that vervet monkey populations often live closer to humans than previously; this close proximity between vervet monkeys and humans is likely to increase due to accelerating human population rates. It is widely accepted that vervet monkeys have adapted to the anthropogenic landscape, becoming densely populated due to increased resource availability. Supporting research has been conducted on semi-urban agricultural populations (Brennan et al., 1985; Chapman et al., 2016; Kappeler et al., 2013; Saj et al., 1999, 2001) and more recently in urban populations (Patterson et al., 2016, 2017, 2018). Further research has also compared vervet monkeys along a gradient of anthropogenic disturbance (Fourie et al., 2015; Loudon et al., 2014), highlighting that with increasing levels of urbanisation more human-food is consumed (Loudon et al., 2014) and males have higher stress levels (Fourie et al., 2015). The results of these two cross-sectional studies provide important findings, independently showing both the benefits (food: Loudon et al., 2014) and costs (stress: Fourie et al., 2015) of urban living, as well as highlighting the variety of habitats vervet monkeys are found in and how these habitats alter adaptive strategies employed by vervet monkeys. Although research has demonstrated vervet monkeys' behavioural flexibility to anthropogenic changes (Brennan et al., 1985; Chapman et al., 2016; Saj et al., 1999, 2001), these studies have only been conducted on mildly disturbed populations near tourist lodges. Research on urban populations has focused predominantly on the human-primate relationship for co-existence (Patterson et al., 2018, 2017, 2016). None of the above studies have simultaneously considered both positive (e.g. human-food) and negative (e.g. aggression from humans) aspects of living in an anthropogenic environment for vervet monkeys, a common constraint of anthropogenic research (McLennan et al., 2017).

1.5 Thesis structure

This thesis presents an assessment of urban influences on the behavioural ecology of urban vervet monkeys. In this introduction, I have given a brief overview of anthropogenic disturbance and its impact on wildlife. I have highlighted the current extent of our knowledge in the field of ethnoprimatology, with respect to behavioural and social structure. Further, I highlighted the lack of behavioural research conducted on urban primates and indicate the suitability of the vervet monkey to assess this. My four data chapters address these gaps in the literature in order to broaden our knowledge of the flexibility of vervet monkeys to human pressures for future wildlife management plans. Each data chapter (Chapters 3-6) is presented in journal article format. Chapter 2 provides details of the study population and field site and outlines general methodology. Chapter 3 assesses the effect of positive and negative aspects of the urban landscape on the ranging patterns of urban vervet monkeys. Chapter 4 expands upon this, assessing the effect of positive and negative aspects of the urban landscape on the time budgets of urban vervet monkeys. Chapter 5 then progresses from general behavioural flexibility to social flexibility using social network analysis to investigate how group and individual social metrics are influenced by human derived food. The final data chapter, Chapter 6, investigates whether parasite load is related to anthropogenic influence along an urbanisation gradient. Finally, Chapter 7 concludes with an overview of the results, discussing the behavioural and social flexibility of vervet monkeys in an urban environment. I emphasise key themes linking the results and suggest how these findings can be interpreted for future management plans.

Aims of the thesis (statement of objectives)

Aim 1. Develop a greater understanding of the behavioural strategies that allow vervet monkeys to adapt to the anthropogenic environment

a. How do anthropogenic influences affect vervet monkey ranging patterns? *(Chapter 3)*

b. How do anthropogenic influences affect the time budget of vervet monkeys? *(Chapter 4)*

Aim 2. Assess the socio-ecological and anthropogenic influences that affect social behaviour of urban vervet monkeys

a. How do anthropogenic influences affect the social networks of urban vervet monkeys? *(Chapter 5)*

Aim 3. Provide recommendations for management protocols for urban vervet monkeys

a. Can parasite load be used to assess urban disturbance along a scale of anthropogenic disturbance? *(Chapter 6)*

b. How can the findings of this thesis influence future management plans? *(Chapter 7)*

Chapter 2

General methodology

This chapter briefly outlines the main methods used throughout this thesis and includes further details on the field sites used for Chapters 3-6. It presents the timescale of the work, including further information on preliminary methods not described in other chapters. Only information on data collection in the field is presented, more specific protocols and details of data extraction and manipulation are presented in each of the following four data chapters.

Ethical statement

This study was purely observational and non-invasive and required no environmental manipulation or direct interaction with the vervet monkeys. Ethical clearance was obtained from Liverpool John Moores University under permit number NK_HT/2017-6. We adhered to the legal requirements of South Africa and the ASAB guidelines for the ethical treatment of primates.

2.1 Study species

2.1.1 Life-history and behavioural overview

Vervet monkeys are medium sized sexually dimorphic African cercopithicoid primates (Turner et al., 1997). Vervet monkeys typically live in multi-male multi-female groups varying in size from as few as two adults, with additional juveniles (Isbell et al., 1991), to as many as 75 individuals (Kavanagh, 1981). They are habitat generalists and have a widespread range throughout Africa. They can tolerate a wide variety of habitats including humid rainforests, semi-deserts, swamps and anthropogenic disturbance, and seem to be limited only by water availability and sleeping sites (McDougall et al., 2010; Wolfheim, 1983). Much past research on vervet monkeys has been conducted during long-term research projects at Amboseli National Park (Brennan et al., 1985; Isbell, 1990; Isbell et al., 1990).

2.2 Field site and study population

2.2.1 Ballito and surrounding neighbourhood

This research project was primarily conducted at Simbithi eco-estate, a private gated estate located on Durban north coast, KwaZulu-Natal, South Africa. The gated estate is located within the coastal town of Ballito, vervet monkeys often left the estate to the surrounding area of Ballito; however, due to safety concerns I never followed them to conduct observations outside the estate. Ballito is a popular residential area with a variety of shopping complexes and leisure facilities. Housing in the area varies from private farmland to densely populated apartment complexes. The town is also a popular holiday destination with both South African and international visitors. Due to the location and financial investment within the area, Ballito has grown exponentially in recent years with larger shopping malls being developed and increased tourism seeing a growth in hotels and leisure facilities.

2.2.2 Eco-estates

Housing demands in South Africa are increasing, causing a changing land use gradient as anthropogenic influences intensify (Donaldson-Selby et al., 2007). Eco-estates are becoming a more popular housing alternative in South Africa (Ballard and Jones, 2011), appealing to a more wealthy class, offering a safe gated environment (Dirsuweit, 2002; Landman, 2012; Roberts, 2012). One of the more appealing factors of the eco-estate mentality is that they encourage conservation strategies, planting indigenous plants only (Ballard and Jones, 2011). Due to private estates unique appeal, their popularity and abundance has grown across South Africa (Ballard and Jones, 2011). These estates have become popular agricultural developments and have thus caused an expansion of many urban areas (Ballard and Jones, 2011). Although they aim to promote environmental awareness and community engagement (Kenna and Stevenson, 2013), it should be noted that any change in habitats and ecosystems can have a domino effect upon the wildlife if not fully considered and well managed (Dobson et al., 2006).

2.2.3 Simbithi Eco-estate

Simbithi eco-estate is the second largest private gated estate within Ballito. Converted from two sugar cane farms in 2004, Simbithi eco-estate was developed to create a luxury urban living environment. The estate management prides itself on the ‘eco’ mentality and implements guidelines within architecture and design for both aesthetical appeal to humans and ecological consideration for wildlife. Within the estate, there are small areas of human-made coastal forest and nature trails (Fig. 2.1). The estate contains a golf course, multiple restaurants, leisure facilities and accommodation varying from apartment complexes to large freestanding homes (Fig. 2.1). Simbithi eco-estate is an ongoing development meaning that there is continual disturbance by workforces and landscape change. Currently the estate has reached approximately 80% of its development potential (Fig. 2.1). In addition to standard urban traffic and noise, the selective mentality of the estate resulted in regular maintenance and preservation of surroundings by a high staff cohort.

The estate is securely fenced off from the surrounding area; however, monkeys are able to leave through small gaps in the fencing structure. Vervet monkeys had an abundant dispersed supply of natural food through the selectively maintained gardens and natural areas within their home range, whereas high value human-food was obtained by entering homes or refuse (Thatcher, *pers. obs*.). This human derived food was opportunistic and clumped. Simbithi management strongly discourage residents from feeding the monkeys; however, residents still fed vervet monkeys within the estate or indirectly fed by littering and bird feeders. Furthermore, vervet monkeys opportunistically foraged on human-food obtained from houses and restaurants. Due to the negative associations with human-food foraging (e.g. entering/damaging property), residents were concerned about populations and in the past 4 years this resulted in an increase in complaints. The ‘eco-team’ within the estate aimed to encourage an equilibrium between residents and wildlife and therefore encouraged research to this end. An increase in vervet monkey population numbers and residential complaints about vervet monkeys being a ‘pest’ species meant that the estate management were keen to facilitate research on human-monkey cohabitation.

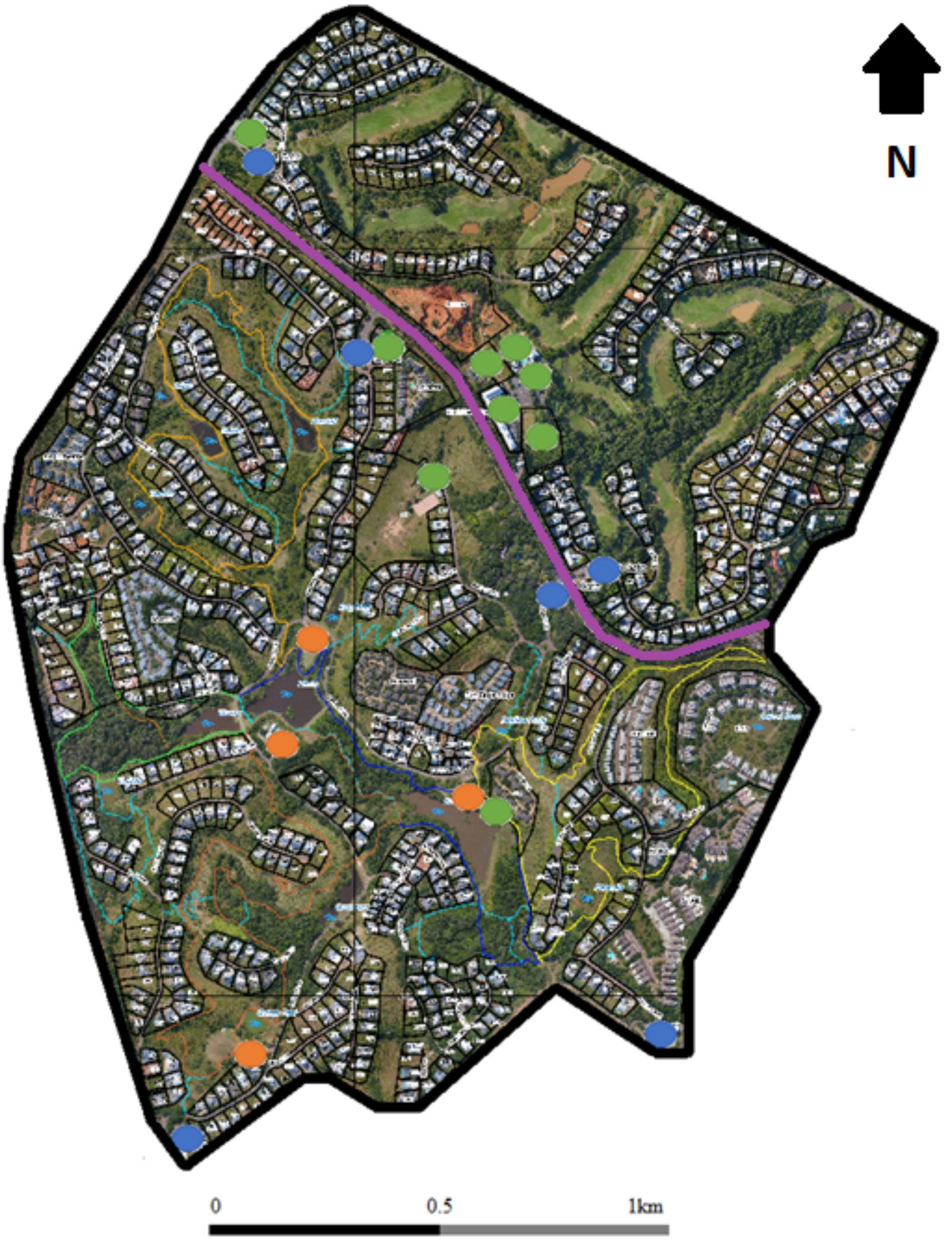

Fig. 2.1 Map showing Simbithi eco-estate, Ballito, Durban north coast, KwaZulu-Natal, South Africa. Black outlined shapes represent residential plots within the estate, those filled in represent the extent of the development (January 2014). Coloured lines represent the ‘nature trails’ within the estate. The thick purple line represents the main road that separates the estate. Orange circles represent community centres. Green circles represent leisure facilities. Blue circles represent entrance/exit gates. Redrawn from http://www.simbithi.co.za/

2.2.4 Additional field sites in Durban and surrounding suburbs

For the analysis in Chapter 6, I visited Simbithi eco-estate and an additional three field sites (Central suburbs of Durban, Bufflesdraai and Ishona Langa Wildlife Sanctuary) to create a rural-periurban-urban gradient scale (Fig. 2.2). As research was already ongoing at these additional sites, vervet monkey groups did not require habituation. The central suburbs of Durban represented an area of high human disturbance, with a high human population and anthropogenic structures. The third site was Bufflesdraai, a waste disposal/industrial site that had limited urban development but regular traffic. Bufflesdraai also had a regeneration process providing valuable resources for vervet monkeys. Finally, Ishona Langa Wildlife Sanctuary, was a private reserve in Ashburton, south of Durban, which was home to a variety of other wildlife. Ishona Langa had limited anthropogenic disturbance with only visiting researchers and two residents.

Fig. 2.2 A map showing the four-field sites used to create a rural-periurban-urban gradient scale (Google, n.d.). Purple circle= Central suburbs of Durban, green circle= Simbithi eco-estate, blue circle= Bufflesdraai and red circle= Ishona Langa Wildlife Sanctuary

2.2.5 Study population at Simbithi Eco-Estate

Initially the eco-team at Simbithi eco-estate estimated that there were five resident groups. After preliminary fieldwork, following and tracking monkeys, I identified seven distinct groups. However, two of these groups spent more time outside of the estate than inside. Due to logistics of both time management and the safety precautions of staying within the gated estate, the five ‘resident’ groups were used within this research project. Group size varied throughout the year, particularly during dispersal (March-June) and birthing season (November-December). Group size ranged from 14-42 individuals (Group size average and composition = **Ballito** (14): 3 males, 6 females, 5 juveniles; **Farmyard** (23): 4 males, 10 females, 9 juveniles; **Savannah** (25): 4 males, 10 female, 11 juveniles; **Goodies** (29): 5 males, 10 females, 14 juveniles; **Heron** (42): 5 males, 14 females, 23 juveniles). Daily point counts of groups were taken at any suitable opportunity following standard point count protocol (Alldredge et al., 2007).

2.2.6 Habituation

Living in an urban area, monkeys were already somewhat habituated to the presence of humans. Nevertheless, from January-February 2016, I spent extended periods at the estate to habituate the monkeys to the presence of one observer at close proximity (10 m) to allow clearer identification of individuals for observations. I considered a group to be sufficiently habituated when I approached to within 10m proximity with no flight response. This proximity decreased over the course of the study and differed between groups and situations.

2.2.7 Identification

All adults were recognisable via distinct appearance. A large proportion of the monkeys had visible scars or injuries (limp, stumped tails etc.) from previous confrontations. Other individuals had less obvious markings, however were identifiable based on size and facial patterning. I created a photo identity guide during the initial phases of fieldwork that facilitated early field observations. Social interactions were not recorded until individual ID was accurate; this was accomplished reliably by May 2016.

2.3. Data collection

2.3.1 Field work schedule

After I conducted habituation and preliminary field work (January-February 2016), the subsequent 12 months were spent conducting the main fieldwork. Between 3-4 weeks were spent each month at Simbithi eco-estate, working 5-7 days a week, from dawn till dusk. The number of days spent in the field varied depending on the success of daily data collection. Initially I aimed to collect a minimum of one full day per group per week; this was not always possible due to issues tracking the monkeys, such as poor visibility or monkeys leaving the confines of the estate. Furthermore, as increased tourist numbers on public holidays often made observations difficult, we avoided fieldwork on public holidays. We aimed to obtain at least one observation per monkey per day and, over the course of the month, collect one observation per monkey in the morning, midday and late afternoon (see section 2.3.2.1). If I was unable to collect all intended observations, then I spent extra field days to acquire these data. This was particularly important in winter when there were ~8 hours of daylight compared to ~16 hours of daylight in summer.

When behavioural fieldwork was not being conducted, I spent time in the laboratory conducting parasite analysis (see 2.3.3) at the University of KwaZulu-Natal, Pietermaritzburg Campus, KwaZulu-Natal, South Africa. Furthermore, after one year of behavioural fieldwork, I spent three months (April-July 2016) conducting more laboratory work.

2.3.2 Behavioural methods

2.3.2.1 Focal animal

I conducted behavioural observations from dawn till dusk, following one group per day. Two monkeys within each group were fitted with GPS (Global Positioning System) collars as part of a separate study. These collars provided invaluable data to my research, allowing me to locate groups at their sleeping site. Furthermore, collars gave GPS recordings at regular intervals that allowed me to track the location of a group if I had lost visual sight of them or they had left the estate. The day was split into three time periods (morning, midday, afternoon), with an aim to collect an observation per time slot per monkey per month for a one-year period (March 2016-February 2017). Twenty min. focal animal observations (Altmann, 1974) were conducted for all adults within each of the five groups. We used an ethogram to conduct observations (Table 2.1), grouping behaviours for time budget categories (Chapter 3) or extracting specific social behaviours (Chapter 5). I collected data using the Prim8 behavioural software (McDonald and Johnson, 2014) on a handheld Lenovo tablet.

2.3.2.2 Group scans

After six months of fieldwork, additional observations were collected to supplement social data in the focal observations, to ensure I collected enough data to sufficiently analyse social interactions for Chapter 5. I extended behavioural data collection by conducting instantaneous group scan samples every 30 min (Altmann, 1974). Again I followed the same ethogram (Table 2.1) and used the Prim8 behavioural software (McDonald and Johnson, 2014) on a handheld Lenovo tablet.

2.3.3 Anthropogenic measures

During dawn until dusk follows of each group, I used all occurrence sampling to record all interactions between humans and vervet monkeys. I identified a human related incident as any occasion when at least one vervet monkey interacted with humans or their possessions (car, house, bin etc.). For positive human incidents, I included any form of human-food consumption (e.g. bread, fruit, pizza), an incident was classed as terminated once all human-food was consumed, if the monkeys then obtained human-food after 20 minutes we classed this as a new event. Negative human incidents were classed as any form of human aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and risk of injury. I classed an incident as terminated once all parties had retreated and we recorded new events if there had been no incident in the prior 20 minutes. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]). I calculated a rate (frequency/month) per group based on how many incidents were observed according to hours of field observation each month.

Table 2.1 Ethogram used to measure the behavioural repertoire of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

Behaviour	Definition	Recipient
Aggression		
Eyebrow raise	Aggressive grimace, in which the eyebrows are raised, and the head is thrust forward [A]	Yes
Vocal threat	Low intensity call or chatter directed to other group member [A]	Yes
Alarm call	Loud harsh sound, mouth open head bobbing, used to highlight threat [A]	No- but note was made on assumed threat (e.g. dog, other group, crowned eagle)
Threat	Monkey opens its mouth without showing its teeth, flaps its ears, stares at its opponent, or slaps its hand on the ground.	Yes
Physical attack	Monkey attacks another animal biting, grabbing, slapping or chasing another monkey	Yes
Aggressive threat	Aggressive head-down stance; hindquarters and tail are held high, while the monkey crouches on its arms with head thrust forward. Monkey advances and retreats rapidly, continually facing and grimacing at the offender.	Yes

Submissive	Submissive behaviour including retreats, turns away, crouches, and facial grimaces [B]	Yes
Redirected aggression	Monkey threatens a subordinate individual, immediately after receiving aggression from a more dominant monkey [B]	Yes
Displace	Another individual moves from their position because of participants movements [C]	Yes
Alliance support	Third party actively joins ongoing conflict and threatens focal individual's opponent [B]	Yes
Other aggressive	Any aggressive behaviour that does not fit into the above categories.	Yes
Affiliative behaviour		
Eliciting vocalisation	Referred to as a ‘war-hor-hor’ sound mouth partially open. Used for approval and contact as well as vision of desired object [A]	
Grooming	Focal monkey grooms another monkey (defined as picking through and/or slow brushing aside the fur of another individual with one or both hands) [D]	Yes
Groomed	Another monkey grooms focal monkey (defined as picking through and/or slow brushing aside the fur of another individual with one or both hands) [D]	Yes
Proximity	Focal monkey within arms distance of another monkey	Yes

Social play	Highly active and non-aggressive social behaviour (including "rough and tumble")[E]	Yes
Other social	Interactions with at least one other monkey including both affiliative and agonistic behaviour that do not fit any above categories[FG]	Yes
Other		
Self-directed	Grooms self, scratches any part of body using hand or foot vigorously[H]	
Yawn	Involuntary opening of mouth widely and inhale due to tiredness or boredom[H]	
Foraging	Actively searching for food items before feeding, including actively moving objects looking for food, cleaning food items and hunting for invertebrates. Also includes directly consuming food items found[FG]	
Resting	Subject is in an inactive posture that excludes interacting with others, in a motionless position for longer than five seconds[F]	
Locomotion	Including all types of locomotion not associated with any other activity, for example walking, running, climbing, and jumping[FG]	
Sexual contact	Mounting, presentation (sexual display), intercourse.	Yes

Positive human incidents	Monkey enters human residence or interacts with other urban structure to obtain human-food or is directly provisioned by humans.
Negative human incidents	Any form of human aggression directed towards vervet monkeys (chase, rocks thrown etc.).
Out of sight	Animal was obscured from view

Reference papers: [A]: (Brain, 1965), [B]: (Fraser and Aureli, 2008), [C]: (Cowlishaw, 1991), [D]: (Schino et al., 1988), [E]: (Fedigan, 1972), [F]: (Saj et al., 1999), [G]: (Ménard et al., 2013), [H]: (Castles et al., 1999)

2.3.4 Natural versus human-food

I recorded consumption using focal animal sampling, noting all events when a monkey was seen foraging (including moving objects/searching for food before feeding) and feeding (manipulating/picking and actually eating items) (Menard et al 2013). I recorded the identity of the food source consumed as either natural food or human food. I classed natural food as any form of plant (including aesthetic garden plants), invertebrates, small vertebrates or eggs consumed. I classed human food as high value human derived resources obtained through provisioning or retrieved from human residence, such as bread and pizza. I also calculated an estimate of natural food availability, following practiced phenology protocol (plants only). I conducted five randomly placed walking transects within each troops' home range noting all specimens $\geq$ 10cm diameter at breast height (Chapman et al., 2005; Marshall and Wich, 2013). I retrospectively identified windows of fruit and flower availability using horticultural records for the region (Bloom, 2010) as in some previous studies (Blake, 1990; Wirminghaus et al., 2001). I ranked fruits according to stage of development using these same records (0= no fruit, 2= unripe, 3= ripe, 4= moribund) to create an estimate of monthly natural food abundance.

2.3.5 Parasitology methods

2.3.5.1 Faecal sampling

For parasite collection and analysis, I followed standardised protocol defined by Gillespie (2006), and made small adjustments to account for facilities and equipment available. I collected faecal samples opportunistically throughout the day, immediately after defecation. Samples were also collected if an animal was trapped or injured and had to be sedated by estate management, upon sedation animals often defecated as a reaction to the administered anaket. I noted the appearance of the sample including consistency (solid, soft, runny), presence of blood or mucus, presence of tapeworms or adult/larval nematodes (if possible), or any other noteworthy features. Using latex gloves, I took a sample of faeces from the centre of the stool (not including any outer elements e.g. vegetation/soil, to avoid contamination by free-living nematodes in the immediate environment). I then homogenised the sample by hand to make sure that there was an even representation of the centre of the faecal matter. I placed approximately 2 g of the homogenised sample into a 15ml wide-mouthed sterile tube that was pre-prepared with 10 ml of 70% ethanol. After sealing the tubes, I labelled them with date, time, species, age class (adult/juvenile) and sex (or monkey ID if known), group and GPS location using a Garmin Etrex 10. I then shook tubes vigorously to maximise contact between sample and ethanol. Samples were stored at an ambient temperature until parasite analysis was conducted.

2.3.5.2 Parasite counts and identification

I conducted all parasite analysis in the UKZN laboratory. I shook tubes to ensure samples were homogenised, I then transferred half of this sample into a 50 ml tube for the centrifuge. I span samples in the centrifuge at 4000 rpm for six min. I removed excess ethanol from the sample, leaving the remaining faecal pellet. I then weighed the tube containing the faecal pellet; subtracting this weight from the original tube weight to give the weight of the faecal sample. I filled the tube to 15 ml with distilled water and shook the tube thoroughly and centrifuged samples were again at 4000 rpm for 6 min. I poured of the supernatant and again weighed the tube and recorded the faecal pellet weight. I added a further 6 ml of distilled water and then shook the sample thoroughly. I next strained the sample through a small sieve (1mm mesh) into a clean beaker, added another 6 ml of distilled water and again strained into the same beaker, I then decanted the strained fluid into a 15 ml falcon tube. I next spun the sample at 4000 rpm for 6 min. and poured the supernatant off leaving only the faecal pellet. I agitated the tube to dislodge the pellet and filled the tube with 15 ml of $NaNO_3$ solution and inverted five times. I used a pipette to take a sample from the centre of the tube and used this to fill both chambers of a McMaster slide.

After two min. when the solution had settled in the McMaster slide, I scanned the slide using the Å~10 objective lens of a compound microscope and identified and counted presence of any parasite eggs, larvae, and cysts. I then scanned the slide under Å~40 objective lens to confirm presence or absence of protozoan cysts. I measured the length and width of individual eggs, cysts, and larvae using a calibrated micrometer, and digitally photographed representatives.

Chapter 3

Positive and negative human interactions influence ranging patterns of vervet monkeys

This paper has been formatted with intention to submit to the International Journal of Primatology.

Generalist species such as vervet monkeys are able to thrive in the urban landscape by taking advantage of the environment's positive attributes such as human-food resources (Kristan et al., 2004). However, utilising urban space comes with costly negative associations, such as aggression from humans and increased risk of injury (Lokschin et al., 2007; Pragatheesh, 2011). In this Chapter, I address how the positive and negative aspects of the anthropogenic landscape influence the ranging behaviour of urban vervet monkeys.

Abstract

Many non-human primates adjust their behaviour and thrive in human-altered habitats, including towns and cities. Studying anthropogenic influences from an animal's perspective can provide a greater understanding of their behavioural flexibility, presenting important information for human-wildlife cohabitation management plans. Currently, such research considers either positive or negative aspects of human-wildlife interactions, and research on potential interactions between these aspects is lacking. Vervet monkeys, *Chlorocebus pygerythrus,* are a suitable species to address this gap in research as they are common across KwaZulu-Natal, South Africa and are tolerant of urbanisation, though they are understudied in urban landscapes. Here we determined how the frequency and nature of human-monkey interactions both positive (food-related) and negative (aggression from humans), affected vervet monkey ranging patterns in an urban environment. Over a year, we assessed the movement patterns of three groups of urban vervet monkeys, considering both 95% and 50% kernel density estimates of their home ranges alongside daily path lengths and path sinuosities using general linear mixed models. Overall, we found that positive and negative human interactions within the urban landscape affected all measures of ranging to some degree. The core home ranges of vervet monkeys increased with a higher rate of positive human incidents and their total home range increased with interaction of both positive and negative human incidents. Furthermore, vervet monkeys were less likely to respond (i.e. increase daily path length or path sinuosity) to human aggression when food rewards were high, suggesting that effective management should focus on education programmes to reduce human-food foraging opportunities. Our results highlight the previously neglected interaction between positive (food-related) and negative (aggression from humans), implying an attraction-avoidance scale for urban vervet monkey ranging patterns.

Introduction

Anthropogenic pressures are a growing issue for wildlife management (McKinney, 2008), particularly with global increases in the rate of anthropogenic changes to land use, including urbanisation. Understanding how wildlife are able to adapt behaviourally in an anthropogenically disturbed environment is essential to provide guidance for human-wildlife cohabitation and conservation management (Dickman, 2010; Hockings et al., 2015; Nowak and Lee, 2013).

As anthropogenic disturbance has increased, so too has research on wildlife living in an anthropogenically altered landscapes (McKinney, 2008). With increased rates of environmental change (Wigginton et al., 2016), almost all wildlife live in an environment that is subject to some level of anthropogenic disturbance (Soulsbury and White, 2015). However, it should be noted that the effects of this environmental change on wildlife varies dramatically with the nature of the disturbance (McKinney, 2008); such as habitat loss (Estrada and Coates-Estrada, 1996), tourism (Brennan et al., 1985; Fuentes et al., 2007; McKinney, 2014) and modified landscapes (Fuentes and Hockings, 2010).

Human-wildlife cohabitation and the associated interactions can be beneficial and/or detrimental to an animal depending on its flexibility (Ditchkoff et al., 2006; McKinney, 2008). The term ‘human-wildlife conflict’ is commonly used to classify negative interactions between humans and wildlife (Graham et al., 2005), however, there is no common term used to classify positive human-wildlife interactions. Currently, there is a bias in literature to focus on these interactions from a human perspective (Soulsbury and White, 2015), yet to understand urban wildlife, possible costs and benefits to the animals should also be considered. The human-modified landscape in urbanised areas provides increased access to anthropogenic food sources; but where wildlife feed on human crops and food, this foraging technique is often viewed as a ‘problem’ behaviour for humans rather than as a beneficial foraging strategy for primates (Riley, 2008; Strum, 2010). From a wildlife perspective, using the urban landscape has many negative consequences, such as increased human aggression and disease transmision (Beisner et al., 2015). However, most studies on the negative effects of the anthropogenic landscape for urban wildlife, measure the avoidance of human inhabited areas (Gehrt et al., 2009; Graham et al., 2009; Prokopenko et al., 2017), rather than directly measuring human aggression towards wildlife. Furthermore, most literature on human–wildlife cohabitation focuses on either positive or negative aspects of human–wildlife interactions (Angelici, 2016; McLennan et al., 2017; Seoraj-Pillai and Pillay, 2016; Woodroffe et al., 2005). No study has yet assessed how human-food consumption and aggression from humans interact to affect ranging patterns.

Some non-human primate species (herein known as primates), such as macaques, baboons and vervet monkeys can adjust and thrive under the challenging pressures of the changing anthropogenic landscape (Priston and McLennan, 2013; Saj et al., 1999; Strum, 1994). Among primates, research has shown a degree of preferences for anthropogenic features that influence habitat selection, e.g. a preference for increased food resources (Bryson-Morrison et al., 2017; Bryson-Morrison et al., 2016; Hoffman and O'Riain, 2012a) and avoidance of noise disturbance (Duarte et al., 2011). Research has also shown how anthropogenic influences affect ranging patterns, generally highlighting that greater anthropogenic disturbance reduces home range size (Altmann and Muruth, 1988; Hoffman and O'Riain, 2011, 2012b; McKinney, 2011; Riley, 2008; Saj et al., 1999; Sha and Hanya, 2013). However, such research has only assessed relatively mild anthropogenic disturbance and knowledge of ranging patterns of urban primates is limited to one study that considered two geographically distant macaque species, showing they responded to anthropogenic disturbance in similar ways, with decreased home range sizes and daily path lengths (Klegarth et al., 2017).

Vervet monkeys, *Chlorocebus pygerythrus*, can thrive in urban landscapes (Patterson et al., 2018, 2017; Saj et al., 1999), exhibiting behavioural flexibility to adapt to anthropogenic disturbance (Chapman et al., 2016). It is therefore an ideal species to examine the effect of variation in human interactions on ranging behaviour. Despite prior research on vervet monkey home range patterns (Isbell et al., 1991; Willems et al., 2009), little is known about the ranging behaviour of urban vervet monkeys which is important for developing appropriate management plans (Beckmann & Berger, 2003; Hoffman & O'Riain, 2012a).

In this study, we consider anthropogenic factors from a monkey's perspective, assessing how positive (human-food) and negative (aggression from humans) anthropogenic factors influenced vervet monkey ranging patterns in an urban environment. We predicted that vervet monkey urban home ranges would decrease because of increased access to calorie-rich resources in the urban environment (Hoffman and O'Riain, 2011; Klegarth et al., 2017). Furthermore, as we found that time spent moving increased after the occurrence of human aggression directed towards vervet monkeys in the study group (Chapter 4); we also predicted that daily path length and path sinuosity (directness of path) would be greater in groups that experienced more aggression from humans.

Methods

Study population

We conducted our study at Simbithi eco-estate, a private gated estate, Ballito, Durban north coast, KwaZulu-Natal, South Africa (29.5140° S, 31.2197° E). The 4.9 km^2 estate was previously two sugar cane farms that were converted to an ecologically considerate urban housing development (Simbithi eco-estate, 2017, *pers. comm.*). The estate contains a variety of housing options along with leisure facilities, restaurants, an equestrian centre, a golf course and small areas of human-made riverine coastal forest. Although discouraged by the estate management, vervet monkeys are fed by humans in residential homes and at leisure facilities. Groups of monkeys obtain human-food from residential kitchens, refuse sites and leisure facilities. Using McKinney's (2015) anthropogenic disturbance classification system, we coded the field site as HG_3LC_5, (H: non-protected high human population density urban area, G_3: >25% of total diet is stolen or provisioned human-foods, varying between groups, L: interactions with locals and researchers daily including provisioning, C_5: reduced predation but association with human conflict).

Seven groups of vervet monkeys lived within Simbithi eco-estate; we studied 3 of these groups that used the housing estate, selecting those that confined their activity to the estate to ensure observer safety because of high crime rates in the local area. Group size varied from 23-42 individuals, average counts: Farmyard group (23): 4 males, 10 females, 9 juveniles; Heron group (42): 5 males, 14 females, 23 juveniles and Savannah group (25): 4 males, 10 female, 11 juveniles. This was the first study of these vervet monkeys, so their history was unknown.

Data Collection

HT conducted all fieldwork following three groups over 12 months from March 2016-February 2017. We followed each group on average for four days a month equalising follows across groups (Means ± SD: Farmyard 3.9 ± 0.57 days, Heron 4.1 ± 0.51, Savannah 4 ± 0.69). We followed groups from dawn to dusk, recording the group location at sunrise at their sleep site and then continuing to record their location every 30 min. standing at the centre of the group with a hand-held global positioning system (GPS) (Dakota 20, Garmin Inc., USA). We used 30-min intervals to calculate all four ranging measures, total home range (95%), core home range (50% KDE), path length and path sinuosity. We chose 30-min intervals to adequately reduce autocorrelation whilst still representing biologically realistic data (Asensio et al., 2012).

We used all occurrence sampling to record all interactions between humans and vervet monkeys during dawn to dusk daily follows. We identified a human related incident as any occasion when human(s) and at least one vervet monkeys interacted. We recorded incidents as positive (human-food) and/or negative (human-monkey aggression). We considered a positive event as terminated once all the human-food had been consumed and recorded new events only when there had been no interactions/human-food consumption for at least 20 minutes. Negative human incidents were classed as any form of human aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and risk of injury. We classed an incident as terminated once all parties had retreated and we recorded new events if there had been no incident in the prior 20 minutes. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]). We calculated a rate (frequency/hour) for both positive and negative human incidents per group for each month.

We screened GPS data from each group for outliers, removing two days of data for the Savannah group because of implausible GPS points (one in June and one in August). We summarised ranging data using four measures. To assess home range, we considered total home range area (95% isopleths) and core area (50% isopleths) (Laver and Kelly, 2008) and analysed GPS points using the kernel density estimator (KDE) (Seaman and Powell, 1996). We measured KDE using the *adehabitat* package in R applying the kernel estimator function *kernelUD* (Calenge, 2006). We calculated daily path length for each group by summing the distances between successive GPS locations using the saga processing toolbox in QGIS (QGIS, 2015). Finally, we assessed the directness of travel routes by calculating the path sinuosity. We used QGIS to obtain the distance between the first and last point of the day, giving us the most direct path length. We calculated path sinuosity by dividing the daily path length by the direct path length (e.g. monkeys that used a less direct path had a higher sinuosity) (Benhamou, 2004).

Statistical analysis

We conducted all analyses using R statistical software version 3.3.2 (R project, 2013) with the significance level set at $P < 0.05$. We specified four generalised liner mixed models using the *lme4* package (Bates et al., 2015). We modelled each ranging measure separately, using monthly values for total and core home range area (N=36) and mean monthly values for daily path length and sinuosity (N=36). Our main results did not change when we used monthly rather than daily values for path calculations; we therefore used monthly path values in our models; so our results were more broadly comparable with the literature. We used the same model structure for all four ranging measures; we created *a priori* maximum model that included mean monthly group size, positive human incidents and negative human incidents as fixed effects as well as including an interaction between positive and negative human incidents. To account for repetition in the data set we included month as a random effect. To ensure data were not auto-correlated monthly we tested data graphically in R using the *lctools* package (Kalogirou, 2016); all responses fell within the confidence intervals and therefore were not temporally auto-correlated. We calculated the VIF (variation inflation factor) of each predictor for inclusion in our model using the *car* package (Fox and Weisberg, 2011), setting the VIF limit at $P< 3$ (Zuur et al., 2010). Dependent variables were not normally distributed according to a Shapiro-Wilks test ($P < 0.05$) and visual inspection using QQ plots (Ghasemi and Zahediasl, 2012). We therefore used general linear mixed models with a Gamma distribution, allowing us to model non-normally distributed data with a random effect.

Due to our small sample size (*N* = 36) in a model with four predictors, we bootstrapped our model to obtain confidence intervals (CI), resampling 1000 times strengthening the model robustness (Yung and Chan, 1999). Furthermore, we used a Kenward-Roger correction in the *afex* package in R (Singmann et al., 2015) to minimize small sample size bias and guard against inflation of Type 1 error rates (McNeish, 2017; Stroup, 2015). We present the Kenward-Roger P values as well as the bootstrapped CI; if the upper and lower CI straddled 0 then we did not consider the variable significant. We assessed the fit of each model by graphically checking residuals for normal distribution and to check the assumptions of our model were not violated.

Ethical note

This study was purely observational. We adhered to the legal requirements of South Africa for the ethical treatment of primates under Liverpool John Moores University ethical permit number NK_HT/2017-6.

Data Availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Results

The three study groups varied in group size, total and core home range size, daily path length and sinuosity, as well as in the frequency of positive and negative incidences with humans (Table 3.1).

Table 3.1. Mean group size, human incidences and monthly ranging metrics ± SD for the three study groups of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

Group	Monthly group size	Positive human incidents (rate per hour)	Negative human incidents (rate per hour)	Total home range (km^2)	Core home range (km^2)	Path length (km)	Path sinuosity
Farmyard	23	0.33 ± 0.71	0.12 ± 0.06	3.96 ± 1.74	0.99 ± 0.31	4.66 ± 3.57	2.77 ± 2.57
Heron	42	1.08 ± 0.71	0.35 ± 0.21	1.89 ± 1.76	1.82 ±0.74	8.66 ± 4.24	8.54 ± 4.83
Savannah	25	0.42 ± 0.27	0.09 ± 0.06	4.17 ± 2.04	0.97 ± 0.95	5.68 ± 2.36	3.31 ± 2.33

Home range

There was a significant positive interaction effect between positive and negative human incidents on total monthly home range (Table 3.2, Fig. 3.1a). Increased positive human incidents decreased home range size; however, increased negative human incidents weakened this effect and a combination of higher positive and negative human incidents increased home range. Additionally, the core monthly home range was significantly larger for urban vervet monkeys that experienced higher levels of positive human incidents (Table 3.3).

Daily path length

There was a negative interaction effect on daily path length (Table 3.4, Fig. 3.1b). Negative human incidents were associated with increased daily path length when positive incidents were low, but when monkeys experienced both high negative and high positive events, they were less likely to move on and daily path length did not increase.

Path sinuosity

There was a significant negative interaction effect between positive and negative human incidents on path sinuosity; when positive human incidents were low, negative human incidents increased path sinuosity, however increasing positive incidents weakened this effect (Table 3.5, Fig. 3.1c).

Table 3.2 Results of GLMM model of factors influencing the total home range area (95% KDE) of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Estimate	Standard error	P value	Upper CI	Lower CI
(Intercept)	4.45	1.22	<0.001	3.91	6.83
Negative human incidents	-7.78	1.65	<0.001	-0.55	-1.71
Positive human incidents	-8.84	0.71	<0.001	-0.47	-2.66
Negative human incidents * Positive human incidents	**5.49**	**0.41**	**0.001**	**2.48**	**0.01**
Group size	0.02	1.77	0.725	0.03	2.091

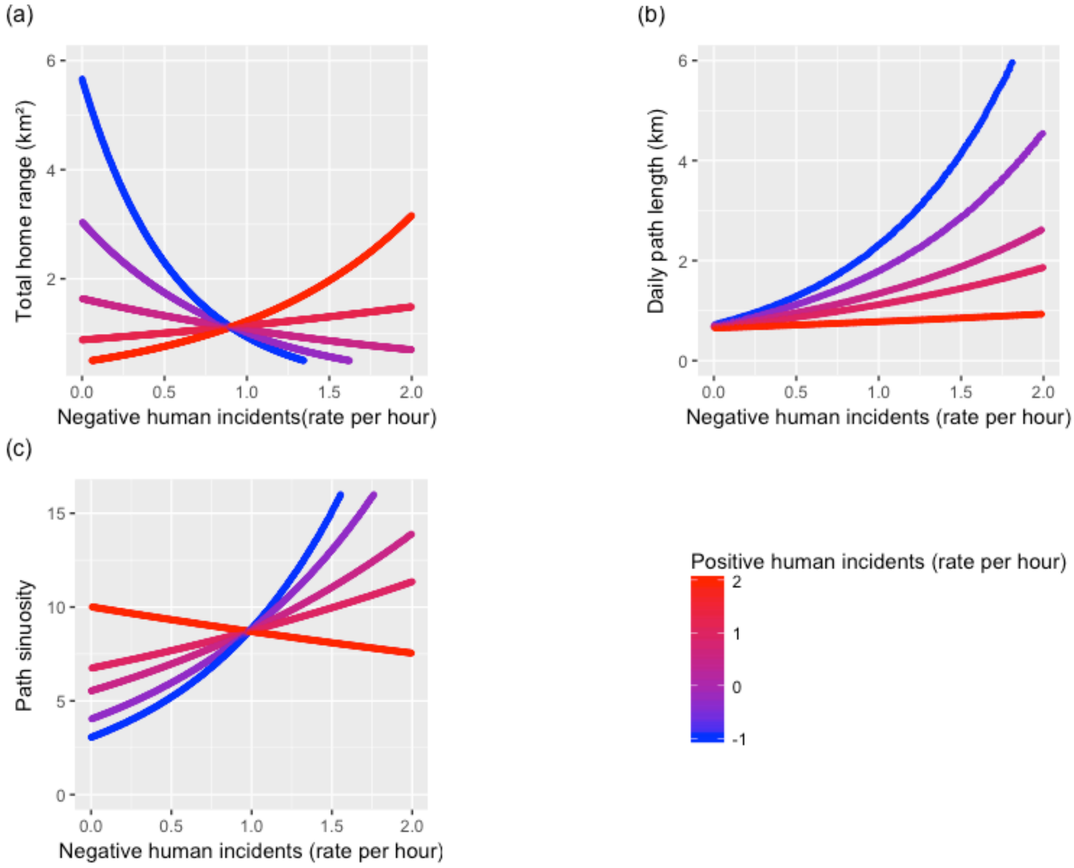

Fig. 3.1 Interaction between mean monthly rate of negative human incidents (rate per/hour) and the mean monthly rate of positive human incidents (rate per/hour) on the ranging patterns of three groups of urban vervet monkeys at Simbithi eco-estate, KwaZulu-Natal, South Africa. Where (a) shows the positive interaction effect on total home range (95% KDE, km^2), (b) shows the negative interaction effect on the daily path length (km) and (c) shows the negative interaction effect on path sinuosity.

Table 3.3 Results of GLMM model of factors influencing the total core range area (50% KDE) of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Estimate	Standard error	P value	Upper CI	Lower CI
(Intercept)	-2.74	0.47	<0.001	-0.66	-5.03
Negative human incidents	1.22	0.66	0.061	-0.91	0.56
Positive human incidents	**2.45**	**0.97**	**0.018**	**3.51**	**1.90**
Negative human incidents * Positive human incidents	0.01	0.68	0.083	-1.62	1.28
Group size	-1.20	0.07	0.546	-0.11	0.06

Table 3.4 Results of GLMM model of factors influencing the daily path length (km) of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Estimate	Standard error	P value	Upper CI	Lower CI
(Intercept)	1.06	0.01	0.078	0.03	1.75
Negative human incidents	-0.01	0.01	0.274	-0.81	0.81
Positive human incidents	-0.01	0.01	0.139	-0.81	0.77
Negative human incidents * Positive human incidents	**-0.05**	**0.01**	**<0.001**	**-0.92**	**-0.84**

Group size	0.26	0.01	0.051	-0.57	0.83

Table 3.5 Results of GLMM model of factors influencing the path sinuosity of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Estimate	Standard error	P value	Upper CI	Lower CI
(Intercept)	1.24	0.19	0.001	3.91	6.96
Negative human incidents	0.06	0.11	0.581	-0.49	1.73
Positive human incidents	0.28	0.10	0.005	0.49	2.67
Negative human incidents * Positive human incidents	**-0.09**	**0.11**	**0.042**	**-2.65**	**-0.06**
Group size	**0.31**	**0.09**	**0.001**	**0.08**	**2.11**

Discussion

All four measures of vervet monkey ranging patterns were influenced by anthropogenic disturbance. Furthermore, the interaction effect between both positive and negative human incidents strongly influenced movement patterns, highlighting vervet monkeys' behavioural flexibility to anthropogenic influence.

The interaction between positive and negative human incidents indicated that when the rate of negative human incidents was low, increasing positive human incidents decreased total home range size; however, increasing negative human incidents weakened this effect and an increased rate of positive and negative human incidents increased total home range size. Previous literature suggests that home range decreases in anthropogenically disturbed primates due to increased access to human resources (Klegarth et al., 2017; Saj et al., 1999). However, we suggest that increased total home range seen in this study, could be an avoidance strategy to reduce the likelihood of human-aggression, when it co-occurs with increased human-food consumption. Our result would therefore support previous research on wildlife in anthropogenic landscapes, showing that wildlife alter their ranging behaviour in order to avoid areas due to increased risk of aggression from humans (African elphants (*Loxodonta africana*), Graham et al., 2009; Elk (*Cervus elaphus),* Prokopenko et al., 2017).

Results also showed that vervet monkey core home range increased with a higher rate of positive human incidents. Research on Tonkean macaques, *Macaca tonkeana*, has showed that they express flexibility in an anthropogenically disturbed habitat, by ranging further to where known resources are predictably available (Riley, 2008). It is possible that vervet monkeys in this study with a higher rate of positive human incidents ranged further in order to increase human-food consumption at predictable locations, thus increased their core home range. In this case the energetic cost of movement was likely outweighed by the benefit of high calorific human-food (e.g. bread, cake, pizza). Although our home range results do not support our prediction for decreased core home range under anthropogenic pressures they do partially support our prediction for the total home range. Overall home range results show a consistent trend for human influences increasing the home range of urban vervet monkey, therefore our results highlight the need to quantitatively measure anthropogenic disturbance.

For daily path length, we found a negative interaction between positive and negative human incidents. Although human aggression increased daily path length, the benefit of human-food appeared to offset this increase, suggesting a decreased likelihood of moving on. Our results support previous findings (Klegarth et al., 2017; Saj et al., 1999), that anthropogenically disturbed primates decrease daily movement due to anthropogenic resources. Further, our results show similar patterns to that of (Chapter 4), supporting the use of a positive negative interaction, showing that vervet monkeys' movement increased with human aggression, yet positive human incidents weakened this affect. Overall, daily path length findings suggest that vervet monkeys' movement is highly dependent on the availability of high value food resources. Crucially, our results suggest that increased human aggression is ineffective in reducing human-food foraging strategies when there is access to human resources.

Our path sinuosity measures showed similar findings to that of our daily path length, that negative human incidents were related to increased path sinuosity; however, with increasing positive human incidents this effect weakened, and paths became more direct. Again, our results support previous literature that suggests vervet monkeys movement is reduced with increased access to high value food (Chapter 4; Saj et al., 1999). Interestingly when there was no negative human incidents, a higher rate of positive human incidents was related to increased path sinuosity. Although this finding is contrasting to our original argument and previous research that suggests human resources should decrease primate movement, some studies have shown primates increase travel to improve spatial feeding strategies (Riley, 2008; Sha and Hanya, 2013). It is possible that increased path sinuosity may be a consequence of vervet monkeys being more exploratory when positive human incidents are high (reward) and negative human interactions are low (deterrent). Results for path sinuosity therefore suggest obtaining high value human derived food is a beneficial foraging strategy (Strum, 2010) and that vervet monkeys use adaptive strategies dependent on human influences, highlighting the complex association of benefits and costs for primates residing in urban areas. Although it should be noted that for these interpretations of path choice, the effect of human interactions could simply be due to the direction of their path, that they did not experience an interaction rather than an effect of human incidents.

We can use our results to make recommendations for more effective human-primate management plans. Our results highlight that vervet monkeys are less likely to respond (i.e. increase daily path length or path sinuosity) to human aggression when food rewards are high. We suggest that plans to minimise human aggression should focus on improving education of preventative measures to reduce opportunities to obtain human-food, particularly reducing access to anthropogenic food or refuse. Although we created an estimate of natural food availability for these groups (see Chapter 2 section 2.3.4 for natural food methods), due to our small data set we did not include natural food in our ranging analysis in order to avoid model over-parametisation; when we did include our natural food estimation within our analysis our main effects did not change. Nevertheless, the interaction between natural food and human-food consumption could provide an interesting view on vervet monkey foraging strategies and therefore should be considered in future research.

In conclusion, our findings highlight the previously overlooked interaction of positive and negative characteristics of urban living (McLennan et al., 2017) that create an attraction-avoidance scale within the anthropogenic landscape. As predicted, ranging patterns in urban vervet monkey groups were strongly affected by anthropogenic influences of the urban landscape.

Chapter 3 summary

In this chapter, the effect of positive and negative aspects of the anthropogenic landscape on multiple aspects of ranging behaviour were considered, including core and total home range, daily path length and path sinuosity. Our results imply an attraction-avoidance scale for urban vervet monkey ranging patterns, highlighting a need to consider the previously overlooked interaction between positive and negative influences of the urban landscape in other aspects of urban wildlife ecology. In the next chapter, I will address the effect of positive and negative human influences applying this same interaction to, time budget analysis.

Chapter 4

Anthropogenic influences on the time budgets of urban vervet monkeys

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In Chapter 3, positive and negative human incidents influenced urban vervet monkey ranging patterns. I therefore expect time spent moving to be affected by human interactions and that this in turn may result in a trade-offs in behaviours, illustrative of the resources and time available to vervet monkeys (Dunbar et al., 2009). In this chapter, I build on Chapter 3's findings and assess flexibility in urban vervet monkey time budgets to anthropogenic influences.

Abstract

Continuing urban developments are ecologically changing many landscapes. A greater understanding of how wildlife adapt behaviourally to these changes is necessary to inform management decisions. Time is a valuable resource to wildlife and a reflection of ecological pressures on the behavioural repertoire of an animal. Data on urban vervet monkey, *Chlorocebus pygerythrus,* time budgets are generally limited and dated. We aimed to investigate the effect of anthropogenic influences, both human-food consumption (positive) and aggression from humans (negative) on the time budgets of vervet monkeys in an urban landscape. We collected 20 min. focal animal observations and used generalised linear mixed models to assess the variation in time budget between five urban vervet monkey groups differing in anthropogenic contact over one year. We recorded positive and negative anthropogenic interactions. Our results showed seasonal influences across all behaviours, following standard ecological predictions. Furthermore, anthropogenic disturbance influenced all aspects of vervet monkey time budgets to some degree. Increased negative human incidents reduced time spent resting, for the other 3 behavioural categories we found a significant interaction between positive and negative human incidents. Increased positive human incidents decreased foraging; however, increased negative human incidents weakened this effect. Movement increased as the rate of positive human incidents decreased, and the rate negative human incidents increased. Lastly, social interactions decreased with negative human incidents; however, this effect weakened with increasing positive human incidents. Overall, vervet monkeys exhibited behavioural flexibility in the urban landscape. We suggest a complex association of costs and benefits to urban living.

Introduction

Increased human populations and urban developments are transforming many wildlife habitats (McKinney, 2006). Human expansion has led to a growing interest in understanding behavioural responses of species to urbanisation for urban management plans (e.g. Jokimäki et al., 2011). Wildlife can adapt to these changes in many ways including modifying foraging behaviour, predator behaviours and activity patterns (Jokimäki et al., 2011). Information on how wildlife adapt behaviourally to these changes can be key for management decisions (Ditchkoff et al., 2006; Marzluff et al., 2001). Time budgets have been applied to a variety of species to study the effect of varying levels of anthropogenic disturbance (e.g. Jokimäki et al., 2011). However, studies including high-density towns and cities are scarce, furthermore, positive associations of urban living for wildlife behaviour are rarely considered, despite being necessary, to develop suitable management plans (McLennan et al., 2017).

Understanding the relationship between an animal and its environment can provide essential information for conservation management and urban planning (Patterson et al., 2018). Time budgets provide a useful method to test ecological hypotheses (Isbell and Young, 1993) as they allow the representation of time allocation where trade-offs in behaviours are illustrative of the resources and time available (Dunbar et al., 2009). Time budget analyses have been employed across urban wildlife to demonstrate the effects of urbanisation and landscape changes (burrowing owls, *Athene cunicularia hypugaea*: Chipman et al., 2008; gray squirrels, *Sciurus carolinensis:* Parker et al., 2014; bottlenose dolphins, *Tursiops aduncus*: Steiner, 2012).

Rapid human population growth and land-use changes have transformed many primate habitats (Estrada et al., 2012; McKinney, 2015) and have resulted in a directional shift towards ethnoprimatology (Fuentes and Hockings, 2010; Hockings et al., 2015; McLennan et al., 2017; Strier, 2017). Although time budgets have been applied to assess primate behavioural flexibility to landscape change, the applications of these findings are largely limited to macaques (*Macaca sp.*) and baboons (*Papio sp.*) (McLennan et al., 2017). Anthropogenic assets such as high value food have been shown to decrease foraging time (Hoffman and O'Riain, 2011; Jaman and Huffman, 2013; Saj et al., 1999; Sha and Hanya, 2013), which often occurs in parallel with a decrease in movement (Jaman and Huffman, 2013; Wong and Candolin, 2015) and associated with an increase in social interactions (Jaman and Huffman, 2013; Saj et al., 1999; Scheun et al., 2015).

Seasonality is a strong predictor of time budgets in wild primates (Fan et al., 2008; Hendershott et al., 2016; Zhou et al., 2007); however, primates living in urban landscapes are often buffered against the effects of seasonality. Reports of seasonality on anthropogenically influenced monkeys are mixed. Some studies show no influence of seasonality, expressing this as a result of a continuous supply of high value resources available (Altmann and Muruth, 1988; Eley, 1989). Recent studies of more anthropogenically disturbed primates have shown that seasonality is influential on time allocation and suggest this to be an adaptive exploitive behaviour (macaques; Jaman and Huffman, 2013, and baboons; van Doorn et al., 2010).

Prior research has assessed aspects of the landscape that influence the success and survival of vervet monkeys, *Chlorocebus pygerythrus,* in a modified anthropogenic environment (Chapman et al., 2016; Patterson et al., 2016). Although studies have considered time budgets of anthropogenically disturbed primates, no study has has yet assessed the flexibility in time budgets of an adapted generalist primate living in such a highly human populated urban setting. Furthermore, past research has only considered the consequences of either human aggression (negative aspects) or access to high value resources (positive aspects) (McLennan et al., 2017). Studies examining the interaction between these negative and positive aspects are needed. As vervet monkeys continue to succeed in the ecologically developing urban landscape, human-wildlife cohabitation often results in negative consequences for vervet monkeys (Wimberger et al., 2010; Wimberger and Downs, 2010). Vervet monkey population expansion in urban lansdscapes raises concerns both for vervet monkey wellbeing (Wimberger et al., 2010; Wimberger and Downs, 2010) and ecological biodiversity conservation (Díaz et al., 2006).

We aimed to investigate the effect of anthropogenic influences, both human-food consumption (positive) and aggression from humans (negative) on the time budgets of vervet monkeys in an urban landscape. In order to do this, our main prediction focussed on ecological and landscape constraints. We predicted that anthropogenic disturbance would affect urban vervet monkeys' time budgets (Jaman and Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). We predicted that positive anthropogenic aspects would decrease movement and foraging and increase social behaviour as a trade off in time availability.

Methods

We conducted our study at Simbithi eco-estate, a private gated housing estate in Durban north coast, KwaZulu-Natal, South Africa (29.5140° S, 31.2197° E). The estate was previously two sugar cane farms that were developed 24 years ago to form a 4.9 km^2estate (Simbithi eco-estate, 2017, *pers. comm.*). The estate was comprised of a variety accommodation options including apartment blocks, retirement complexes and general housing within a green mosaic. The estate had other anthropogenic leisure developments including restaurants, shops, fitness facilities, a golf course and a hotel. The estate encouraged wildlife research to help biodiversity management plans. Residents had mixed responses to vervet monkey presence ranging from actively encouraging vervet proximity to humans (intentional feeding by humans) to actively deterring vervet monkeys from human property (human aggression).

Vervet monkeys are commonly found in urban settings of KwaZulu-Natal and therefore provided a candidate model to assess behavioural flexibility under anthropogenic changes (Chapman et al., 2016; Saj et al., 1999). The estate contained seven groups of vervet monkeys (Simbithi eco-estate, 2017, *pers. comm.*), although this study only considered the five groups that regularly stayed within the borders of the estate. Group size varied from 14-42 individuals (Ballito (14): 3 males, 6 females, 5 juveniles; Farmyard (23): 4 males, 10 females, 9 juveniles; Savannah (25): 4 males, 10 female, 11 juveniles; Goodies (29): 5 males, 10 females, 14 juveniles; Heron (42): 5 males, 14 females, 23 juveniles). This was the first study on these groups, so their history was unknown. Most monkeys were well habituated to humans due to the regular proximity to human residence. All adult vervet monkeys were identifiable via distinguishable markings, therefore, all 71 adult vervet monkeys were observed for this study.

We collected data from March 2016 - February 2017. We conducted observations from dawn until dusk (up to 8h in winter and 16h in summer) for a minimum of three weeks per month. Where possible we conducted a minimum of one observation per monkey per month, spread throughout the day (mean ± SD number of observations per group in the morning = 217 ± 33, midday = 251 ± 19 and afternoon = 286 ± 40). In total 3774 focal animal observations were conducted across all groups, averaging 650 ± 173 minutes per monkey.

We used focal animal sampling techniques (Altmann, 1974) to observe each individual for 20 min., sampling all group members before repeating observations in each month. We chose four key mutually exclusive categories to represent time budget defined as foraging: a monkey actively searching for food items before feeding and directly consuming food items found (food items included: plants, aesthetic garden plants and human derived food) (Ménard et al., 2013; Saj et al., 1999); movement: included all types of locomotion not associated with any other activity, for example walking, running, climbing, and jumping (Ménard et al., 2013; Saj et al., 1999); resting: monkey in an inactive posture that excludes interacting with others, in a motionless position for longer than five seconds (Saj et al., 1999); social: monkey interacting with at least one other monkey including both affiliative and agonistic behaviours (Ménard et al., 2013; Saj et al., 1999).

During dawn until dusk follows of each group, we used all occurrence sampling to record all interactions between humans and vervet monkeys. We identified a human related incident as any occasion when at least one vervet monkey interacted with humans or their related possessions (car, house, bin etc.). For positive human incidents we included any form of human-food consumption (e.g. bread, fruit, pizza). An incident was classed as terminated once all human-food was consumed, if the monkeys then obtained human-food after 20 minutes we classed this as a new event. Negative human incidents were classed as any form of human aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and risk of injury. We classed an incident as terminated once all parties had retreated and we recorded new events if there had been no incident in the prior 20 minutes. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]).

To support our monthly human values, we also created an estimated monthly value of natural food availability, classing natural food as any form of plant including aesthetic garden plants. Following practiced phenology protocol, we conducted five randomly placed walking transects within each group's home range noting all specimens $\geq$ 10cm diameter at breast height (Marshall and Wich, 2013). We retrospectively identified windows of fruit and flower availability using horticultural records for the region as in some previous studies (Blake, 1990; Wirminghaus et al., 2001). We ranked fruits according to stage of development using these same records (0= no fruit, 2= unripe, 3= ripe, 4= moribund) to create an estimate of monthly natural food abundance. We split our data seasonally based on the four calendar seasons (summer: November-March, spring: September-October, autumn: April-June, winter: July-September) (SANBI, 2017).

Statistical analyses

For human values, we calculated a monthly rate (per hour) per group based on how many incidents were observed according to hours of field observation each month. For behavioural observations we converted the total duration(s) of behaviour to percentage of time spent performing that behaviour per focal observation. Behavioural data were found to be not normally distributed using the Shapiro-Wilk's test ($p \leq 0.001$) (Ghasemi and Zahediasl, 2012). We calculated the variation inflation index of each predictor for inclusion in our model using the *car* package (Fox and Weisberg, 2011), setting the inclusion level at <3 (Zuur et al., 2010). All data were analysed using R statistical software version 3.3.2 (R project, 2013) and the significance level set at $p \leq 0.05$.

As data were non-parametric, we ran a generalised linear mixed model on each behavioural category as the dependent variable using the *lme4* package (Bates et al., 2015). We created *a priori* maximum models that included positive human incidents, negative human incidents, natural food availability, group size and season as fixed effects. To control for repeated observations on individuals we included monkey identity as a random effect. Furthermore, we ran an interaction between positive and negative human incident rates. We ran all models with a gamma error distribution using a log link function.

To test whether the fixed effects explained variation, we used a likelihood ratio test (‘Anova’ command set to “Chisq”) comparing the maximum model against our null model (dependent variable plus one) (Zuur et al., 2009). If the maximum model was significantly better, we then ran a second likelihood ratio test on the maximum model to test the significance of each fixed effect (Zuur et al., 2009).

Results

Although we did not statistically test the relationship between natural food availability and time spent foraging on different food resources, we provide a visual representation (Fig. 4.1). We show that when high natural food is available monkeys increase their foraging on natural food sources; however, time spent feeding on human-food did not decrease in the same way as time feeding on natural food increased.

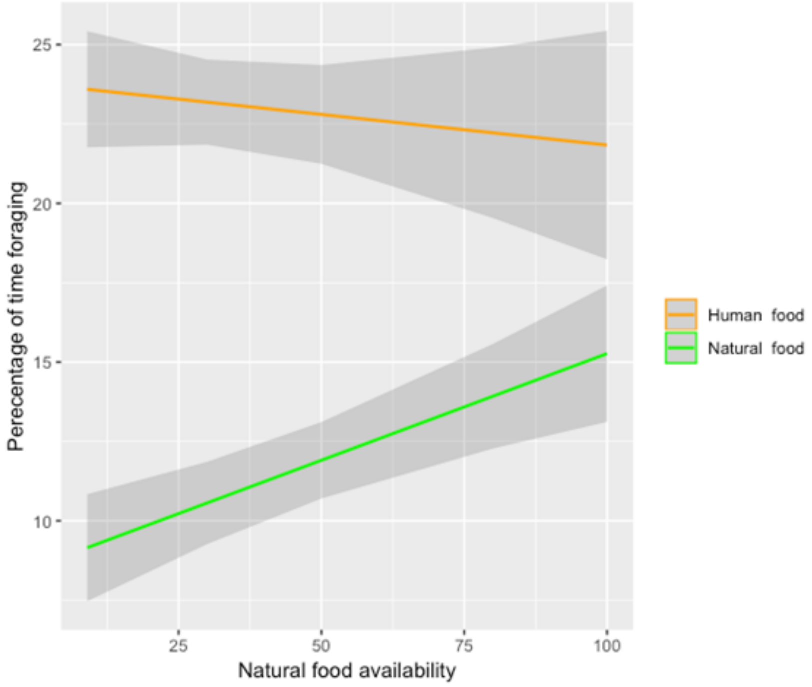

Fig. 4.1 Relationship between the percentage of time spent foraging on natural food and human-food in relation to natural food availability of urban vervet monkeys at Simbithi eco-estate, KwaZulu-Natal, South Africa. Dark grey areas represent 95% confidence intervals.

Natural Food

Increased natural food availability had a positive effect on time spent foraging (F_1=2.14, $p \underline{=} 0.032$, Table 4.1).

Anthropogenic disturbance

The interaction effect between positive and negative human incidents showed that percentage of time spent foraging was less when positive human incidents were low and negative human incidents were high; however a higher rate of positive incidents and less negative human incidents were related to an increase in time spent foraging (F_1=32.26, $p < 0.001$, Table 4.1, Fig. 4.2a). The interaction between positive and negative human incidents showed that their movement increased as the rate of positive human incidents decreased, and the rate negative human incidents increased (F_1=3.9, $p = 0.045$, Table 4.2, Fig. 4.2b). Increased negative human incidents had a negative effect on time spent resting (F_1=12.29, $p \leq 0.001$, Table 4.3). The interaction effect between positive and negative human incidents showed that greater positive human incidents increased vervet monkey socialising time, but when they experienced both low negative and low positive human incidents their time spent socialising was significantly less (F_1=5.12, $p = 0.025$, Table 4.4, Fig. 4.2c).

Seasonality

Vervet monkey foraging was significantly affected by seasonality (F_3=96.79, $p = \leq 0.001$, Table 4.1), with less time spent foraging in summer than any other season. In addition, their time spent moving (F_3=14.7, $p = 0.002$, Table 4.2) and resting (F_3=64.41, $p \leq 0.001$, Table 4.3) was significantly affected by seasonality as vervet monkeys moved less and rested more in summer than any other season and more time resting in autumn than in winter and spring. Finally, their time spent socialising was also affected by seasonality (F_3=60.74, $p \leq 0.001$, Table 4.4) as this was significantly higher in summer than all other months.

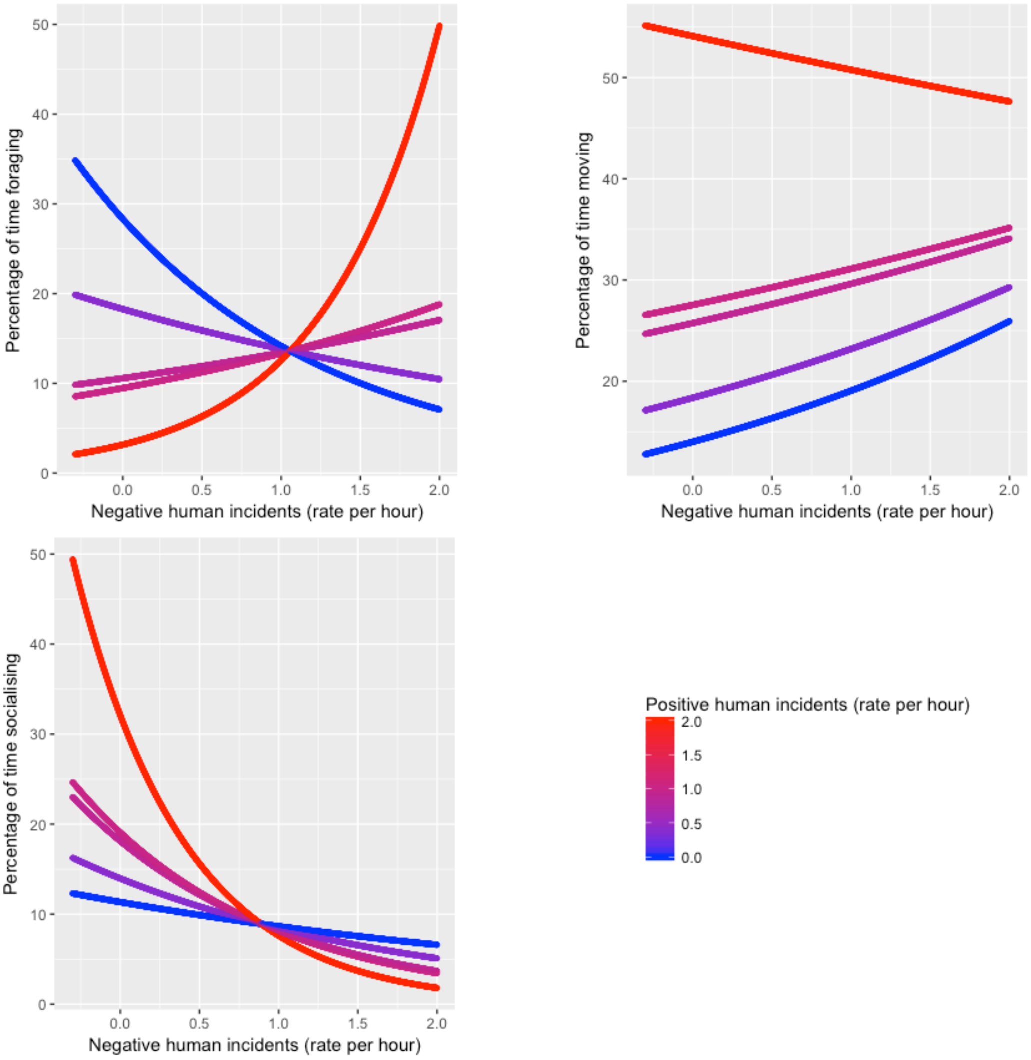

Fig. 4.2 Interaction between negative human incidents and positive human incidents on the time budgets of urban vervet monkeys at Simbithi eco-estate, KwaZulu-Natal, South Africa. (a) shows the positive significant effect on the percentage of time spent foraging, (b) shows the negative significant effect on the percentage of time spent moving and (c) shows the negative significant effect on the percentage of time spent socialising

Table 4.1 Output of GLMM and likelihood ratio test on urban vervet monkey foraging behaviour, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.05	0.20	15.20	≤0.001		
Negative human incidents	-0.69	0.18	-3.85	≤0.001	1.22	0.027
Positive human incidents	-1.10	0.15	-7.36	≤0.001	32.26	≤0.001
Negative human incidents * Positive human incidents	**1.04**	**0.22**	**4.78**	**≤0.001**	**22.84**	**≤0.001**
Group size	**0.02**	**0.01**	**3.33**	**0.001**	**11.11**	**0.001**
Natural food	**0.01**	**0.00**	**2.14**	**0.032**	**4.60**	**0.032**
Season					**96.79**	**≤0.001**
Autumn – Spring	**-0.31**	**0.10**	**-3.04**	**0.002**		
Autumn – Summer	**-0.82**	**0.10**	**-8.67**	**≤0.001**		
Autumn – Winter	0.04	0.09	0.40	0.687		
Summer – Spring	**0.52**	**0.08**	**6.36**	**≤0.001**		
Summer – Winter	**0.86**	**0.10**	**8.35**	**≤0.001**		
Spring – Winter	**0.34**	**0.09**	**3.73**	**≤0.001**		

Table 4.2 Output of GLMM and likelihood ratio test on urban vervet monkey movement behaviour, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.09	0.04	80.50	≤0.001		
Negative human incidents	0.10	0.02	5.41	≤0.001	24.72	≤0.001
Positive human incidents	0.21	0.02	11.54	≤0.001	40.86	≤0.001
Negative human incidents * Positive human incidents	**-0.03**	**0.02**	**-2.00**	**0.046**	**3.90**	**0.045**
Group size	**-0.18**	**0.03**	**-6.08**	**≤0.001**	**38.19**	**≤0.001**
Natural food	0.01	0.02	0.57	0.567	0.14	0.707
Season					**14.70**	**0.002**
Autumn - Spring	0.00	0.04	-0.02	0.986		
Autumn - Summer	**0.09**	**0.04**	**2.12**	**0.034**		
Autumn - Winter	-0.04	0.04	-1.10	0.273		
Summer - Spring	**-0.09**	**0.03**	**2.73**	**0.006**		
Summer - Winter	**-0.13**	**0.04**	**-3.41**	**0.001**		
Spring - Winter	-0.04	0.04	-0.94	0.346		

Table 4.3 Output of GLMM and likelihood ratio test on urban vervet monkey resting behaviour, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	1.95	0.09	21.78	≤0.001		
Negative human incidents	**-0.15**	**0.05**	**-2.88**	**0.004**	**12.29**	**≤0.001**
Positive human incidents	0.04	0.05	0.70	0.483	0.56	0.451
Negative human incidents * Positive human incidents	-0.02	0.04	-0.45	0.654	0.20	0.655
Group size	**-0.12**	**0.04**	**-2.73**	**0.006**	**7.43**	**0.006**
Natural food	-0.05	0.05	-0.97	0.330	0.95	0.330
Season					**64.41**	**≤0.001**
Autumn - Spring	**0.27**	**0.12**	**2.18**	**0.029**		
Autumn - Summer	**0.81**	**0.11**	**7.35**	**≤0.001**		
Autumn - Winter	**0.26**	**0.12**	**2.12**	**0.034**		
Summer - Spring	**0.55**	**0.10**	**5.46**	**≤0.001**		
Summer - Winter	**0.55**	**0.13**	**-4.36**	**≤0.001**		
Spring - Winter	-0.01	0.12	-0.08	0.938		

Table 4.4 Output of GLMM and likelihood ratio test on urban vervet monkey social behaviour, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Model summary				Likelihood ratio test	
Term	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.07	0.11	28.09	≤0.001		
Negative human incidents	-0.26	0.05	-5.29	≤0.001	55.28	≤0.001
Positive human incidents	0.09	0.06	1.61	0.108	3.15	0.08
Negative human incidents * Positive human incidents	**-0.09**	**0.04**	**-2.26**	**0.024**	**5.12**	**0.025**
Group size	0.02	0.08	0.19	0.850	0.04	0.850
Natural food	-0.08	0.05	-1.51	0.131	2.28	0.131
Season					**60.74**	**≤0.001**
Autumn - Spring	-0.08	0.12	-0.67	0.501		
Autumn - Summer	**-0.66**	**0.11**	**-5.84**	**≤0.001**		
Autumn - Winter	0.14	0.10	1.37	0.172		
Summer - Spring	**0.80**	**0.12**	**6.52**	**≤0.001**		
Summer - Winter	**0.74**	**0.11**	**-6.76**	**≤0.001**		
Spring - Winter	0.05	0.11	0.48	0.632		

Discussion

As predicted, anthropogenic disturbance influenced all four aspects of the time budgets of urban vervet monkeys to some degree. Moreover, the interplay between positive and negative human incidents influenced three of the four behavioural categories. Results highlighted how urban vervet monkeys have adapted behaviourally to the ecologically changing anthropogenic landscape.

As expected, increasing anthropogenic food consumption by vervet monkeys significantly reduced their time spent foraging. Foraging results support previous research on provisioned vervet monkeys that high nutritional value human-food provides more energy in smaller amounts in a shorter amount of time decreasing foraging requirements (Brennan et al., 1985; Jaman and Huffman, 2013; Saj et al., 1999). The interaction effect between positive and negative human incidents showed that when positive incidents were low and negative incidents were high, vervet monkeys spent less time foraging; however, when positive human incidents were high and negative human incidents were low their foraging time increased. Notably, our interaction between positive and negative human incidents suggests that if vervet monkeys have access to high value anthropogenic food then despite human-aggression their time spent foraging will increase. It should be noted however, that vervet monkeys have cheek pouches, an anatomical adaptation that has been defined as a key feature of adaptive cercopithecines (Humle and Hill, 2016). Therefore, the use of cheek pouches to store and consume food may have affected vervet monkey foraging rates. Future studies should incorporate the use of check pouches into their methods, this supportive data on check pouch use could provide a greater insight into vervet monkey foraging strategies, particularly over a desirable resource such as human-food.

Time spent moving was greater when vervet monkeys experienced a higher rate of negative human incidents, although this effect decreased with more frequent positive human incidents. Previous research would suggest that access to high value resources should lessen the need to search for food and hence reduce time spent moving (Saj et al., 1999), supporting our findings. However, the interaction effect suggests that time spent moving is not only affected by successfully obtaining high value anthropogenic food resources, but is also associated with increased human aggression. Movement behaviour therefore suggests that vervet monkeys may be less likely to move on in response to human aggression, when high value human-food is available, supporting findings of Chapter 3.

Notably, vervet monkey social behaviour increased with a greater rate of positive human incidents, supporting previous research, which has shown that access to high value food items results in decreased foraging time and increased time available for social behaviour (Jaman and Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). The negative interaction effect between both anthropogenic factors showed that negative human incidents offset this, decreasing social behaviour. This could be due to the increased tension and aggression related to high value resources or as an outcome of aggression from humans to monkeys (Fuentes and Hockings, 2010). It is possible that human aggression affects vervet monkey social cohesion; however, further study is required to investigate the impact of urban living on vervet monkey social systems and how both positive and negative associations affect social behaviour both together and individually. Even so, as increased negative human incidents also reduced time spent resting, it could be suggested that human-aggression is generally costly to urban vervet monkey time budgets.

Although most historical research on urban primates has found no influence of seasonality (Altmann and Muruth, 1988; Eley, 1989), our research did show an effect of seasonality across all behaviours, supporting more recent studies that have shown that seasonality is influential on urban species (macaques: Jaman & Huffman, 2013 and baboons: van Doorn et al., 2010). Trends found followed expected patterns of energetic constraints (Borg et al., 2015; McFarland et al., 2015). An unexpected finding was the seasonal effect of foraging. We expected that with access to high value food vervet monkeys would be less reliant on seasonally influenced natural food (Naughton-Treves et al., 1998); however, our results indicated that their foraging was significantly higher in autumn and winter. We suggest that this is due to a high reliance on attractive garden plants (Chaves and Bicca-Marques, 2017; Hoffman and O'Riain, 2011; Wimberger and Hill, 2017). Nevertheless, it should be noted that our measure of natural food availability in this study is based on a retrospective estimate; future studies should apply a proper phenological assessment of natural food, such as those proposed by Marshall and Wich (2013), to further understand urban vervet monkey foraging strategies. Overall, results for seasonality support previous research on urban baboons, showing how their adaptive generalist qualities have allowed them to take advantage of all aspects within their habitat (van Doorn et al., 2010). Seasonality results further highlight the exploitive nature of vervet monkeys and their behavioural flexibility, taking advantage of the most nutrient rich available resources, including seasonally influenced resources. Furthermore, the relationship we highlight between food choice, implied fluctuation if foraging behavior dependent on natural food availability, therefore, the seasonal variations in food availability and food consumption provide an interesting point for further analysis.

Management implications

Anthropogenic influences on the time budgets of vervet monkeys revealed independent and interlinking effects, which is a previously neglected area of ethnoprimatology research (McLennan et al., 2017). By developing our knowledge of urban ecology and behavioural adaptations, we can directly improve human-monkey relationships for the benefit of both parties through appropriate management plans (Soulsbury and White, 2015). We suggest that management should target preventing opportunities for vervet monkeys to forage on human-food, which appears to drive human aggression. Housing estates should implement education programmes that encourage residents to reduce vervet monkey access to anthropogenic food (e.g. by securing refuse bins, reducing access points into houses, storing food items securely), with the aim to improve human-wildlife cohabitation within urban areas for vervet monkey and human well-being, as well as ecological biodiversity conservation.

Chapter 4 summary

In this chapter, I built upon results from Chapter 3, analysing the same interaction effect between positive and negative influences on urban vervet monkey daily time budgets. Again, this chapter highlighted the complex relationship between the costs and benefits to urban living, demonstrating how vervet monkeys have behaviourally adapted to the urban landscape. In the next chapter, I expand on the behavioural flexibility highlighted in this chapter, and further assess the impact of these anthropogenically influenced variables on the sociality of urban vervet monkeys.

Chapter 5

Using social networks to explore the social flexibility of urban vervet monkeys

This has paper has been formatted with intention to submit to Animal Behaviour.

In the previous two chapters, I investigated the effects of positive and negative anthropogenic influences on the general behavioural ecology of urban vervet monkeys. In this chapter my research will focus on vervet monkey social interactions in the urban landscape. Social flexibility of wildlife has been shown to be plastic and adaptive to change (review: Smil, 2003), therefore, social flexibility has been suggested as an important characteristic required to survive anthropogenic change (Ditchkoff et al., 2006); however, this has not yet been studied in urban wildlife. Applying the principles of socio-ecological theory to vervet monkey behaviour allows us to test their social flexibility in the urban landscape. Social network analysis is a powerful tool to monitor changes in social structure. Here, I apply social network analysis to assess ecological influences on vervet monkey social associations.

Abstract

Changes in landscape profiles caused by anthropogenic pressures directly influence both ecological and social challenges for many species; however, generalist species such as the vervet monkey, *Chlorocebus pygerythrus,* thrive under these pressures. Behavioural flexibility to anthropogenic pressures is most evident in foraging and social behaviour. The availability of human-food sources to urban primates represents clumped, monopolisable food that has the potential to increase contest competition. How these anthropogenic food sources may impact the social structure of urban primates is not yet known. Accumulating evidence across many taxa indicates that social connectedness increases measures of reproductive success. Social network analysis allows us to identify changes in network structure that may have fitness consequences. Using social network analysis, we investigated the effect of anthropogenic food on the social cohesion of five vervet monkey groups living in urban KwaZulu-Natal, South Africa. Over six months we conducted group scan samples every 30-min on each group for a minimum of 4 days per month. We created grooming and aggression matrices and calculated measures of group (density, clustering coefficient and distance) and individual (eigenvector centrality and degree) connectedness. We analysed the effect of foraging on natural and human-related food sources on each network metric using linear mixed models. Anthropogenic food influenced almost all social metrics. At the group level, foraging on anthropogenic food was related to increased density and cohesion in both grooming and aggression networks. At the individual level increasing anthropogenic food affected high-ranking monkeys most: eigenvector centrality and outdegree in aggression networks increased with rank. We show for the first time how social network analysis can be a useful tool to document urban effects on wildlife groups, highlighting the social flexibility of these urban dwellers.

Introduction

Behavioural flexibility is the response of an individual/group to environmental change (Kappeler & Kraus, 2010; Schradin, 2013). Additionally, social flexibility of wildlife has been shown to be plastic to change (review: Smil, 2003). It is commonly accepted that successful adaptation to urban changes is due to resource exploitation (Diquelou et al., 2015) and social flexibility (Skandrani et al., 2017), thus, many studies have highlighted the importance of behavioural flexibility in urban species (Aguiar et al., 2014; Bateman & Fleming, 2014; Skandrani et al., 2017; Slabbekoorn, 2013; Widdows & Downs 2016, 2018).

The urban landscape is widely acknowledged as an important ecological system (Fuentes and Hockings, 2010), yet our understanding of social adaptations within this ecological system are relatively limited (Lacy and Martins, 2003; Skandrani et al., 2017). Evidence is accumulating that social network positions have fitness consequences (e.g. Royle et al., 2012) and therefore an animal's social network is expected to respond flexibly to environmental change (Snijders et al., 2017). However, there has been no clear assessment so far of the association between urban ecology and sociality. Previously, social network analysis on bottlenose dolphins (*Tursiops truncates*) demonstrated that individuals adjusted their group cohesiveness to improve feeding efficiency at anthropogenic food patches (Pace et al., 2011). More recently, research on spotted hyena (*Crocuta crocuta*) indicated that clans in less disturbed areas had shorter path lengths indicating that they were more closely associated; however, anthropogenic disturbance and provisioning were only assumed within this study and not directly measured (Belton et al., 2018). Understanding the interaction between anthropogenic food and ecological factors on social dynamics is important to develop our understanding of wildlife flexibility to the urban landscape (Couzin, 2006).

Feeding competition is one of the most fundamental factors affecting fitness in animals (Chapman, Rothman, & Lambert, 2012). Understanding how the distribution of food resources influences the nature of feeding competition is a central feature of ecological explanations of social structure and organisation (e.g. Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). Changes in landscape profiles caused by anthropogenic pressures directly influence food distribution and availability, altering ecological and social challenges for many species (Chilvers and Corkeron, 2001). Anthropogenic suburbs provide habitats that are productive and well maintained, providing abundant dispersed resources (McKinney, 2002), particularly in selectively maintained gate communities (Ballard and Jones, 2011). Furthermore, anthropogenic environments also bring benefits such as increased access to high value, patchy, monopolisable human-food resources. The socio-ecological model predicts that high value monopolisable resource distribution gives rise to strong within group competition (WGC) (Sterck et al., 1997; van Schaik & van Noordwijk, 1998; Wrangham, 1980) and when coupled with low between-group contest competition, should create groups that are more cohesive. Within such groups, small supportive networks should form with key central individuals (van Schaik, 1989), a more linear despotic hierarchy should be apparent, and females should form frequent coalitions to maintain rank-related benefits (Isbell, 1991; Isbell & Young, 2002; Sterck et al.,1997). The effect of such ecological pressures on social structure has not yet been applied to intragroup variation in urban wildlife; nevertheless, using the rationale of WGC to test these ecological pressures allows a greater understanding of both group and individual adaptations to urbanisation.

Behavioural flexibility has desirable fitness benefits within the urban ecosystem (Sol et al., 2013), particularly for adaptive generalist species such as the vervet monkey, *Chlorocebus pygerythrus* (Chapman et al., 2016). Vervet monkeys are a highly social species that live in multimale-multifemale groups, are female philopatric and have strict female and male hierarchies (e.g. Borgeaud & Bshary, 2015; Seyfarth & Cheney, 1984). Previous social network studies have shown the strong influence of female philopatry and rank on vervet monkey social metrics (Borgeaud et al., 2017; Henzi et al., 2013; Josephs et al., 2016; Young et al., 2017). Vervet monkeys therefore provide a suitable model to test social flexibility in an urban matrix.

In our study, vervet monkeys had an abundant dispersed supply of natural food through the selectively maintained gardens and natural areas within their home range, whereas high value human-food was obtained by entering homes or refuse (Thatcher, *pers. obs.*), these human-foods were therefore opportunistic and clumped. Based on socioecological theory we expected that greater exploitation of these high value human-foods and less dependence on natural food resources would increase WGC. We therefore made a *group level prediction*: (*a*) groups that foraged on these clumped human-food resources more frequently would increase their grooming connections and aggressive interactions, thus network density (both grooming and aggression) should increase and distance should decrease compared to those that fed primarily on natural food resources, as group living animals can adopt multiple competitive foraging strategies (Isbell et al., 1991) we predicted a negative interaction between natural food and human-food. We further predicted (*b*) that an increase in differentiated relationships should lead to an increase in sub-grouping. At the *individual level* we predicted that (*a*) due to the strict linear hierarchy associated with increased WGC, higher ranked individuals would obtain more anthropogenic food and therefore be more central within their group grooming and aggression networks. Finally, due to female philopatry in vervet monkeys, we predicted that (*b*) females would receive more grooming and aggression than males and be more central. We made no specific predictions about human aggression; however, we included it as an additional level of anthropogenic disturbance to human-food consumption.

Methods

Subjects and study site

We studied five groups of urban vervet monkeys in Simbithi eco-estate, Ballito, Durban north coast, KwaZulu-Natal (S:29.3029, E:31.131). Simbithi eco-estate is a gated housing estate, converted from sugar cane farms to create a complex urban mosaic. The estate was comprised of a variety of urban complexes, structures and housing options, along with areas of human-made coastal forest and managed walking trails.

We conducted our study from September 2016- February 2017. Group size varied from ~14-42 individuals (Ballito [14]: 3 males, 6 females, 5 juveniles; Farmyard [23]: 4 males, 10 females, 9 juveniles; Savannah [25]: 4 males, 10 females, 11 juveniles; Goodies [29]: 5 males, 10 females, 14 juveniles; Heron [42]: 5 males, 14 females, 23 juveniles).

We studied only adult vervet monkeys and all adults were individually recognisable from distinct markings. No researchers had studied these groups previously, so population genetic history was unknown. The study period did not include the dispersal and mating seasons (April-July), therefore numbers of adults across groups were relatively stable. We collected data during spring (September-October) and summer (November-March) periods within KwaZulu-Natal (SANBI, 2017).

Behavioural data collection

HT collected vervet monkey behaviour data from dawn until dusk (~12 h in spring and ~16 h in summer). We conducted instantaneous group scans every 30 min for a 10-min period, recording both grooming and aggressive interactions including the identity of the social partner/s. We also noted the occurrence of any dominance interactions and aggressive competition ad lib. We recorded the frequency of aggressive between-group encounters (Kitchen et al., 2004) using all occurrence sampling. We collected all data using the Prim8 behavioural software (McDonald and Johnson, 2014) on a handheld Lenovo tablet.

We used all occurrence sampling to record all interactions between humans and vervet monkeys during dawn to dusk daily follows. We identified a human related incident as any occasion when at least one vervet monkeys interacted with humans or human possessions (e.g. houses, bins and cars). We classified incidents as positive (human-food consumption) or negative (human aggression towards monkeys). For positive human incidents we included any form of human-food consumption and recorded a new event if the monkeys had not foraged on human-food in the previous 20 minutes. Negative human incidents were classed as any form of human aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and risk of injury. We classed an incident as terminated once all parties had retreated and we recorded new events if there had been no incident in the prior 20 minutes. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]). We recorded natural food using focal animal sampling, noting all events when a monkey was seen foraging for (including moving objects/searching for food before feeding) and feeding on (manipulating/picking and actually eating items) (Ménard et al., 2013) natural food; natural food included any form of plant including aesthetic garden plants.

Association measures

We constructed directed weighted matrices for grooming and aggression per month. All networks were constructed from scan data to ensure equal sample sizes across individuals. We calculated measures of network structure using UCInet (Borgatti, Everett and Freeman, 2002). To quantify group level social associations, we used three common network parameters including density, distance and a clustering coefficient (Croft et al., 2008). Density is a measure of dyadic connections (ties) in a population with respect to the potential number of ties; high scores representing a saturated network and low scores a sparse network. We further assessed distance as a measure of direct social interaction. We calculated the average distance between pairs within a network, allowing us to assess how well connected a group was. The global clustering coefficient measures how clustered a network is, e.g. how many 'cliques' are within a network.

To assess individual metrics, we used three common network parameters: eigenvector centrality and degree centrality (Croft et al., 2008). We used a weighted matrix to calculate eigenvector centrality and a binary matrix to assess degree. Again, we assessed both grooming and aggressive associations. The eigenvector centrality coefficient is a measure of how connected an individual is within its network considering the centrality of those to whom they are connected (Croft et al., 2008). Binary degree centrality measures how many direct ties an individual has and is useful to measure partner diversity (Croft et al., 2011); an individual with more ties has higher centrality. Outdegree refers to the number of ties that originate from the focal whilst indegree is the number of ties directed at the focal.

Statistical analyses

We calculated a rate (frequency/hour) for the two human incident measures and natural food. We calculated both a group and individual frequency for separate analysis of our individual and group level prediction. We conducted all statistical analyses using R statistical software version 3.3.2 (R project, 2013). We calculated a normalised David's rank using the *Steepness* package (Leiva and De Vries, 2011). We created 12 linear mixed models in total using the *lme4* package (Bates et al., 2015) with each social metric as the dependent variable. We created three models for our group metrics and three models for our individual metric models, and we ran these for both aggression and grooming behaviours. Within each model, each row represented a mean monthly social metric calculated for either each of the five groups or each individual. We constructed two separate *a priori* model structures to address our separate predictions. We included an interaction between positive human incidents and natural food to assess our group level prediction of clumped human-food increasing WGC. For our individual level predictions, we ran an interaction between positive human incidents with rank, and sex as a main effect, to assess our predictions of the effect of anthropogenic food and rank, and sex on network metrics.

Group level prediction: Group social metric~ positive human incidents*natural food + negative human incidents + group size + (1| group identity)

Individual level prediction: Individual social metric~ sex*positive human incidents + rank*positive human incidents + negative human incidents + natural food + group size + (1| group identity/monkey identity)

Because of non-independence issues with network data we used the *boot* package (Canty and Ripley, 2017; Davison and Hinkley, 1997) in R to run our model and bootstrap the confidence intervals of our model parameters (Lusseau et al., 2009). We ran all tests using 1000 permutations. If the upper and lower CI straddled 0 then we did not consider the effect significant. We assessed the fit of each model graphically checking residuals for normal distribution.

Results

We observed each vervet monkey group for a minimum of 3 days a month and collected a total of 279 h for Ballito, 335 h for Farmyard, 327 h for Savannah, 298 h for Goodies and 336 h for Heron. Only the results of intragroup interactions are presented, as we witnessed just six aggressive intergroup encounters over 6 months.

Networks showed clear variation between vervet monkey groups and social metrics. We found consistent effects of positive human incidents increasing group cohesion and centrality measures (Fig. 5.1, Table 5.1, Table 5.4).

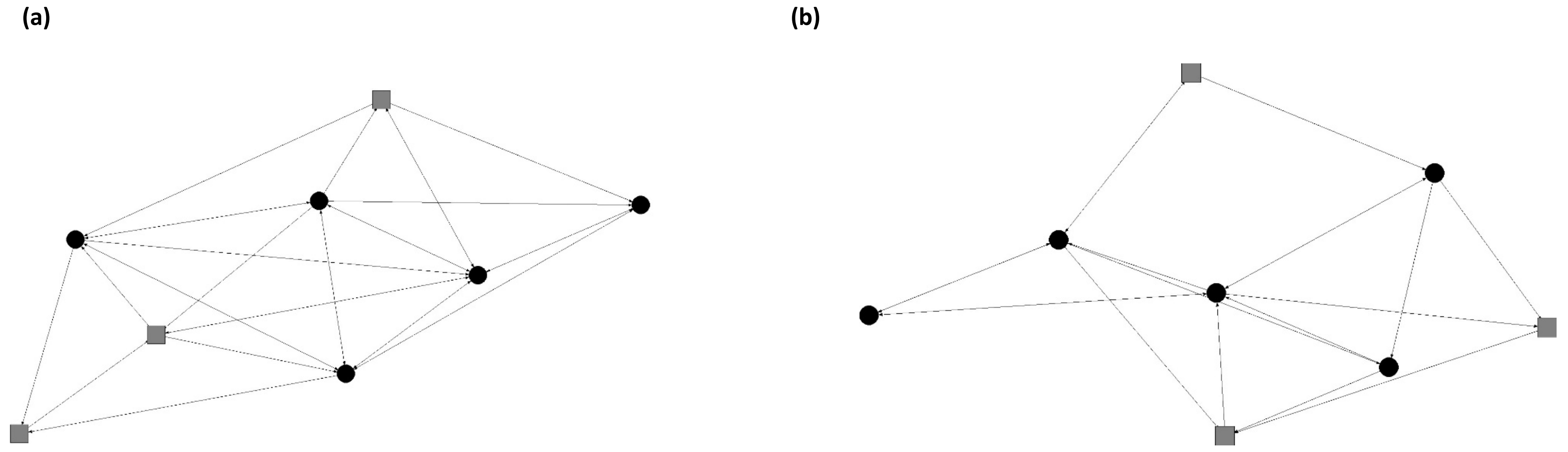

Fig. 5.1 Example sociogram representing the Ballito vervet monkey group. Black circles represent female monkeys and grey squares represent male monkeys, the networks have been spring embedded. Networks represent two separate months, where (**a**) is the month with the highest rate of positive human incidents and (**b**) is a month with lowest positive human incidents

Group level prediction

Table 5.1 Summary of significant effects from the LMM for the group level predictions for both grooming and aggression. We present both our predicted outcome and significant results where confidence intervals did not straddle 0, + and - signs show the directionality of the effect

		Positive human incidents		Natural food		Positive human incidents* Natural food	
		Predicted	Result	Predicted	Result	Predicted	Result
Grooming	Density	+	+	-	-	-	+
	Clustering	+	+	-		-	
	Distance	-	-	+		-	-
Aggression	Density	+	+	-	-	-	+
	Clustering	+	+	-		-	
	Distance	-	-	-		-	

Group level prediction a

We found a positive interaction effect between natural food and positive human incidents on grooming density, supporting group level prediction *a* for grooming. Grooming density increased with positive human incidents and this effect was strengthened by increased foraging on natural food (Table 5.2, Fig. 5.2a). Supporting this, we found a negative interaction effect on grooming distance (Table 5.2, Fig. 5.2b); distance decreased with an increasing rate of positive human incidents; however, this effect weakened with increasing natural food. Aggression metrics also met our group level prediction *a*. We found that a greater rate of positive human incidents was significantly related to decreased distance within the network. Furthermore, for aggression network density, we found a significant positive interaction between positive human incidents and natural food. Increased frequency of positive human incidents was associated with a sharp increase in density; however, when the rate of natural food decreased, density significantly decreased (Table 5.3, Fig. 5.2c).

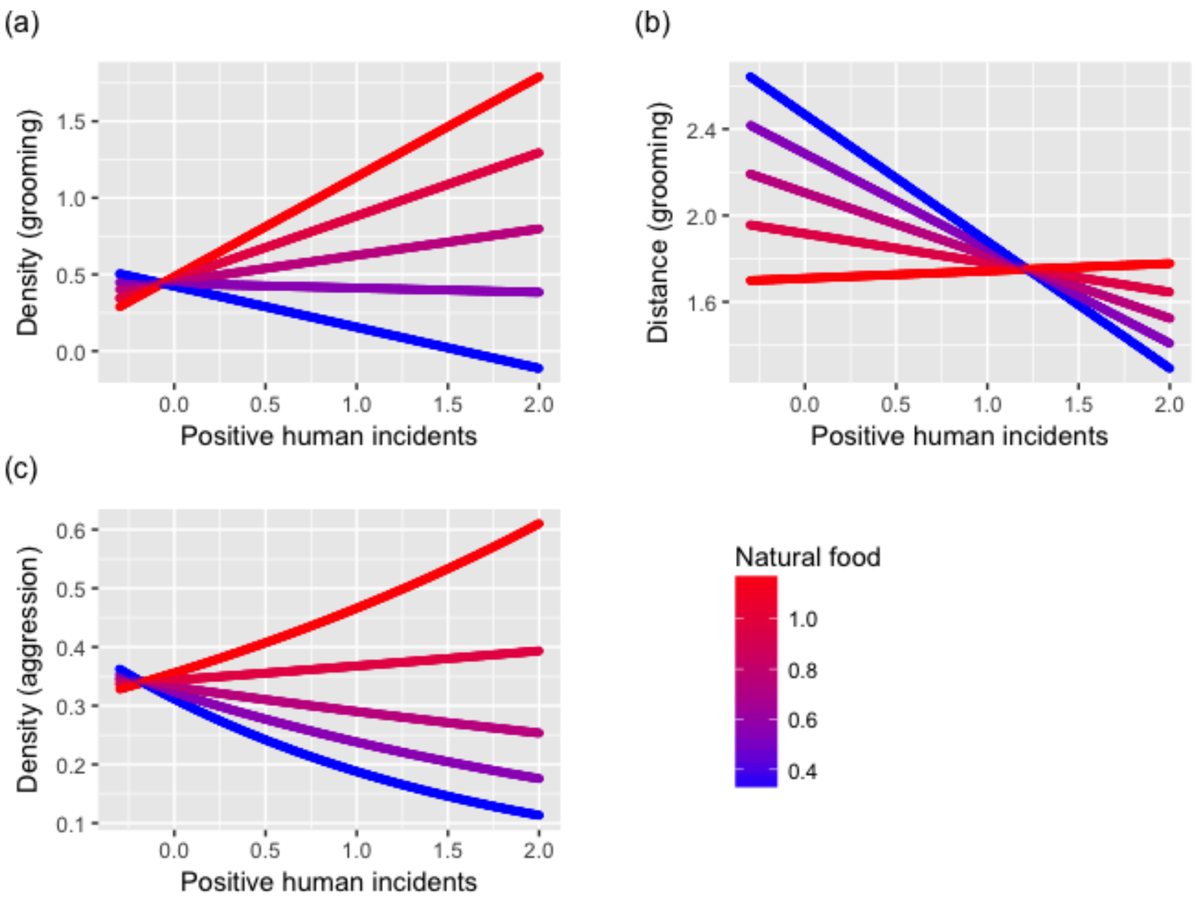

Fig. 5.2 Interaction between group natural food rate per hour and group positive human incidents rate per hour on group level social metrics of urban vervet monkeys at Simbithi eco-estate, KwaZulu-Natal, South Africa. Where (a) shows the positive effect on grooming density, (b) shows the negative effect on grooming distance and (c) shows the positive effect on aggression density

Group prediction b subgrouping

A higher rate of positive human incidents was positively related to increased clustering coefficients, for both grooming (Table 5.2) and aggression (Table 5.3), supporting group level prediction *b* for grooming. There was no significant interaction between the rate of positive human incidents and natural food for clustering coefficient.

Table 5.2 LMM output and bootstrapped confidence intervals for group level grooming metrics of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Effect	Estimate	Standard error	CI lower	CI upper
Density	(Intercept)	1.63	0.19	1.26	2.01
	Negative human incidents	-0.02	0.08	-0.18	0.13
	Positive human incidents	0.63	0.11	-0.42	-0.04
	Natural food	-0.40	0.18	0.06	0.76
	Group size	-0.33	0.17	-0.71	0.01
	Positive human incidents* Natural food	**0.26**	**0.13**	**0.51**	**0.02**
Clustering coefficient	(Intercept)	0.28	0.04	0.23	0.74
	Negative human incidents	-0.01	0.01	-0.03	0.02
	Positive human incidents	**0.13**	**0.02**	**-0.02**	**-0.58**

	Natural food	-0.06	0.03	-0.08	0.03
	Group size	0.05	0.03	-0.148	0.07
	Positive human incidents* Natural food	-0.01	0.00	0.05	-0.03
Distance	(Intercept)	2.58	0.33	1.93	3.24
	Negative human incidents	-0.07	0.13	-0.36	0.19
	Positive human incidents	-0.18	0.20	-3.82	-4.20
	Natural food	-0.44	0.31	-1.05	0.17
	Group size	0.36	0.28	-0.25	0.94
	Positive human incidents* Natural food	**-0.11**	**0.12**	**-0.23**	**-0.04**

Table 5.3 LMM output and bootstrapped confidence intervals for group level aggression social metrics of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Effect	Estimate	Standard error	CI lower	CI upper
Density	(Intercept)	0.29	0.16	0.77	1.37
	Negative human incidents	0.06	0.01	-0.02	0.01
	Positive human incidents	0.12	0.01	0.11	0.04
	Natural food	-0.04	0.02	0.01	0.09
	Group size	0.00	0.01	-0.02	0.00
	Positive human incidents* Natural food	**0.14**	**0.00**	**0.13**	**0.21**
Clustering coefficient	(Intercept)	0.28	0.04	0.21	0.36
	Negative human incidents	-0.01	0.01	-0.04	0.02
	Positive human incidents	**0.07**	**0.02**	**0.02**	**0.11**

	Natural food	-0.06	0.03	-0.13	0.01
	Group size	0.05	0.03	-0.02	0.13
	Positive human incidents* Negative human incidents	-0.04	0.02	-0.08	0.01
Distance	(Intercept)	0.70	0.43	-0.49	0.33
	Negative human incidents	0.01	0.03	-0.02	0.47
	Positive human incidents	**-0.09**	**0.04**	**-0.21**	**-0.73**
	Natural food	0.00	0.00	-0.32	0.47
	Group size	**0.08**	**0.01**	**0.27**	**1.10**
	Positive human incidents* Natural food	0.00	0.00	-0.22	0.14
	Positive human incidents* Negative human incidents	-0.02	0.00	-0.48	0.01

Individual level prediction

Table 5.4 Summary of significant effects from the LMM for the individual level predictions for both grooming and aggression. We present both our predicted outcome and significant results where confidence intervals did not straddle 0, + and - signs show the directionality of the effect

		Sex		Positive human incidents* Rank	
		Predicted	Result	Predicted	Result
Grooming	Eigenvector	♀	♀	+	
	Indegree	♀	♀	+	+
	Outdegree	♀	♀	+	
Aggression	Eigenvector	♀		+	+
	Indegree	♀		+	
	Outdegree	♀		+	+

Individual prediction a

Individual level prediction *a* was not supported by our grooming metrics but was supported by our aggression metrics (Table 5.5 and 5.6). Unexpectedly we found a significant negative interaction between positive human incidents and rank for indegree. Individuals' indegree increased with rank when rates of positive human incidents were low; however, as the rate of positive human incidents increased, indegree increased across ranks (Table 5.5, Fig 5.3a). We found a positive interaction between positive human incidents and rank for both aggression eigenvector centrality and outdegree (Table 5.6, Fig. 5.3b,c). When positive human incidents were high, aggression eigenvector centrality of higher-ranking monkeys increased; however, when positive human incidents were low, aggression connectedness (eigenvector centrality) decreased (Fig. 5.3b). When rate of positive human incidents increased, aggression outdegree increased with rank; however, when the rate of positive human incidents was low, the effect of rank weakened (Fig. 5.3c).

Individual prediction b

In support of individual level prediction *b* we found that females were significantly more central than males for all three measures of grooming centrality (Table 5.5); however, we found no differences between males and females for aggression metrics (Table 5.6).

Individual metrics and negative human incidents

Although we made no predictions for negative human incidents, we found that negative human incidents significantly affected all vervet monkey individual metrics, but no group metrics. Increased rates of negative human incidents had a significant positive effect on grooming eigenvector centrality score; however, negative human incidents had a significant negative effect on indegree and outdegree (Table 5.5). A greater rate of negative human incidents had a significant positive effect on all three aggressive centrality measures (Table 5.6).

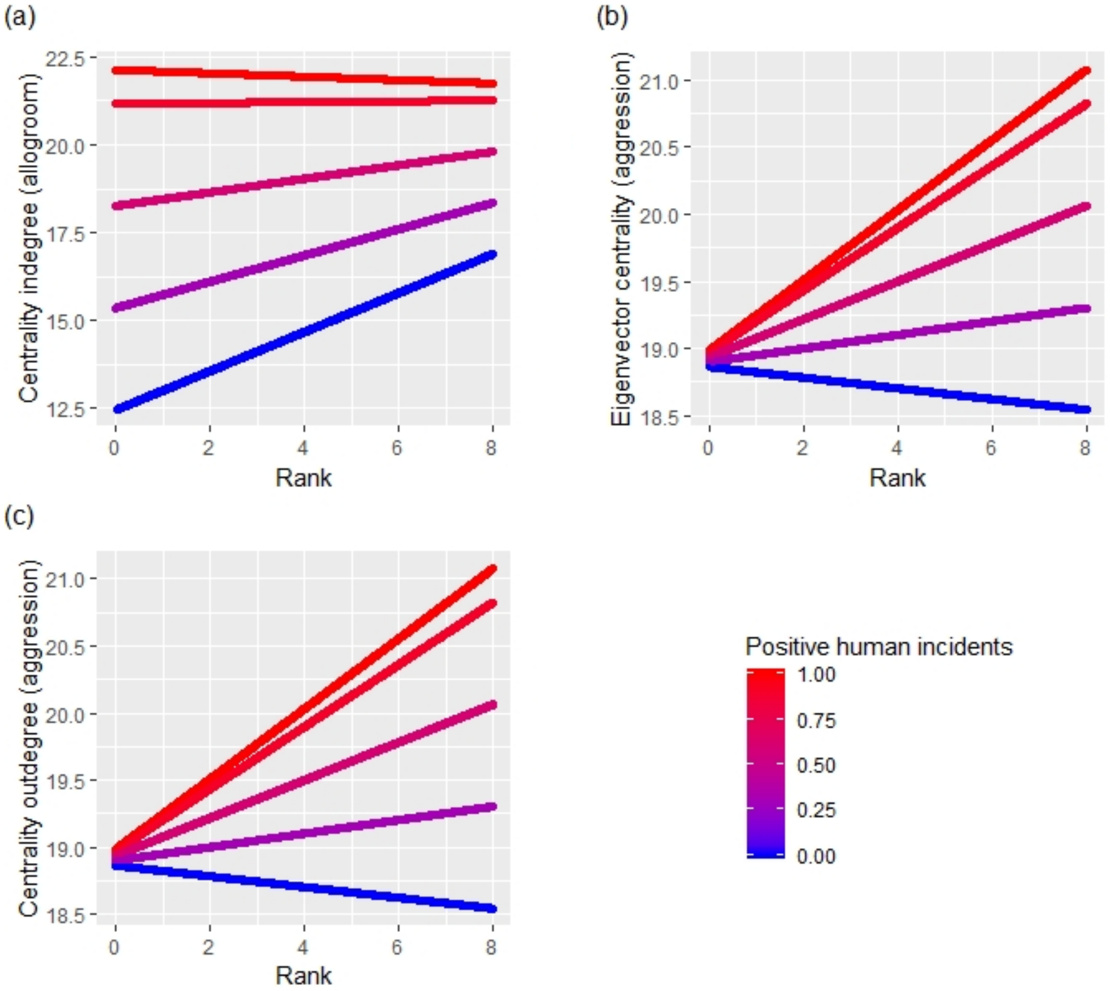

Fig. 5.3 Interaction between rank and individual positive human incidents rate per hour on individual level social metrics of urban vervet monkeys at Simbithi eco-estate, KwaZulu-Natal, South Africa. Where (a) shows the negative effect on grooming indegree, (b) shows the positive effect on aggressive eigenvector centrality and (c) shows the positive effect on aggressive centrality outdegree

Table 5.5 LMM output and bootstrapped confidence intervals for individual level grooming social metrics of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Effect	Estimate	Standard error	CI lower	CI upper
Eigenvector centrality	(Intercept)	0.29	0.03	0.20	0.34
	Positive human incidents	**0.06**	**0.02**	**0.02**	**0.12**
	Negative human incidents	**0.01**	**0.01**	**0.06**	**0.20**
	Natural food	0.01	0.01	-0.01	0.02
	Group size	**-0.05**	**0.01**	**-0.09**	**-0.03**
	Rank	0.00	0.01	-0.01	0.02
	Sex	**-0.15**	**0.03**	**-0.20**	**-0.07**
	Rank*Positive human incidents	0.00	0.01	-0.01	0.01
	Sex*Positive human incidents	0.01	0.02	-0.02	0.06

Indegree	(Intercept)	23.11	2.39	18.67	28.52
	Positive human incidents	0.42	0.81	-0.93	2.02
	Negative human incidents	**-0.88**	**0.31**	**-1.26**	**-0.02**
	Natural food	-0.12	0.26	-0.26	0.42
	Group size	-1.15	1.08	-2.31	1.29
	Rank	0.13	0.30	-0.68	0.66
	Sex	**-14.81**	**2.04**	**-19.00**	**-11.21**
	Rank*Positive human incidents	**-2.53**	**0.20**	**-0.14**	**-0.92**
	Sex*Positive human incidents	1.09	0.78	-0.42	2.01
Outdegree	(Intercept)	23.29	2.96	16.51	28.64
	Positive human incidents	0.19	0.69	-2.53	0.22
	Negative human incidents	**-0.04**	**0.27**	**-0.05**	**-1.24**

	Natural food	**-0.39**	**0.21**	**-0.77**	**-0.04**
	Group size	-0.33	0.99	-1.25	2.17
	Rank	0.05	0.27	-0.53	0.86
	Sex	**-12.79**	**2.40**	**-17.29**	**-7.83**
	Rank*Positive human incidents	-0.20	0.17	-0.25	0.46
	Sex*Positive human incidents	0.40	0.66	-0.67	1.57

Table 5.6 LMM output and bootstrapped confidence intervals for individual level aggression social metrics of urban vervet monkeys, Simbithi eco-estate, KwaZulu-Natal, South Africa

	Effect	Estimate	Standard error	CI lower	CI upper
Eigenvector centrality	(Intercept)	0.20	0.03	0.15	0.30
	Positive human incidents	0.00	0.02	-0.02	0.06
	Negative human incidents	**0.01**	**0.01**	**0.05**	**0.02**
	Natural food	0.00	0.01	-0.01	0.02
	Group size	-0.02	0.02	-0.05	0.02
	Rank	0.01	6.57	-0.01	0.02
	Sex	0.04	0.04	-0.05	0.12
	Rank*Positive human incidents	**0.08**	**0.00**	**0.05**	**0.02**
	Sex*Positive human incidents	-0.01	0.02	-0.05	0.02

Indegree	(Intercept)	5.03	1.67	1.95	8.52
	Positive human incidents	0.05	0.21	-0.63	0.29
	Negative human incidents	**0.26**	**0.08**	**0.10**	**0.51**
	Natural food	0.04	0.06	-0.08	0.17
	Group size	0.21	0.32	-0.42	0.79
	Rank	0.08	0.09	-0.25	0.26
	Sex	-0.79	1.24	-3.32	1.51
	Rank*Positive human incidents	0.01	0.05	-0.08	0.16
	Sex*Positive human incidents	-0.17	0.21	-0.54	0.23
Outdegree	(Intercept)	5.21	1.78	2.12	9.73
	Positive human incidents	1.50	0.56	0.39	2.96
	Negative human incidents	**1.05**	**0.23**	**1.87**	**0.75**

	Natural food	0.23	0.18	-0.06	0.64
	Group size	-1.18	0.80	-2.68	0.54
	Rank	0.09	0.19	-0.51	0.38
	Sex	1.33	1.03	-0.90	3.44
	Rank*Positive human incidents	**1.31**	**0.13**	**0.08**	**0.68**
	Sex*Positive human incidents	0.68	0.53	-1.72	0.30

Discussion

Ethnoprimatology, the study of human and non-human primate interactions, is an ever-widening field due to the increasing rates of anthropogenic change (Fuentes & Hockings, 2010; McKinney, 2015; McKinney & Dore, 2018; McLennan et al., 2017). Here, we provided the first findings of wildlife social flexibility in an urban landscape. All social metrics, both group and individual, appeared to be influenced by either positive or negative aspects of urban living. We presented data on intragroup associations only, as intergroup encounters were relatively rare, indicating aggressive intergroup competition was low.

Group level predictions

All group level metrics were influenced by the rate of human-food consumption. Furthermore, for our group level prediction *a* we found that our interaction between positive human incidents and natural food showed similar effects on group formation for both grooming and aggression networks. Our interaction had a positive effect on grooming and aggression network density but a negative effect of grooming network distance. This suggests that when human-food consumption was high, aggressive competition within the group increased and grooming connections also increased. These findings support established socioecological theories of alliance support over a clumped resource (Hockings et al., 2012; van Schaik, 1989).

We also found a main effect of positive human incidents on the clustering coefficient in both grooming and aggression networks, indicating that with increasing human-food consumption, sub-group formation increased supporting our group level prediction *b.* It is possible that increasing clique formation is beneficial to the formation of supportive alliances, in order to obtain high value resources (van Schaik, 1989);

however, further research would be necessary to look at the relationship between alliance support and human-food consumption support this theory.

Overall, group metrics showed that greater human-food consumption was related to increased group cohesion supporting previous work by Hockings et al (2012) that found chimpanzee (*Pan troglodytes verus*) groups became more cohesive during crop foraging. Group metric results support the idea that group living animals modify the nature of their social relationships to increase their competitive power over desirable food resources (Sterck et al., 1997). These findings develop our knowledge of the flexibility in social structure of vervet monkeys in an urban setting.

Individual level predictions

For our individual level prediction *a*, that higher ranked individuals would be more central with increased human-food consumption, we found a negative interaction between positive human incidents and rank on grooming indegree. Interestingly, positive human incidents reduced the effect of rank on grooming, such that the grooming indegree of lower ranking individuals increased to a comparable level with high-ranking individuals. There was no such effect on grooming outdegree indicating that lower ranking individuals became more attractive to groom but themselves did not groom more partners. It is possible that with a higher frequency of positive human incidents, high-ranking individuals could no longer monopolise all human-food resources, suggesting that a high rate of human-food consumption can lead to more egalitarian grooming patterns (Sterck et al., 1997). It could be argued that this increase in social value irrespective of rank was due to potential coalitionary support required and may have represented a social exchange (Schino, 2007).

We found an interaction between positive human incidents and rank for aggressive eigenvector centrality, showing that the aggressive connections of higher ranking vervet monkeys increased with a higher rate of positive human incidents. The same was true of aggression outdegree; higher rates of positive human incidents were related to an increased number of partners to whom aggression was given by high-ranking individuals. These findings supported our individual level prediction *a*, based on the socio-ecological model, that high value resources (positive human incidents) promote a more despotic dominance style that leads to different consequences for individuals of high/low rank (Isbell, 1991; Sterck et al., 1997).

Our individual level prediction *b* was met. We found that females were more central in their grooming networks, having a higher centrality for all three individual metrics than males. The influence of sex reflects increased female centrality in a female philopatric species (Seyfarth and Cheney, 1984), and supports previous social network studies that have shown females are more central within their networks than males in female philopatric species (Borgeaud et al., 2017; Henzi et al., 2013; Josephs et al., 2016; Young et al., 2017).

We found an unexpected, yet consistent, trend of negative human incidents across aggression and grooming metrics at the individual level. All measured aggression parameters increased with increasing frequency of negative human incidents; it is possible that increased aggression outdegree and indegree between individuals was a result of human-induced redirected aggression. Redirected aggression between primates is a relatively common behaviour where the individual that received aggression is more likely to aggress its conspecifics (e.g. Cheney & Seyfarth, 1989). We also found that grooming eigenvector centrality increased, whilst both grooming indegree and outdegree decreased, with a higher rate of negative human incidents. Previous primate literature has shown that grooming is used to alleviate stress and anxiety (e.g. Wittig et al., 2008). If human aggression increases stress and anxiety in vervet monkeys, we might expect to see all grooming centrality measures positively increase. However, previous literature has shown that under situations of increased tension, female primates may reduce their number of grooming partners, focusing on high quality relationships (De Waal, 1987; Judge et al., 2006; Koyama and Aureli, 2018; Wittig et al., 2008). Further research on this population of vervet monkeys has shown that individuals direct grooming at individuals of greater competitive power as a conflict avoidance strategy (Thatcher, *pers. obs.*), which would support the theory of reduced grooming partners when vervet monkeys are subject to high rates of human aggression.

Currently social network analysis is rarely used to study anthropogenically disturbed wildlife (Bejder et al., 2009; Belton et al., 2018). We provided an assessment of five groups of vervet monkeys that showed social flexibility to living in a highly anthropogenic landscape. Our results largely comply with socioecological predictions, showing that when more reliant upon clumped high value anthropogenic resources, group cohesion increases, possibly because individuals attempt to increase their individual resource holding potential and competitive power over anthropogenic food resources. Previous work has demonstrated the importance of social network analysis in pathogen transfer (MacIntosh et al., 2012), and considering the increased parasite load found in urban primates (Chapter 6), further application of social networks to urban wildlife could provide important information not just for fitness benefits of animals, but also human-wellbeing (Díaz et al., 2006).

Chapter 5 summary

In this chapter, I used social network analysis to assess social flexibility of urban vervet monkeys. I found that both group and individual social metrics were influenced by *anthropogenic variables and, as in Chapters 3 and 4, results highlighted the strong role of human-food consumption on the behavioural ecology of urban vervet monkeys. In the next chapter, I consider whether parasite load can be used as a measure of anthropogenic disturbance and its potential as a management tool.*

Chapter 6

Using parasitic load to measure the effect of anthropogenic disturbance on vervet monkeys

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In this thesis so far, I have demonstrated how vervet monkeys have adapted behaviourally to anthropogenic changes in their ecosystem. Anthropogenic disturbance is increasing at a substantial rate (Mackenstedt et al., 2015), consequently most primates studies are now able to include some level of anthropogenic disturbances within their data (McLennan et al., 2017). The effects of anthropogenic disturbance vary dramatically in their impact across landscapes (Niemelä and Kotze, 2009). We suggest that vervet monkeys are a candidate model to assess the impact of anthropogenic disturbance using parasite load as they can adapt to multiple levels of anthropogenic disturbance (Chapman et al., 2016). In this chapter, we use a scale of urbanisation to test the use of parasite load as an effective measure of anthropogenic disturbance.

Abstract

Vervet monkeys, *Chlorocebus pygerythrus*, thrive in urban areas of KwaZulu-Natal, South Africa, and present a suitable model to assess parasitic load as a measure of anthropogenic disturbance, such as urbanisation. We collected vervet monkey faecal samples from four study sites representing a gradient of land use and urbanisation. We assessed faecal parasites using the faecal flotation method calculating eggs per gram and parasite richness. Overall 58% of samples had some level of parasitic infection. Both group size and anthropogenic disturbance had a significant positive effect on eggs per gram and parasite richness. Results therefore show that increased urbanisation increases parasite load in vervet monkeys. This study provides essential information on urban monkey parasite infections, as well as highlighting the applicability of using parasite load to measure the effect of urbanisation on wildlife.

Introduction

Dramatic increases in human populations have resulted in drastic changes to the function and biodiversity of the natural ecosystem (Bonier et al., 2006; Sauvajot, 1998). Though effects are species specific, certain wildlife species have been able to adapt to ecological changes and thrive in these conditions (McLennan et al., 2017). However, the stresses of an expanding anthropogenic environment can have negative consequences for wildlife such as poor body condition and increased parasite load (Borg et al., 2015; Soto-Calderón et al., 2016). Understanding the effects of anthropogenic disturbance, such as urbanisation, on host–parasite relationships and zoonotic transmission has implications not only for the health of humans and their livestock, but also for wildlife conservation and biodiversity (Cable et al., 2017; Humle and Hill, 2016; Soulsbury and White, 2015).

Urbanisation varies dramatically from large cities to small settlements, therefore, the effects are difficult to quantitatively measure (Bennett and Gratton, 2012; Mackenstedt et al., 2015; Niemelä and Kotze, 2009). Urbanisation creates unique habitats through a process of increasing human populations and anthropogenic structures (Werner, 2011). With the continuing encroachment of anthropogenic pressures, most wildlife studies include some level of human disturbance in their data (e.g. McLennan et al., 2017). However, with the exception of Lane et al.'s (2011) study on *Macaca fascicularis*, few primate studies include highly human-populated urban areas. Furthermore, the majority of anthropogenic parasite studies focus on comparisons between only two study sites. However, the results of these studies show varying effects of increasing urbanisation on zoonotic transmission and parasite infection rates (Cable et al., 2017). Creating a quantitative measure for urban influences is complex, but currently a gradient scale from rural to urban is the most commonly acknowledged method (Bennett and Gratton, 2012; Bradley and Altizer, 2007; Shochat et al., 2007).

Vervet monkeys, *Chlorocebus pygerythrus*, are a common generalist primate that has become highly populated within urban areas of KwaZulu-Natal, South Africa (Patterson et al., 2016, 2017, 2018). They are, therefore, a suitable model to investigate anthropogenic influences on wildlife parasite load. Furthermore, they frequently forage on anthropogenic food sources increasing opportunities for zoonotic transmission (Eley, 1989; Hahn et al., 2003; Hegglin et al., 2015). Research into anthropogenic influences on parasite load in vervet monkeys is limited to two studies (Gaetano et al., 2014; Valenta et al., 2017). Gaetano et al.'s (2014) research suggests that ecological factors are better predictors of parasitism concentrations than anthropogenic contact. However, the applicability of their findings is limited by both small sample size and relatively short time span. Valenta et al. (2017) reported a higher parasite richness in vervet monkeys in an anthropogenic disturbed habitat compared with historical data in less disturbed vervet monkey populations. However, they were unable to interpret their results clearly due to variation in sample sizes and methods across historical studies. Finally, the habitats assessed in both studies had low anthropogenic stress, highlighting a need to assess a wider range of anthropogenic influences on vervet monkeys.

Methods

We aimed to establish whether a relatively low-cost methodological approach to assessing parasite load could reflect an urbanisation gradient. We used four sites throughout KwaZulu-Natal, South Africa. We chose study sites to reflect anthropogenic influences along a rural– periurban–urban gradient (Table 1), including the previously neglected category of a highly human-populated urban area. Vervet monkey group size information was collected using standard point count protocol (Hutto et al., 1986). We obtained human populations and anthropogenic structure numbers from site officials and governmental records (STATS SA, 2017) (Table 6.1). We calculated anthropogenic structure per km^2 in QGIS (QGIS, 2015) by overlaying a grid and counting anthropogenic topography (Table 6.1).

Table 6.1 Information on vervet monkey faecal parasite samples collected from four sites representing a rural–periurban–urban gradient in KwaZulu-Natal, South Africa. Sites have also been classified using McKinney's standardised classification system (McKinney, 2015)

Site	Human density per km^2	Anthropogenic structure per km^2	Group size	Mean no. samples (± SD) per month	McKinney classification
Private reserve	2	2	20	49 (9 ± 0.7)	CDEB
			49	27 (4.5 ± 1.21)	
			16	31 (5 ± 0.3)	
Industrial land	48	4	22	28 (4 ± 0.3)	DDIC
Gated estate	2970	275	12	24 (4 ± 0.2)	HG3LC
			23	23 (4 ± 0.3)	
			27	27 (5 ± 0.3)	
			42	31 (5 ± 0.3)	
City centre	3100	352	28	22 (4 ± 0.2)	HKPO
			35	24 (4 ± 0.4)	

We collected vervet monkey faecal samples over 6 months from October 2016–March 2017. We collected 286 specimens immediately after defecation following standard sampling techniques, storing them in 70% ethanol (Gillespie, 2006).

Vervet monkey samples were prepared for analyses using the faecal flotation method (Gillespie, 2006). We pipetted the prepared sample from the centre of the tube into chambers of a McMaster slide. The slide was assessed using standard methods (Cringoli et al., 2004). We used an electron phase microscope to scan the slide using a A° * 10 objective lens and identified parasite eggs based on morphology. Digital photographs were taken of any vervet monkey parasites observed.

We converted raw data from the McMaster analysis to eggs per gram (Dunn and Keymer, 1986) and compiled information on parasite richness per sample. We classed vervet monkeys as infected if their faecal sample had one or more parasite(s) and present the percentage of samples infected.

We analysed data using R statistical software version 3.3.2 (R project, 2013). Data for both eggs per gram and parasite richness were not normally distributed (Shapiro–Wilks test, $p \leq 0.001$) (Ghasemi & Zahediasl, 2012). We ran two generalised linear models, with eggs per gram and parasite richness as separate dependent variables. We tested eggs per gram with a poisson distribution and log link suitable for frequency data and species richness with a Gamma distribution and log link for non-normal data. For both models, to avoid collinearity, we combined human density per km2 and anthropogenic structure per km2 to create a fixed effect. We created *a priori* maximum model that included both anthropogenic influence km^2 and group size as fixed effects. Generalised linear models were specified using the lme4 package (Bates et al., 2015). To test whether the fixed effects explained variation we used a likelihood ratio test ('anova' command set to 'Chisq') to compare the maximum model against the null model (Zuur et al., 2009). Furthermore, we bootstrapped our confidence intervals to account for uneven sampling within our data set (Davison and Hinkley, 1997).

Results

Overall, 58% of the 286 vervet monkey samples had some level of parasitic infection. Parasites identified were *Coccidia* sp., *Strongyloides* sp., *Tricuris* sp., *Ascaris* sp. and *Oesophagostomum* sp. Eggs per gram were significantly higher in vervet monkeys from more urbanised sites (Table 6.2, Fig. 6.1a). Increasing vervet monkey group size also had a significant positive effect on eggs per gram (Table 6.2, Fig. 6.1b). Parasite richness was significantly higher in vervet monkeys inhabiting more urbanised habitats (Table 6.3, Fig. 6.2a). Increasing group size also had a significant positive effect on vervet monkeys' parasite richness (Table 6.3, Fig. 6.2b).

Table 6.2 Output of GLMM and likelihood ratio test on the eggs per gram of vervet monkey faecal samples (n = 286) collected along a rural–periurban–urban gradient in KwaZulu-Natal, South Africa

Fixed effects	Estimate	Standard error	Bootstrapped confidence intervals		Likelihood ratio test	
			Lower	Upper	Chisq	P value
Intercept	1.45	1.64				
Anthropogenic influence km^2	2.84	4.51	0.02	0.02	35.83	$\leq$0.001
Group size	6.34	1.93	0.12	0.12	11.17	0.001

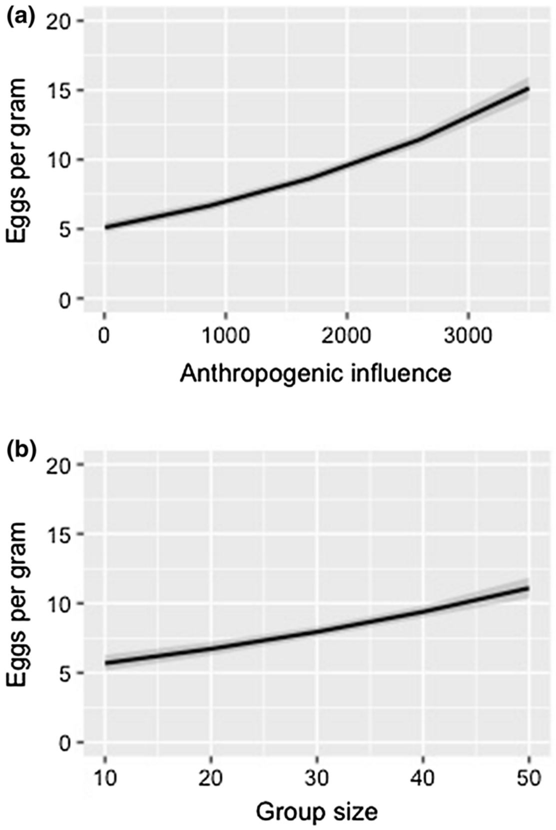

Fig. 6.1 Eggs per gram obtained from vervet monkey faecal samples collected from four sites representing a gradient of urbanisation in KwaZulu-Natal, South Africa, where (a) shows the positive significant effect of increased anthropogenic influence on eggs per gram of vervet monkeys ($p \leq 0.001$), and (b) shows the positive significant effect of group size on eggs per gram of vervet monkeys ($p = 0.001$)

Table 6.3 Output of GLMM and likelihood ratio test on the parasite richness in vervet monkey faecal samples (n = 286) collected along a rural–periurban–urban gradient in KwaZulu-Natal, South Africa

Fixed effects	Estimate	Standard error	Bootstrapped confidence intervals		Likelihood ratio test	
			Lower	Upper	Chisq	P value
Intercept	- 8.87	2.39				
Anthropogenic influence km^2	2.47	4.34	0.01	0.03	29.96	≤0.001
Group size	1.23	5.38	0.01	0.02	5.27	0.021

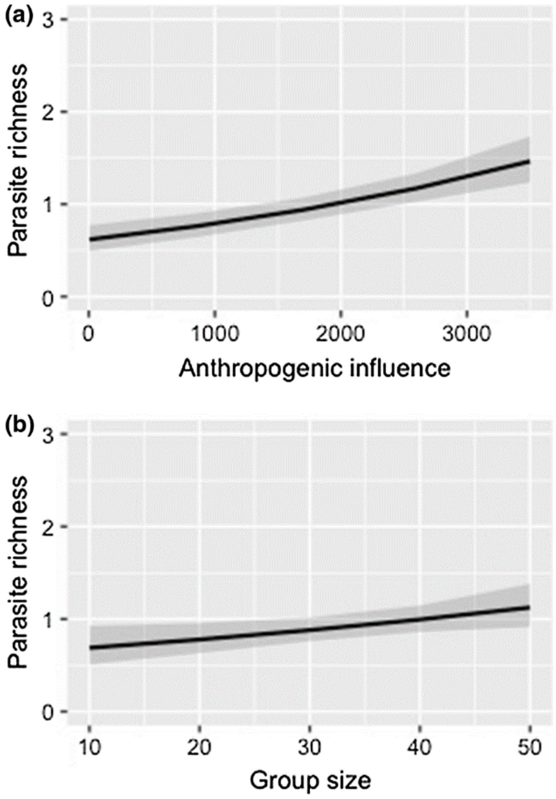

Fig. 6.2 Parasite richness obtained from vervet monkey faecal samples collected from four sites representing a gradient of urbanisation in KwaZulu-Natal, South Africa where

(a) shows the positive significant effect of increased anthropogenic influence on parasite richness of vervet monkeys ($p \leq 0.001$), and (b) shows the positive significant effect of group size on parasite richness of vervet monkeys ($p = 0.021$)

Discussion

Parasite eggs per gram and species richness were significantly higher in vervet monkeys living in areas of higher human density and greater anthropogenic structure than in lower human density and anthropogenic structure, supporting previous studies (e.g. Valenta et al., 2017). As expected, vervet monkey group size was a significant predictor across sites for both eggs per gram and parasite richness.

Overall, our findings suggest that increased urbanisation increases parasite load in vervet monkeys. Past results into the effects of anthropogenic disturbance on primate parasite load are mixed (Cable et al., 2017), although the majority of studies have compared only disturbed and undisturbed categories (Gillespie and Chapman, 2008). Here, we analysed a gradient of urbanisation, crucially including a highly human-populated urban area.

Anthropogenic pressures in dense urban environments, such as city centres, can have a negative impact both at an individual level (body condition: Eley, 1989; Scheun et al., 2015) and at a group level (group stability: Sinha & Mukhopadhyay, 2013). Supporting this, we found that parasite eggs per gram and richness were greater when anthropogenic pressures were higher. Increased anthropogenic influences results in increased contact with humans for wildlife, that can facilitate disease transmission (Eley, 1989; Hahn et al., 2003; Hegglin et al., 2015). A greater public awareness of the need to minimise human-food foraging opportunities for vervet monkeys could limit contact and reduce exposure to potential pathogens for both species. This is especially important considering the nature of human derived food, these foods generally contain a greater starch content, which can contribute to increased parasite concentrations in host species (Becker et al., 2015; Weyher et al., 2006).

It should be noted that parasite load can be influenced by many other factors, such as socioecological pressures and climatic variation (Altizer et al., 2003). Previous studies have shown that increased stress can result in immunosuppression increasing parasite load (Padgett and Glaser, 2003), particularly under increased anthropogenic pressures (Klaus et al., 2018). Also, it is possible that zoonosis and parasite transmission could be facilitated by increased presence and competition with other wildlife and domestic companion animals (Mackenstedt et al., 2015). Future studies should consider controls within their methodology to account for these difficulties in determining the cause of parasite load (Gillespie, 2006).

Although the vervet monkey parasite species found in our study were consistent with those found in other studies on urban primates, without genetic analysis we were unable to look at the direct transmission effects of these parasites. A greater understanding of zoonotic transmission would be a valuable asset, both from the perspective of human well-being and ecological biodiversity conservation (Díaz et al., 2006). Our findings highlight the suitability of the faecal flotation protocol as a relatively low-cost sampling method to monitor host–parasite responses to urbanisation in species such as vervet monkeys. Such methodology could be included in urban management plans on a wider scale to assess the relationship between anthropogenic ecological change and wildlife health. We recommend if future academics are to consider implementing the methods presented in this paper, they should consider blind analysis, to strengthen our current methodology.

Our study is the first to provide baseline parasite data on vervet monkeys living in relatively highly urbanised areas. The wide range of sites used allowed us to conduct a controlled comparison of the effect of anthropogenic influences across a rural–periurban–urban gradient. Results highlight that increased urbanisation is related to both increased eggs per gram and parasite richness in vervet monkeys. The study provides an important foundation for these successful urbanites. As urbanisation increases, a greater understanding of urban exploiters' adaptations to ecological changes is important.

Chapter 6 summary

In this final data chapter, I assessed parasite load along a rural–periurban–urban gradient and found that parasite richness and abundance increased with anthropogenic disturbance and suggest the importance of this information for possible zoonotic transmission. Data presented in this chapter show that a simple low-cost methodology that requires little training could be implemented on a wider scale to assess anthropogenic change and monitor wildlife health.

Chapter 7

General discussion

In this thesis, I have assessed the behavioural flexibility of vervet monkeys under quantified anthropogenic pressures. In this chapter, I summarise the main results and highlight general trends with reference to the research aims set out in Chapter 1, discuss how they contribute to the field of ethnoprimatology and make recommendations for human-vervet monkey management programmes.

Aim 1: Develop a greater understanding of the behavioural strategies that allow vervet monkeys to adapt to the anthropogenic environment

7.1 Behavioural flexibility

The first two data chapters of this thesis considered ranging (Chapter 3) and time budget (Chapter 4) behaviour to assess how vervet monkey's behaviour is influenced by human interactions within the urban environment. Current knowledge of these primate behaviours in a highly urbanised landscape is limited (Klegarth et al., 2017; Chipman et al., 2008; Parker, Gonzales, & Nilon, 2014; Steiner, 2012). Results presented in Chapter 3 and 4 indicated that all four measures of ranging behaviour and all four time-budget categories were affected by anthropogenic disturbance. These findings support the notion that vervet monkeys are behaviourally flexible to the urban landscape and anthropogenic pressures.

Current research focuses primarily on negative repercussions of human-primate interactions, with a distinct lack of research considering both positive and negative aspects (McLennan et al., 2017). As such, I ran an interaction between both positive and negative human influences on our ranging and time budget analysis. This interaction showed that negative human incidents increased daily path length when positive incidents were low, however, with increasing positive human incidents this effect weakened, and paths became shorter (Chapter 3). This suggests that monkeys will take shorter journeys if they have increased access to human-food, but if the rate of positive human incidents decreases and negative human incidents increases, these routes will become longer and less direct. Previous research has shown that supplementary feeding, through active provisioning and waste food consumption, can reduce the home range of urban wildlife (Tennent and Downs, 2008; Widdows and Downs, 2015); however, prior to this thesis, this has not been shown in urban dwelling primates.

Changes in ranging behaviour has consequences for foraging, moving, resting and social components of individuals' time budget. I found that our result for moving time budget behaviour (Chapter 4) corresponded with our result for path choice (Chapter 3). Time spent moving was higher with increased negative human incidents, yet positive human incidents weakened this effect. Results for movement patterns (Chapter 3 & 4), suggested that vervet monkeys' movement was highly dependent on the value of food resources available, supporting past research (Saj et al., 1999). Results highlight that vervet monkeys were less likely to move in response to human aggression when high value food was available.

The interaction of positive and negative human incidents was also significant for foraging and socialising time budget behaviours, vervet monkeys increased time spent performing these behaviours when positive human incidents were high. It is possible that decreased daily ranging patterns (Chapter 3) and movement (Chapter 4), provided more time and energy to perform other behaviours (Dunbar et al., 2009). Results on foraging behaviour indicated that if vervet monkeys have access to high value anthropogenic food, then despite human-aggression, their time spent foraging would increase. Although our results are contrary to previous anthropogenic time budget studies showing a reduction in time foraging in human altered landscapes (Jaman and Huffman, 2013), this may point to a methodological difference between studies, as our foraging behaviour included eating as well as searching for food. Thus, this increase in foraging behaviour likely reflects that vervet monkeys took more time consuming these high value items and that this did not represent an increase in energy expenditure. Our interaction also showed that vervet monkey social behaviour increased with a greater rate of positive human incidents; however, negative human incidents offset this, decreasing social behaviour. Increased time spent socialising supports previous studies, where reduced movement allowed for more time socialising under high anthropogenic conditions (Jaman and Huffman, 2013).

Overall, I found the interaction between positive and negative human incidents to be significant for three ranging measures and three time budget categories. I therefore suggest that the interplay between positive and negative aspects of the urban environment creates a complex attraction-avoidance scale, and that to fully understand behavioural adaptations under anthropogenic pressures both of these aspects must be considered. Predominantly, results from Chapters 3 and 4 highlights, that vervet monkeys respond to the urban landscape by altering their behaviour under periods of increased human resources to benefit from the potentially high calorific intake.

Overall, results of this thesis support literature on general adaptive primate species in the anthropogenic landscape, suggesting behavioural flexibility to anthropogenic pressures, particularly increased human resources (Bryson-Morrison et al., 2017; Bryson-

Morrison et al., 2016; Hoffman and O'Riain, 2012a; Saj et al., 1999; Sha and Hanya, 2013). Interestingly most studies of anthropogenically disturbed primates show behavioural flexibility, highlighting that time spent moving and foraging was reduced to allow for greater time to socialise (Jaman and Huffman, 2013; Saj et al., 1999; Scheun et al., 2015), moderately supporting the results of this thesis; however, these previous studies only compare study sites with no measure of anthropogenic disturbance. My analysis considers a quantified measure of human-monkey interactions, including both positive and negative aspects of this interaction, to show a complimentary finding, suggesting behavioural flexibility to the multiple facets of urban living. Further research would allow us to test if this adaptive behaviour of vervet monkeys is an expression of behavioural flexibility, as well as highlight potential fitness benefits.

Aim 2: Assess the socio-ecological and anthropogenic influences that affect social behaviour of urban vervet monkeys

7.2 Social flexibility

Our understanding of social flexibility in response to anthropogenic pressures and resources is limited (Lacy and Martins, 2003; Skandrani et al., 2017), but important for developing our knowledge of whether, or how, wildlife adapt to urban landscapes (Couzin, 2006; McLennan et al., 2017). In Chapter 5, I provided results that support the principles of socio-ecological theory, which with increasing WGC (indexed by human-food consumption), groups were more cohesive and expressed a linear despotic hierarchy.

In Chapter 4 I used time budget analysis to highlight the value of human interactions to vervet monkey social behaviour; our positive-negative human interaction scale showed that vervet monkey socialised more when positive human incidents were higher; however, negative human incidents offset this decreasing social behaviour. In Chapter 5, I further explored the role of human interactions on social behaviour, considering social interactions at a group and individual level and found supporting results to my time budget analysis (Chapter 4). For both group and individual measures, social network analysis emphasised the importance of human-food consumption on vervet monkey social structure. For example, I found an interaction between natural food consumption and positive human incidents on group social metrics that suggested when human-food consumption was high, grooming connections also increased. Results support the hypothesis that vervet monkeys modify their social relationships to increase competitive power when feeding on monopolisable resources (Sterck et al., 1997). Recent studies have shown that flexibility in social structure has long-term fitness benefits for population growth and success (Royle et al., 2012) and longevity (Silk et al., 2010). Feeding competition is one of the most fundamental factors affecting fitness in animals (Chapman et al., 2012), considering the strong role of human-food on social interactions highlighted in both Chapters 4 and 5, it is likely that flexibility in vervet monkeys' network composition in response to food competition is adaptive.

Aim 3: Provide recommendations for management protocols for urban vervet monkeys

7.3 Parasite monitoring tool

Although I have highlighted the flexible behaviour of vervet monkeys to anthropogenic influences (Chapters 3-5), it should be noted that urban living can have fitness costs, such as increased parasite load (Borg et al. 2015; Soto-Calderón et al. 2016). In Chapter 6, I used a rural-periurban-urban gradient scale to show that more anthropogenically disturbed habitats had higher parasite richness and abundance, providing the first parasite reference level for highly urbanised vervet monkeys.

Chapter 6 highlighted the suitability of the faecal flotation protocol as a relatively low-cost sampling method to monitor host-parasite responses to urbanisation in species such as vervet monkeys. This faecal flotation protocol could be used in future wildlife management programmes to monitor changing anthropogenic pressures. Identification of urban parasites provided in Chapter 6 are therefore important to implement suitable management procedures for biodiversity wellbeing, particularly as human-wildlife co-habitation increases (Cable et al., 2017)

It should be considered that parasite load can be affected by multiple variables, to fully understand the effect of urbanisation on parasite load further exploration is needed. Numerous studies have highlighted the association between grooming networks and parasite load, noting that social interactions and positioning can increase parasite transmission rate (Altizer et al., 2003; MacIntosh et al., 2012). As I have highlighted interesting social trends in this thesis (Chapters 4 and 5), it is possible that social flexibility may influence parasite load in urban vervet monkeys and therefore would provide an interesting topic for future research. Furthermore, previous research has shown increased human-wildlife interactions and human-food consumption opportunities increases zoonotic transmission (Eley, 1989; Hahn et al., 2003; Hegglin et al., 2015). In Chapter 3, I found that positive and negative aspects of urbanisation interacted to affect urban vervet monkey ranging patterns, highlighting how the attractiveness of human-food increased human-monkey interactions. Increased proximity between vervet monkeys and residents, as well as direct provisioning, could therefore lead to increased parasite transmission as shown in previous studies (Hegglin et al., 2015). Nevertheless, simple management strategies to reduce human interactions could be employed to anticipate this risk of transmission. Overall, behavioural aspects of this thesis could be considered in future research to further understand parasite transmission rates for the benefits of human-primate cohabitation and human-wellbeing (Díaz et al., 2006).

7.4 Suggestions for management

Human-wildlife interactions pose one of the greatest threats to the survival and success of many species (Dickman, 2010). Acquiring further knowledge on the impact of urbanisation on wildlife populations is therefore 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 (Strum, 2010; Woodroffe et al., 2005). It has been suggested that successful management requires multiple strategies focused on reducing rates of human aggression and improving human perceptions (Hockings et al., 2015; Nowak and Lee, 2013; Priston and McLennan, 2013). A common theme throughout this thesis has been how the interplay of both positive and negative aspects of the urban environment creates a complex attraction-avoidance scale (Chapters 3 & 4). I recommend management strategies consider both positive and negative aspects of urban living for vervet monkeys. I will disseminate my findings to management at Simbithi eco-estate, providing them with a synopsis of my findings and recommendations, and published papers.

The effects of the positive and negative interaction have important implications for management, suggesting that increased human aggression will not necessarily reduce the ‘unwanted’ behaviour of vervet monkeys. Therefore, trategies should aim to prevent/reduce opportunities for human-food consumption that may support human-wildlife cohabitation. Education is commonly suggested as the primary management tool for the benefit of human-wildlife cohabitation (e.g. Spencer et al., 2007; Tchamba, 1996; Treves & Karanth, 2003). I suggest programmes disseminate simple preventative measures to local residents that can reduce human aggression and minimise unnecessary maltreatment of vervet. For example, within houses I propose that residents should ensure that food is not accessible by (i) minimising access into their property by shutting windows and doors or using screens at open doors and windows to prevent monkeys entering houses and (ii) not leaving food on display e.g. fruit bowls, and securely storing all food items in storage jars and cupboards. However, research has shown that educational measures are not always successful if implemented with a lack of reinforcement, or without a competent assessment of their implementation (Baruch-Mordo et al., 2011). As such, I suggest that the estate management should be pro-active in their measures, providing educational sessions, as well as leaflets, and enforcing residents' efforts to reduce opportunities for human-food consumption. Monitoring the frequency of human-food consumption after such preventative measures have been applied may provide valuable data of success, which would encourage greater participation among residents.

In addition, management can also contribute to reducing human-food consumption opportunities by securing all bins with latches or locks that make it harder for vervet monkeys to access the food waste. Management could also focus on human-food consumption that occurs within their own leisure facilities (e.g. restaurants and golf club), discouraging intentional feeding of vervet monkeys and encouraging immediate disposable of food and waste. Reduction of food availability and human-food consumption opportunities has proven to be successful in previous management plans (e.g. Strum, 2010). Implementation of simple regulations to prevent opportunistic human-food consumption and provisioning by humans should in turn reduce human aggression, improve vervet monkey welfare and increase biodiversity wellbeing in respect to zoonotic transmission (Chapter 6).

The positive-negative human interaction scale highlighted that not only is human aggression ineffectual, but also showed that human-food influences vervet monkey behaviour. Management could therefore consider implementing artificial food patches, to encourage monkeys to feed at these select sites instead of entering human residence. Kaplan and colleagues (2011) showed that artificial food patches could be used to alter baboon movement patterns away from anthropogenic areas. Kaplan and colleagues found that baboons would feed at these patches; however, they would only consistently do so when access to waste was minimised and food patches were maintained. Based on the results of Kaplan and colleagues research, it could therefore be suggested that a combination of preventing access to human-food/residence and well-maintained artificial food patches could be used to reduce negative interactions between vervet monkeys and humans. It should be noted that supplementary food patches are likely to be dominated by higher ranked individuals and may therefore have rank dependent reproductive benefits and costs (King et al., 2008; Strum, 2010). Furthermore, artificial feeding patches increase proximity and encounter rates between individuals, hence increasing chances for parasite transmission (Klaus et al., 2018).

In order to be effective, artificial food patches would need to be increased to a sufficient amount and be well dispersed, allowing lower rank monkeys to have a greater chance of feeding there. It is likely that dispersing food in a closed dense urban setting, such as Simbithi eco-estate, could increase vervet monkey proximity to human homes and increase the likelihood of negative human–nonhuman primate relationships. In order to enforce artificial food patches as an alternative foraging source for urban primate management, the methodology needs more grounded research into the amount of food needed, the quality of food fed to be effective, the amount of time this food should be available and the long term social and ecological effects. Furthermore, if supplementary food patches are considered in future management, they should be closely monitored as over-provisioning could increase population growth rates and demography (Rodriguez-Hidalgo et al., 2010). Although there is some research suggesting artificial food patches can be used to alter species' ranging behaviour (American black bear (*Ursus americanus*), Fersterer et al., 2001; moose (*Alces alces*), Sahlsten et al., 2010), I believe that the implementation of food patches as a management tool is not yet justified and requires further research.

An alternative to managing artificial food patches, could be to increase natural food resources within the estate for vervet monkeys. In Chapter 4 I showed that as natural food availability increased vervet monkeys would forage more on these natural food resources. Therefore, additional natural food resources could be planted, providing a sustainable management plan for the benefit of human-primate cohabitation. However, it is important to highlight Simbithi is an 'eco-estate' and therefore already has numerous natural areas that are regularly maintained (see Chapter 2), yet these resources are not fully exploited by the vervet monkeys. For this management strategy to be considered, more research would need to be conducted on vervet monkeys plant preferences and a more thorough phenological assessment of the estate (see 7.4.1). Therefore, based on current knowledge, I suggest management at Simbithi eco-estate focus their efforts on preventing vervet monkeys' access to human derived food.

7.5 Limitations of study

7.5.1 Natural food

One limitation of this study is the assessment of natural food, although I originally intended to assess natural food availability with traditional methods (Marshall and Wich, 2013), using transects and quadrats to assess food availability monthly, this was not possible due to methodological limitations. I therefore used a combination of both a retrospective estimate of food availability and behavioural observations of food consumption, choosing the most relevant calculation dependent on the research hypothesis. Although methods may not be accurate of all food available, I feel it is a justifiable representation of natural food and is adequate for the assessments conducted. Nevertheless, I suggest that if future scholars are to conduct similar research they should fully assess natural food availability, considering more traditional primate field methods (Marshall and Wich, 2013). Furthermore, I also suggest that as the field of ethnoprimatology continues to grow researchers should consider how we define 'natural food'. In this study population 'natural food' consisted of horticultural food resources either those in residential gardens or those in selectively maintained walking trails throughout the estate. This horticultural food represented a seasonally varying food resource to the vervet monkeys and the only natural food available to them. However, in other anthropogenic studies horticultural plants or similar crops may be seen as human-derived. As the term natural food and wild food are commonly used to describe the primary 'natural' food resource to primates, natural food is a suitable reflection on the study site. However, as anthropogenic research continues a review of suitable terminology and definitions would facilitate for more comparable research across populations.

7.5.2 Behavioural observations

As was expressed in the general methods (Chapter 2), the initial behavioural data collection methods set out for this study were extended in order to increase data. Data collection was sufficient for the analysis performed within this thesis to address my aims and hypothesis; nevertheless, on reflection employing a combination of scans and individual focal observations sooner would have created a stronger data set. I therefore recommend that if researchers were to replicate these methods, performing similar analysis both focal observations and group scans should be used to form a larger, more detailed data base from the onset. Behavioural observations were also limited by the frequency that certain groups left the estate, to compensate extra field days had to be dedicated to behavioural observations. Future scholars should consider these limitations of losing visual contact with the group, for example by observing fewer groups, or by obtaining more preliminary information on group movement patterns.

7.5.3 Cheek pouches

In addition to extending behavioural observations, on reflection some further acknowledgement or inclusion of the function of cheek pouches would have provided a greater insight into vervet monkeys foraging strategies. Cheek pouches are an adaptive anatomical quality of cercopithecines (Lambert, 2005; Lambert and Rothman, 2015). As a result of these anatomical adaptations cercopithecines are acknowledged to be adaptive, using a retrieve-and-retreat foraging strategy (Murray, 1975). It is likely that this foraging strategy has allowed cercopithecines to prosper in the anthropogenic environment (Humle and Hill, 2016). Previous research has shown how cheek pouch use can be influenced by socio-ecological pressures (Lambert, 2005), therefore it is likely that changes in food abundance in the anthropogenic landscape may alter foraging time and hence energy expenditure for urban vervet monkeys (Chapter 3 and 4). Furthermore, as group demography can affect cheek pouch use, it is likely that rank and group competition may also be influenced by cheek pouch use (Chapter 5). The use of cheek pouches was not considered within the methods of this thesis originally due to time limitations and visual feasibility; however, I would strongly recommend that they are included in future studies on anthropogenic populations of cercopithecine species. A group scan every 30 minutes would provide enough data to be able to assess this anatomical adaptation, without hindering other data collection. This additional information would provide a further insight into the adaptive foraging strategies employed by cercopithecines in the anthropogenic landscape.

7.5.4 Wider applicability

The gated estates used for this research provided a unique safe habitat to conduct research, which vervet monkeys exploited using various strategies. This in-depth study of the anthropogenic influences on the behavioural ecology of vervet monkeys provides the first thorough assessment in a highly modified human habitat by assessing ranging patterns, time budgets, social behaviour and faecal parasite load. Gated estates provide a variety of human influences as well as a safe environment for urban wildlife research such as that presented in this thesis. Nevertheless, it should be noted that as this thesis provides the first research to use these unique habitats to study primate behavioural ecology, findings should be applied with caution to other populations. We strongly encourage scholars to take advantage of these safe urban settlements to conduct further research. Continuing research within this unique habitat will allow a better understanding of population numbers and dynamics, assessing not only the flexibility of urban vervet monkeys, but also the fitness consequences of urban exploitation.

7.6 Future study

7.6.1 Further data exploration

Chapter 3 used GPS data to show that both negative and positive human interactions influenced ranging patterns of urban vervet monkeys. Human-wildlife cohabitation is acknowledged to cause increased negative associations between humans and wildlife (Dickman, 2010). A prior study by Hoffman and O'Riain (2012) considered the relationship between spatial distribution and baboon-human cohabitation to initiate landscape management recommendations, to reduce this negative baboon-human relationship. I therefore intend to develop Hoffman and O'Riain's work, using GPS co-ordinates from each human-vervet interaction to see if there are any patterns between landscape characteristics and human-interactions. This analysis will also highlight if there are any 'hotspots' where there are particularly high rates of human-food consumption or human-monkey aggression. This information would further help facilitate management plans, knowing which houses may need greatest guidance preventing vervet monkey access, or where may be the most suitable place to initiate artificial food patches/tree planting.

Chapter 4 (Fig 4.1) highlights an interesting trend between time spent foraging on human and natural food in relation to the availability of natural food. It is to be expected that there would be an interesting relationship between natural and human-food consumption, particularly considering seasonal variations in food availability. This relationship between human interactions and food resources has been considered in crop foraging species (Chaves and Bicca-Marques, 2016); however, the relationship in the urban landscape between horticultural resources and human-food has not yet been considered. I therefore aim to conduct further analysis exploring this relationship between food consumption and food availability. When recording foraging behaviour, I made a detailed description of food choice, e.g. fruit, leaves etc. and later grouped these into either human or natural food. This extra information and analysis will provide a more detailed perspective on the opportunistic foraging tactics of urban vervet monkeys, complementing the findings of Chapter 3 and 4.

7.6.2 Anthropogenic interactions

Human-wildlife interactions are generally classed as the interactions resulting from the shared landscape between people and wildlife, resulting in both positive, negative and neutral outcomes for humans and wildlife (Dickman, 2010; Humle and Hill, 2016; Nyhus, 2016). In this thesis, I show the benefit of measuring both positive and negative aspects of urban living for vervet monkeys, previously highlighted to be a shortcoming of ethnoprimatology literature (McClennan et al., 2017). The results of this thesis highlight the importance of considering both benefits and costs of urban living as they provide an advanced view of urban primates' strategies.

Human-nonhuman primate interactions can have varying consequences for humans too. For example, positive outcomes such as seed dispersal (Chapman and Onderdonk, 1998) and financial benefits (e.g. tourism) (Hvenegaard, 2014) as well as negative repercussions for humans such as livestock predation (Sogbohossou et al., 2011) and crop loss (Hill, 2000). Therefore, I suggest that future studies should include a measure of human benefit and costs within their methodology. This would provide a complimentary addition to the data collected in this study and allow a better understanding of the multiple facets that create the human-wildlife interface (Nyhus, 2016). By acknowledging the fact that humans create their environment yet monkeys generally respond to the changes within their environment, we will develop an understanding of human perception towards primate interactions. This additional information will help direct management plans, providing an indication of likely public participation or retaliation.

As a primate's behaviour towards a human is thought to be a reflection of a human's behaviour towards a primate (and vice versa), this interaction between human and non-human primate behaviour should be considered in future analysis. For example, it is likely that negative human aggression towards vervet monkeys will affect vervet monkey's retaliation towards humans with increased aggression. It is therefore important to acknowledge that human and vervet monkey interactions are not independent and that understanding both human and monkey behaviour is imperative in the urban landscape.

7.6.3 Measuring anthropogenic disturbance

As most primate species are now subject to some level of anthropogenic disturbance (Clutton-Brock and Janson, 2012) the interest in the human-primate interface is ever-growing, resulting in a surge in ethnoprimatology studies (McKinney and Dore, 2018). Currently most research that focuses on the anthropogenic interface classifies disturbance by habitat type. McKinney (2015) highlighted that as the wealth of ethnoprimatology literature grows a moderated form of classification is needed to compare research. McKinney's classification system uses a flow-chart system to represent the level of disturbance for four categories (landscape, human-nonhuman primate interface, diet and predation risk), providing each research site/study group with a code. McKinney's classification was used to describe the study site in Chapter 3 and compare sites of disturbance in Chapter 6. Although McKinney's classification had some application in highlighting differences between sites, at large I found the interface challenging. The interface provided by McKinney requires the researcher to use only the classifications provided in the flowchart to categorise primate disturbance; however, these categories are broad and could be subjective to the researcher. Furthermore, for the variable of ‘human-nonhuman primate interface’ there is not a suitable classification for the vervet monkey population at Simbithi eco-estate. Urban primates often interact with humans by foraging on human-food or entering human-property, McKinney’s interface does not provide a suitable category for this interaction, instead the closest option assumes that humans are provisioning primates via direct interactions rather than a dependence on opportunistic human-food consumption. Furthermore, considering the increasing rate of anthropogenic disturbance (McKinney and Dore, 2018), it is questionable why currently only two papers (Rodrigues, 2017; Thatcher et al., 2018) use McKinney’s classification to code their study site, likely highlighting issues with using the system.

It cannot be denied that McKinney’s classification system, or something of similar nature, is necessary. Considering this clear gap in the literature, I suggest an alternative measure is necessary for future comparison between studies. I suggest that future academics consider a mean of quantitatively measuring anthropogenic disturbance. Currently only a limited number of studies use a rate per hour to assess anthropogenic disturbance similar to that used in this thesis (Hsu et al., 2009; McKinney et al., 2015; Riley and Wade, 2016). To acknowledge that anthropogenic interactions can be influenced by both human and primate behaviour, I suggest that future studies create four rates of interactions, measuring positive and negative interactions from both the human and primate perspective. Although it should be noted that these four measures are unlikely to be independent, a representation of these different rates within future studies will allow a truthful measurement of human-primate interactions. Furthermore, the human-primate interface is also influenced by landscape and habitat features (Hoffman and O’Riain, 2012a), I therefore suggest future studies should create a measure of habitat fragmentation, using a similar measure (anthropogenic disturbance per km^2) to that used in Chapter 6. I suggest that if future academics apply these simple measures of anthropogenic disturbance to future research it can create a cross comparable quantified measure of anthropogenic disturbance. Greater facilitation of cross-comparison research will aid future collaborations and support management plans.

7.7 Conclusion

Through multiple assessments of vervet monkey behavioural ecology, I document the behavioural flexibility of vervet monkeys to anthropogenic changes. In addition, I assess the previously neglected interaction between human-food and human-aggression, showing that human-food influences all assessed aspects of vervet monkey behavioural ecology. This finding has important repercussions for future management concerns of vervet monkeys, highlighting that aggression towards vervet monkeys is not an effective deterrent when human-food consumption opportunities are high, and that efforts should focus towards minimising vervet monkey access to human-food.

Overall, this thesis has used quantified anthropogenic influences to provide a unique insight into urban primate ecology, providing complimentary evidence to the already emerging field. This study considers quantified anthropogenic influences from the view of primates, importantly analysing an integrated approach that considers not only negative aspects of human-monkey interactions but also positive aspects. It therefore provides an insight into the possible strategies used by these urbanites, essential for management recommendations. We suggest more ethnoprimatology studies should look at methods to quantifiably measure disturbance instead of broadly classifying field sites. More consistent use of quantified disturbance will allow for future collaborations and comparisons between studies.

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Appendix 1

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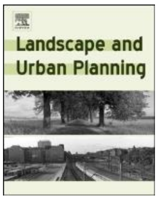

Research Paper

Anthropogenic influences on the time budgets of urban vervet monkeys

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ABSTRACT

Continuing urban developments are ecologically changing many landscapes. A greater understanding of how wildlife adapt behaviorally to these changes is necessary to inform management decisions. Time is a valuable resource to wildlife and a reflection of ecological pressures on the behavioral repertoire of an animal. Data on urban vervet monkey, *Chlorocebus pygerythrus*, time budgets are generally limited and dated. We aimed to investigate the effect of anthropogenic influences, both human food consumption (positive) and human-monkey conflict (negative) on the time budgets of vervet monkeys in an urban landscape. We collected 20 min. focal animal observations and used generalized linear mixed models to assess the variation in time budget between five urban vervet monkey groups differing in anthropogenic contact over one year. We recorded anthropogenic interactions as positive and/or negative. Our results showed seasonal influences across all behaviors. Furthermore, anthropogenic disturbance influenced all aspects of time budget to some degree. We found a positive interaction effect between positive and negative human incidents on foraging, and a negative interaction effect on movement and social behavior. Overall, vervet monkeys exhibited behavioral flexibility in the urban landscape. We suggest a complex association of costs and benefits to urban living.

1. Introduction

Increased human populations and urban developments are transforming many wildlife habitats (McKinney, 2006). Human expansion has led to a growing interest in understanding behavioral responses of species to urbanization for urban management plans (e.g. Jokimäki et al., 2011). Wildlife has been shown to adapt to these changes in many ways including modifying foraging behavior, predator behaviors and activity patterns (Jokimäki et al., 2011). Information on how wildlife adapt behaviorally to these changes can be key for management decisions (Ditchkoff, Saalfeld, & Gibson, 2006; Marzluff, Bowman, & Donnelly, 2001). Time budgets have been applied to a variety of species to study the effect of varying levels of anthropogenic disturbance (e.g. Jokimäki et al., 2011). However, studies including high-density towns and cities are scarce, furthermore, positive associations of urban living for wildlife behavior are rarely considered, despite being necessary, to develop suitable management plans (McLennan, Spagnoletti, & Hockings, 2017).

Understanding the relationship between an animal and its environment can provide essential information for conservation management and urban planning (Patterson, Kalle, & Downs, 2018). Time budgets provide a useful method to test ecological hypotheses (Isbell & Young, 1993) as they allow the representation of time allocation where trade-offs in behaviors are illustrative of the resources and time available (Dunbar et al., 2009). Time budget analyses have been employed across urban wildlife to demonstrate the effects of urbanization and landscape changes (burrowing owls, *Athene cunicularia hypugaeaa* : Chipman et al., 2008; gray squirrels, *Sciurus carolinensis:* Parker, Gonzales, & Nilon, 2014; bottlenose dolphins, *Tursiops aduncus*: Steiner, 2012).

Rapid human population growth and land-use changes have transformed many primate habitats (Estrada, Raboy, & Oliveira, 2012; Mckinney, 2015) and have resulted in a directional shift towards ethnoprimatology (Fuentes & Hockings, 2010; Hockings et al., 2015; McLennan et al., 2017; Strier, 2017). Although time budgets have been applied to assess primate behavioral flexibility to landscape change, the applications of these findings are largely limited to macaques (*MACACA* sp.) and baboons (*Pappio* sp.) (McLennan et al., 2017). Anthropogenic assets such as high value food have been shown to decrease foraging time (Hoffman & O'Riain, 2011; Jaman & Huffman, 2013; Saj, Sicotte, & Paterson, 1999; Sha & Hanya, 2013) which often occurs in parallel with a decrease in movement (Jaman & Huffman, 2013; Wong & Candolin, 2015) and associated with an increase in social interactions (Jaman & Huffman, 2013; Saj et al., 1999; Scheun, Bennett, Ganswindt,

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& Nowack, 2015).

Seasonality is a strong predictor of time budgets in wild primates (Fan, Ni, Sun, Huang, & Jiang, 2008; Hendershott, Behie, & Rawson, 2016; Zhou et al., 2007), however, primates living in urban landscapes are often buffered against the effects of seasonality. Reports of seasonality on anthropogenically influenced monkeys are mixed. Some studies show no influence of seasonality, expressing this as a result of a continuous supply of high value resources available (Altmann & Muruth, 1988; Eley, 1989). Recent studies of more anthropogenically disturbed primates have shown that seasonality is influential on time allocation and suggest this to be an adaptive exploitive behavior (macaques; Jaman & Huffman, 2013, and baboons; Van Doorn, O'Riain, & Swedell, 2010).

Prior research has assessed aspects of the landscape that influence the success and survival of vervet monkeys, *Chlorocebus pygerythrus*, in a modified anthropogenic environment (Chapman et al., 2016; Patterson, Kalle, & Downs, 2016). Although studies have considered time budgets of anthropogenically disturbed primates, no study has yet assessed the flexibility in time budgets of an adapted generalist primate living in such a highly human populated urban setting. Furthermore, past research has only considered the consequences of either human/wildlife conflict (negative aspects) or access to high value resources (positive aspects) (McLennan et al., 2017). Studies examining the interaction between these negative and positive aspects are needed. As vervet monkeys continue to succeed in the ecologically developing urban landscape, the human wildlife conflict between vervet monkeys and local residents continues to grow with negative consequences for vervet monkeys (Wimberger & Downs, 2010; Wimberger, Downs, & Perrin, 2010). Vervet monkey population expansion in urban lansdscapes raises concerns both for vervet monkey wellbeing (Wimberger & Downs, 2010; Wimberger, Downs, et al., 2010) and ecological biodiversity conservation (Díaz, Fargione, Iii, & Tilman, 2006)

We aimed to investigate the effect of anthropogenic influences, both human food consumption (positive) and human-monkey conflict (ne- gative) on the time budgets of vervet monkeys in an urban landscape. In order to do this, our main prediction focused on ecological and land- scape constraints. We predicted that anthropogenic disturbance would affect urban vervet monkeys' time budgets (Jaman & Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). We predicted that positive an- thropogenic aspects would decrease movement and foraging and in- crease social behavior as a trade off in time availability.

2. Methods

We conducted our study at Simbithi eco-estate, a private gated housing estate in Durban north coast, KwaZulu-Natal, South Africa (29.5140° S, 31.2197° E). The estate was previously two sugar cane farms that were developed 20 years ago to form a 430 ha estate (Simbithi eco-estate, 2017, pers. comm.). The estate was comprised of a variety accommodation options including apartment blocks, retirement complexes and general housing within a green mosaic. The estate had other anthropogenic leisure developments including restaurants, shops, fitness facilities, a golf course and a hotel. The estate encouraged wildlife research to help biodiversity management plans. Residents had mixed responses to vervet monkey presence ranging from actively encouraging vervet proximity to humans (intentional feeding by humans) to actively deterring vervet monkeys from human property (human aggression).

Vervet monkeys are commonly found in urban settings of KwaZulu-Natal (Thatcher, Downs, & Koyama, 2018) and therefore provided a candidate model to assess behavioral flexibility under anthropogenic changes (Chapman et al., 2016; Saj et al., 1999). The estate contained seven groups of vervet monkeys (Simbithi eco-estate, 2017, pers. comm.), although this study only considered the five groups that regularly stayed within the borders of the estate. Group size varied from 14 to 42 individuals (Ballito (14): 3 males, 6 females, 5 juveniles; Farmyard (23): 4 males, 10 females, 9 juveniles; Savannah (25): 4 males, 10 female, 11 juveniles; Goodies (29): 5 males, 10 females, 14 juveniles; Herron (42): 5 males, 14 females, 23 juveniles). This was the first study on these groups so their history was unknown. Most monkeys were well habituated to humans due to the regular proximity to human residence. Two months were spent prior to commencing behavioral observations identifying monkeys. All adult vervet monkeys were identifiable via distinguishable markings, therefore, all 71 adult vervet monkeys were observed for this study.

We collected data from March 2016 to February 2017. We conducted observations from dawn until dusk (up to 8 h in winter and 16 h in summer) for a minimum of three weeks per month. Where possible we conducted a minimum of one observation per monkey per month, spread throughout the day (mean ± SD number of observations per group in the morning = 217 ± 33, midday = 251 ± 19 and afternoon = 286 ± 40). In total 3774 focal animal observations were conducted across all groups, averaging 650 ± 173 min per monkey.

We used focal animal sampling techniques (Altmann, 1974) to observe each individual for 20 min, sampling all group members before repeating observations in each month. We chose four key mutually exclusive categories to represent time budget defined as foraging: a monkey actively searching for food items before feeding and directly consuming food items found (food items include, plants, aesthetic garden plants and human derived food) (Ménard et al., 2013; Saj et al., 1999); movement: included all types of locomotion not associated with any other activity, for example walking, running, climbing, and jumping (Ménard et al., 2013; Saj et al., 1999); resting: monkey in an inactive posture that excludes interacting with others, in a motionless position for longer than five seconds (Saj et al., 1999); social: monkey interacting with at least one other monkey including both affiliative and agonistic behaviors (Ménard et al., 2013; Saj et al., 1999).

During dawn until dusk follows of each group, we used all occurrence sampling to record all interactions between humans and vervet monkeys. We identified a human related incident as any occasion when at least one vervet monkey interacted with humans or their related possessions (car, house, bin etc.). For positive human incidents we included any form of human-food consumption (e.g. bread, fruit, pizza). An incident was classed as terminated once all human food was consumed, if the monkeys then obtained human food after 20 min we classed this as a new event. Negative human incidents were classed as any form of human-monkey aggression directed towards vervet monkeys (chase, rocks thrown etc.). Such interactions represent a cost to the vervet monkey due to the energy expended (running away) and risk of injury. We classed an incident as terminated once all parties had retreated and we recorded new events if there had been no incident in the prior 20 min. Positive and negative human incidents were not mutually exclusive, a human event could be coded twice as both positive and negative (e.g. monkey takes food from human house [positive] and is chased away [negative]). To support our monthly human values we also created an estimated monthly value of natural food availability. Following practiced phenology protocol we conducted five randomly placed walking transects within each group's home range noting all specimens ≥10 cm diameter at breast height (Marshall & Wich, 2013). We retrospectively identified windows of fruit and flower availability using horticultural records for the region as in some previous studies (Blake, 1990; Wirminghaus, Downs, Symes, & Perrin, 2001). We split our data seasonally based on the four calendar seasons (summer: November-March, spring: September-October, autumn: April-June, winter: July-September) (SANBI, 2018).

2.1. Statistical analyses

For human values, we calculated a monthly rate (per hour) per group based on how many incidents were observed according to hours of field observation each month. For behavioral observations we converted the total duration(s) of behavior to percentage of time spent performing that behavior per focal observation. Behavioral data were found to be not normally distributed using the Shapiro-Wilk's test ($p \leq 0.001$) (Ghasemi & Zahediasl, 2012). We calculated the variation inflation index of each predictor for inclusion in our model using the CAR package (Fox et al., 2007), setting the inclusion level at < 3 (Zuur, Ieno, & Elphick, 2010). All data were analyzed using R statistical software (R project, 2013) and the significance level set at $p \leq 0.05$.

As data were non-parametric we ran a generalized linear mixed model on each behavioral category as the dependent variable using the *lme4* package (Bates, 2010). We created *A priori* maximum models that included positive human incidents, negative human incidents, natural food availability, group size and season as fixed effects. We controlled for repeated observations on individuals we included monkey identity as a random effect. Furthermore, we ran an interaction between positive and negative human incident rates. We scaled all our variables to produce a better fitting model. We ran all models with a gamma error distribution using a log link function.

To test whether the fixed effects explained variation we used a likelihood ratio test ('Anova' command set to "Chisq") comparing the maximum model against our null model (dependent variable plus one) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). If the maximum model was significantly better, we then ran a second likelihood ratio test on the maximum model to test the significance of each fixed effect (Zuur et al., 2009).

3. Results

3.1. Anthropogenic disturbance

The interaction effect between positive and negative human incidents showed that percentage of time spent foraging was less when positive human incidents were low and negative human incidents were high, however a higher rate of positive incidents and less negative human incidents were related to an increase in time spent foraging ($F_1 = 32.26$, $p \leq 0.001$; Table 1, Fig. 1a). The interaction between positive and negative human incidents showed that their movement increased as rate of positive human incidents decreased and the rate negative human incidents increased ($F_1 = 3.9$, $p = 0.045$; Table 2, Fig. 1b). Increased negative human incidents had a negative effect on time spent resting ($F_1 = 12.29$, $p \leq 0.001$; Table 3). The interaction effect between positive and negative human incidents showed that greater positive human incidents increased vervet monkey socializing time, but when they experienced both low negative and low positive human incidents their time spent socializing was significantly less ($F_1 = 5.12$, $p = 0.025$; Table 4, Fig. 1c).

3.2. Group size

Vervet monkeys spent more time foraging with increasing group size ($F_1 = 11.11$, $p = 0.001$, Table 1). Vervet monkeys spent less time moving ($F_1 = 38.19$, $p \leq 0.001$, Table 2) and resting ($F_1 = 7.43$, $p = 0.006$, Table 3) with increasing group size.

3.3. SEASONALITY

Vervet monkey foraging was significantly affected by seasonality ($F_1 = 96.79$, $p = \leq 0.001$, Table 1), with less time spent foraging in summer than any other season. In addition, their time spent moving ($F_1 = 14.7$, $p = 0.002$, Table 2) and resting ($F_1 = 64.41$, $p \leq 0.001$, Table 3) was significantly affected by seasonality as vervet monkeys moved less and rested more in summer than any other season and more time resting in autumn than in winter and spring. Finally, their time spent socializing was also affected by seasonality ($F_1 = 60.74$, $p \leq 0.001$, Table 4) as this was significantly higher in summer than all other months.

4. Discussion

As predicted, anthropogenic disturbance influenced all four aspects of the time budgets of urban vervet monkeys to some degree. Moreover, the interplay between positive and negative human incidents influenced three of the four behavioral categories. Results highlighted how urban vervet monkeys have adapted behaviorally to the ecologically changing anthropogenic landscape.

As expected, increasing anthropogenic food consumption by vervet monkeys significantly reduced their time spent foraging. Foraging results support previous research on provisioned vervet monkeys that high nutritional value human food provides more energy in smaller amounts in a shorter amount of time decreasing foraging requirements (Brennan, Else, & Altmann, 1985; Jaman & Huffman, 2013; Saj et al., 1999). The interaction effect between positive and negative human incidents showed that when positive incidents were low and negative incidents were high, vervet monkeys spent less time foraging, however, when positive human incidents were high and negative human incidents were low their foraging time increased. Notably, our interaction between positive and negative human incidents suggests that if vervet monkeys have access to high value anthropogenic food then despite human-aggression their time spent foraging will increase.

Time spent moving was greater when vervet monkeys experienced a higher rate of negative human incidents, although this effect decreased with more frequent positive human incidents. Previous research would suggest that access to high value resources should lessen the need to search for food and hence reduce time spent moving (Saj et al., 1999),

Table 1
Output of GLMM and likelihood ratio test on urban vervet monkey foraging behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

Term	Model summary				Likelihood ratio test	
	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.05	0.20	15.20	≤0.001		
Negative human incidents	−0.69	0.18	−3.85	≤0.001	1.22	0.027
Positive human incidents	−1.10	0.15	−7.36	≤0.001	32.26	≤0.001
Negative human incidents * Positive human incidents	1.04	0.22	4.78	≤0.001	22.84	≤0.001
Group size	0.02	0.01	3.33	0.001	11.11	0.001
Natural food	0.00	0.00	2.14	0.032	4.60	0.032
Season					96.79	≤0.001
Autumn – Spring	−0.31	0.10	−3.04	0.002		
Autumn – Summer	−0.82	0.10	−8.67	≤0.001		
Autumn – Winter	0.04	0.09	0.40	0.687		
Summer – Spring	0.52	0.08	6.36	≤0.001		
Summer – Winter	0.86	0.10	8.35	≤0.001		
Spring – Winter	0.34	0.09	3.73	≤0.001		

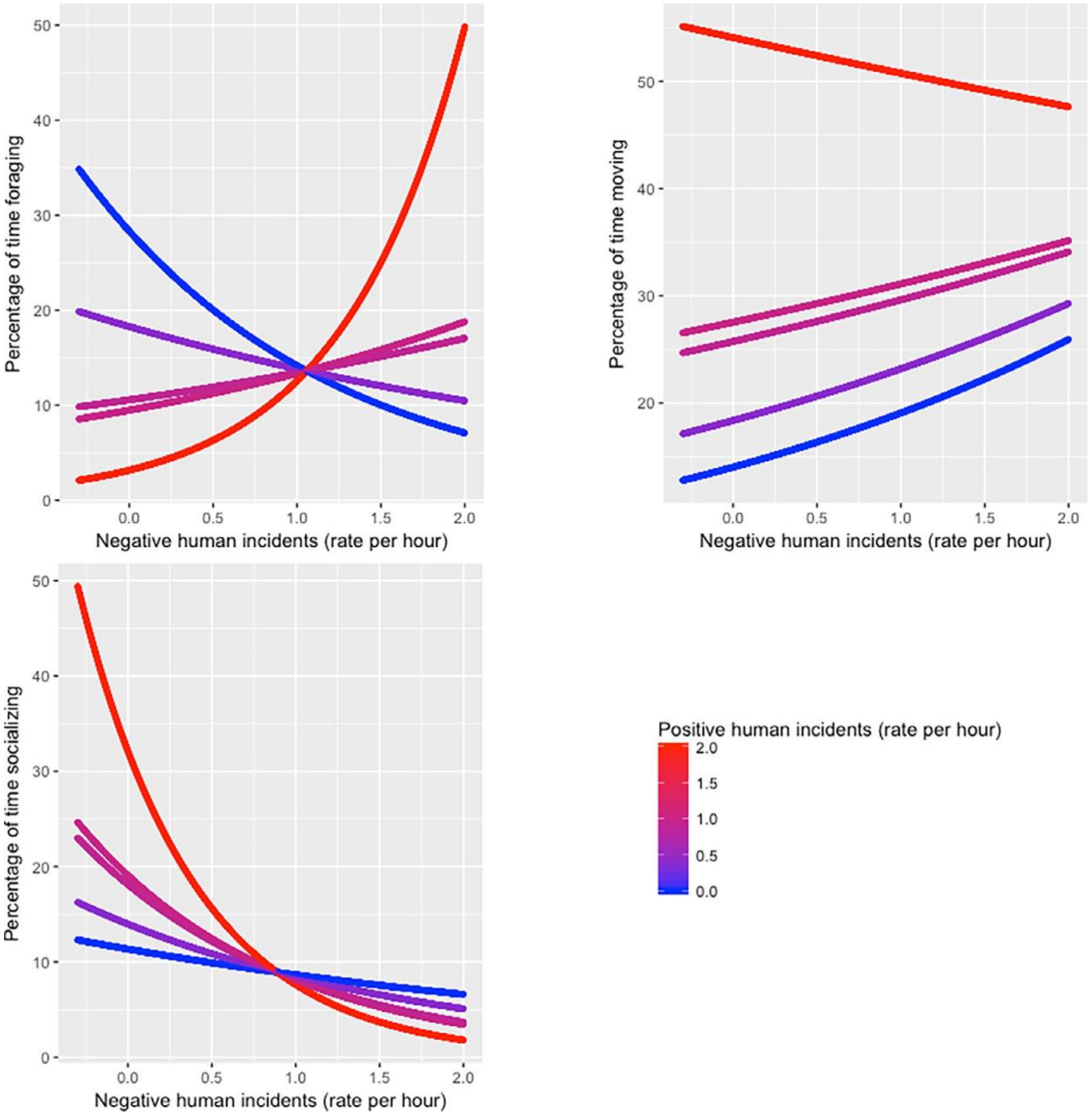

Fig. 1. Interaction between negative human incidents and positive human incidents on the time budgets of urban vervet monkeys at Simbithi Eco-estate, North Durban, KwaZulu-Natal, South Africa. (a) Shows the positive significant effect on the percentage of time spent foraging, (b) shows the negative significant effect on the percentage of time spent moving and (c) shows the negative significant effect on the percentage of time spent socializing.

supporting our findings. However, the interaction effect suggests that time spent moving is not only affected by successfully obtaining high value anthropogenic food resources, but is also associated with increased human aggression. Movement behavior therefore suggests that vervet monkeys may be less likely to move on in response to human aggression when high value human foods are available, supporting recent findings by Thatcher et al (*in prep*).

Notably, vervet monkey social behavior increased with a greater rate of positive human incidents, supporting previous research, which has shown that access to high value food items results in decreased foraging time and increased time available for social behavior (Jaman & Huffman, 2013; Saj et al., 1999; Scheun et al., 2015). The negative interaction effect between both anthropogenic factors showed that negative human incidents offset this, decreasing social behavior. This could be due to the increased tension and aggression related to high value resources or as an outcome of human wildlife conflict (Fuentes & Hockings, 2010). It is possible that human-conflict affects social cohesion, however further study is required to investigate the impact of urban living on vervet monkey social systems and how both positive and negative associations affect social behavior both together and individually. Even so, as increased negative human incidents also reduced time spent resting, it could be suggested that human-aggression is generally costly to urban vervet monkey time budgets.

Although most historical research on urban primates has found no influence of seasonality (Altmann & Muruth, 1988; Eley, 1989), our research did show an effect of seasonality across all behaviors, supporting more recent studies that have shown that seasonality is still influential on urban species (macaques: Jaman & Huffman, 2013 and baboons: Van Doorn et al., 2010). Trends found followed expected patterns of energetic constraints (Borg et al., 2015; McFarland, Henzi, Barrett, & Wanigaratne, 2015). An unexpected finding was the seasonal effect of foraging. We expected that with access to high value food

Table 2
Output of GLMM and likelihood ratio test on urban vervet monkey movement behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

Term	Model summary				Likelihood ratio test	
	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.09	0.04	80.50	≤0.001		
Negative human incidents	0.10	0.02	5.41	≤0.001	24.72	≤0.001
Positive human incidents	0.21	0.02	11.54	≤0.001	40.86	≤0.001
Negative human incidents * Positive human incidents	−0.03	0.02	−2.00	0.046	3.90	0.045
Group size	−0.18	0.03	−6.08	≤0.001	38.19	≤0.001
Natural food	0.01	0.02	0.57	0.567	0.14	0.707
Season					14.70	0.002
Autumn – Spring	0.00	0.04	−0.02	0.986		
Autumn – Summer	0.09	0.04	2.12	0.034		
Autumn – Winter	−0.04	0.04	−1.10	0.273		
Summer – Spring	0.09	0.03	2.73	0.006		
Summer – Winter	−0.13	0.04	−3.41	0.001		
Spring – Winter	−0.04	0.04	−0.94	0.346		

Table 3
Output of GLMM and likelihood ratio test on urban vervet monkey resting behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

Term	Model summary				Likelihood ratio test	
	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	1.95	0.09	21.78	≤0.001		
Negative human incidents	−0.15	0.05	−2.88	0.004	12.29	≤0.001
Positive human incidents	0.04	0.05	0.70	0.483	0.56	0.451
Negative human incidents * Positive human incidents	−0.02	0.04	−0.45	0.654	0.20	0.655
Group size	−0.12	0.04	−2.73	0.006	7.43	0.006
Natural food	−0.05	0.05	−0.97	0.330	0.95	0.330
Season					64.41	≤0.001
Autumn – Spring	0.27	0.12	2.18	0.029		
Autumn – Summer	0.81	0.11	7.35	≤0.001		
Autumn – Winter	0.26	0.12	2.12	0.034		
Summer – Spring	0.55	0.10	5.46	≤0.001		
Summer – Winter	−0.55	0.13	−4.36	≤0.001		
Spring – Winter	−0.01	0.12	−0.08	0.938		

Table 4
Output of GLMM and likelihood ratio test on urban vervet monkey social behavior, Simbithi Eco-estate, Durban North Coast, KwaZulu-Natal, South Africa.

Term	Model summary				Likelihood ratio test	
	Estimate	Standard error	Statistic	P value	Chisq	P value
(Intercept)	3.07	0.11	28.09	≤0.001		
Negative human incidents	−0.26	0.05	−5.29	≤0.001	55.28	≤0.001
Positive human incidents	0.09	0.06	1.61	0.108	3.15	0.08
Negative human incidents * Positive human incidents	−0.09	0.04	−2.26	0.024	5.12	0.025
Group size	0.02	0.08	0.19	0.850	0.04	0.850
Natural food	−0.08	0.05	−1.51	0.131	2.28	0.131
Season					60.74	≤0.001
Autumn – Spring	−0.08	0.12	−0.67	0.501		
Autumn – Summer	−0.66	0.11	−5.84	≤0.001		
Autumn – Winter	0.14	0.10	1.37	0.172		
Summer – Spring	0.80	0.12	6.52	≤0.001		
Summer – Winter	0.74	0.11	−6.76	≤0.001		
Spring – Winter	0.05	0.11	0.48	0.632		

vervet monkeys would be less reliant on seasonally influenced natural food (Naughton-Treves, Treves, Chapman, & Wrangham, 1998), however, our results indicated that their foraging was significantly higher in autumn and winter. We suggest that this is due to a high reliance on attractive garden plants (Chaves & Bicca-Marques, 2017; Hoffman & O'Riain, 2011; Wimberger & Hill, 2017). Results for seasonality support previous research on urban baboons, showing how their adaptive generalist qualities have allowed them to take advantage of all aspects within their habitat (Fruteau, Voelkl, van Damme, & Noë, 2009; van Doorn et al., 2010). Seasonality results further highlight the exploitive nature of vervet monkeys and their behavioral flexibility, taking advantage of the most nutrient rich available resources, including seasonally influenced resources.

5. Management implications

Anthropogenic influences on the time budgets of vervet monkeys revealed independent and interlinking effects, which is a previously neglected area of ethnoprimatology research (McLennan et al., 2017). By developing our knowledge of urban ecology and behavioral adaptations, we can directly improve human-monkey relationships for the benefit of both parties through appropriate management plans

(Soulsbury & White, 2015). We suggest that management should target preventing opportunities for vervet monkeys to forage on human food which appear to drive human-monkey conflict. Housing estates should implement education programmes that encourage residents to reduce vervet monkey access to anthropogenic food availability (e.g. by securing refuse bins, reducing access points into houses, storing food items securely), with the aim to reduce human-wildlife conflict within urban areas for vervet monkey and human well-being, as well as ecological biodiversity conservation.

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Appendix 2

Thatcher, H. R., Downs, C. T., & Koyama, N. F. (2018). Using Parasitic Load to Measure the Effect of Anthropogenic Disturbance on Vervet Monkeys. EcoHealth. 15, 676-681.

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Short Communication

Using Parasitic Load to Measure the Effect of Anthropogenic Disturbance on Vervet Monkeys

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Abstract: Vervet monkeys, Chlorocebus pygerythrus, thrive in urban areas of KwaZulu-Natal, South Africa, and present a suitable model to assess parasitic load as a measure of anthropogenic disturbance, such as urbanization. We collected vervet monkey faecal samples from four study sites representing a gradient of land use and urbanization. We assessed faecal parasites using the faecal flotation method calculating eggs per gram and parasite richness. Overall, the more urban vervet monkey populations had a significantly higher parasite richness and abundance. Our study shows the applicability of using parasite load to measure the effect of urbanization on wildlife.

Keywords: Zoonosis, Transmission, Human–wildlife, Land-use gradient, Management

Dramatic increases in human populations have resulted in drastic changes to the function and biodiversity of the natural ecosystem (Sauvajot 1998; Bonier et al. 2006). Though effects are species specific, certain wildlife species have been able to adapt to ecological changes and thrive in these conditions (McLennan et al. 2017). However, the stresses of an expanding anthropogenic environment can have negative consequences for wildlife such as poor body condition and increased parasite load (Borg et al. 2015; Soto-Caldero´n et al. 2016). Understanding the effects of anthropogenic disturbance, such as urbanization, on host–parasite relationships and zoonotic transmission has implications not only for the health of humans and their livestock, but also for wildlife conservation and biodiversity (Soulsbury and White 2015; Humle and Hill 2016; Cable et al. 2017).

Urbanization varies dramatically from large cities to small settlements, and therefore, the effects are difficult to quantitatively measure (Niemela¨ and Kotze 2009; Bennett and Gratton 2012; Mackenstedt et al. 2015). Urbanization creates unique habitats through a process of increasing human populations and anthropogenic structures (Werner 2011). With the continuing encroachment of anthropogenic pressures, most wildlife studies include some level of human disturbance in their data (e.g. McLennan et al. 2017). However, with the exception of Lane et al.'s (2011) study on *Macaca fascicularis*, few primate studies include highly human-populated urban areas. Furthermore, the majority of anthropogenic parasite studies focus on comparisons between only two study sites. However, the results of these studies show varying effects of increasing urbanization on zoonotic transmission and parasite infection rates (Cable et al. 2017). Creating a quantitative measure for urban influences is complex, but currently a gradient scale from rural to urban is the most commonly

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acknowledged method (Bradley and Altizer 2006; Shochat et al. 2007; Bennett and Gratton 2012).

Vervet monkeys, *Chlorocebus pygerythrus*, are a com-mon generalist primate that has become highly populated within urban areas of KwaZulu-Natal, South Africa (Pat-terson et al. 2016; 2017; 2018). They are, therefore, a suit-able model to investigate anthropogenic influences on wildlife parasite load. Furthermore, they are frequent rai-ders of anthropogenic food sources increasing opportunities for zoonotic transmission (Eley 1989; Hahn et al. 2003; Hegglin et al. 2015). Research into anthropogenic influences on parasite load in vervet monkeys is limited to two studies (Gaetano et al. 2014; Valenta et al. 2017). Gaetano et al.'s (2014) research suggests that ecological factors are better predictors of parasitism concentrations than anthropogenic contact. However, the applicability of their findings is limited by both small sample size and relatively short time span. Valenta et al. (2017) reported a higher parasite richness in vervet monkeys in an anthropogenic disturbed habitat compared with historical data in less disturbed vervet monkey populations. However, they were unable to interpret their results clearly due to variation in sample sizes and methods across historical studies. Finally, the habitats assessed in both studies had low anthropogenic stress, highlighting a need to assess a wider range of anthropogenic influences on vervet monkeys.

We aimed to establish whether a relatively low-cost methodological approach to assessing parasite load could reflect an urbanization gradient. We used four sites throughout KwaZulu-Natal, South Africa. We chose study sites to reflect anthropogenic influences along a rural–periurban–urban gradient (Table 1), including the previously neglected category of a highly human-populated urban area. Vervet monkey troop size information was collected using standard point count protocol (Hutto et al. 1986). We obtained human populations and anthropogenic structure numbers from site officials and governmental records (STATS SA, 2017) (Table 1).

We collected vervet monkey faecal samples over 6 months from October 2016–March 2017. We collected 286 specimens immediately after defecation following standard sampling techniques, storing them in 70% ethanol (Gillespie 2006).

Vervet monkey samples were prepared for analyses using the faecal flotation method (Gillespie 2006). We pipetted the prepared sample from the centre of the tube into chambers of a McMaster slide. The slide was assessed using standard methods (Cringoli et al. 2004). We used an electron phase microscope to scan the slide using a A * 10 objective lens and identified parasite eggs based on morphology. Digital photographs were taken of any vervet monkey parasites observed.

We converted raw data from the McMaster analysis to eggs per gram (Dunn and Keymer 1986) and compiled information on parasite richness per sample. We classed vervet monkeys as infected if their faecal sample had one or more parasite(s) and present the percentage of samples infected.

Table 1. Information on Vervet Monkey Faecal Parasite Samples Collected from Four Sites Representing a Rural–Periurban–Urban Gradient in KwaZulu-Natal, South Africa.

Site	Human density per km^2	Anthropogenic structure per km^2	Group size	Mean no. samples (± SD) per month	McKinney classification
Private reserve	2	2	20	49 (9 ± 0.7)	CDEB
			49	27 (4.5 ± 1.21)	
			16	31 (5 ± 0.3)	
Industrial land	48	4	22	28 (4 ± 0.3)	DDIC
Gated estate	2970	275	12	24 (4 ± 0.2)	HG$_3$LC
			23	23 (4 ± 0.3)	
			27	27 (5 ± 0.3)	
			42	31 (5 ± 0.3)	
City centre	3100	352	28	22 (4 ± 0.2)	HKPO
			35	24 (4 ± 0.4)	

Sites have also been Classified Using McKinney's Standardized Classification System (2015).

We analysed data using R v3.3.2 (R Project 2017). Data for both eggs per gram and parasite richness were not normally distributed (Shapiro–Wilks test, p 0.001) (Ghasemi and Zahediasl 2012). We ran two generalized linear models, with eggs per gram and parasite richness as separate dependent variables. We tested eggs per gram with a Poisson distribution and log link suitable for frequency data and species richness with a gamma distribution and log link for non-normal data. For both models, to avoid collinearity, we combined human density per km^2 and anthropogenic structure per km^2 to create a fixed effect. We also included vervet monkey troop size as a fixed effect. Generalized linear models were specified using the lme4 package (Bates 2010). To test whether the fixed effects ex-plained variation we used a likelihood ratio test ('anova' command set to 'Chisq') to compare the maximum model against the null model (Zuur et al. 2009). Furthermore, we bootstrapped our confidence intervals to account for un-even sampling within our data set (Davison and Hinkley 1997).

Overall, 58% of the 286 vervet monkey samples had some level of parasitic infection. Parasites identified were *Coccidia* sp., *Strongyloides* sp., *Tricuris* sp., *Ascaris* sp. and *Oesophagostomum* sp. Eggs per gram were significantly higher in vervet monkeys from more urbanized sites (Table 2, Fig. 1a). Increasing vervet monkey troop size also had a significant positive effect on eggs per gram (Table 2, Fig. 1b). Parasite richness was significantly higher in vervet monkeys inhabiting more urbanized habitats (Table 3, Fig. 2a). Increasing troop size also had a significant positive effect on vervet monkeys' parasite richness (Table 3, Fig. 2b).

Parasite eggs per gram and species richness were significantly higher in vervet monkeys living in areas of higher human density and greater anthropogenic structure than in lower human density and anthropogenic structure, supporting previous studies (e.g. Valenta et al. 2017). As expected, vervet monkey troop size was a significant predictor across sites for both eggs per gram and parasite richness.

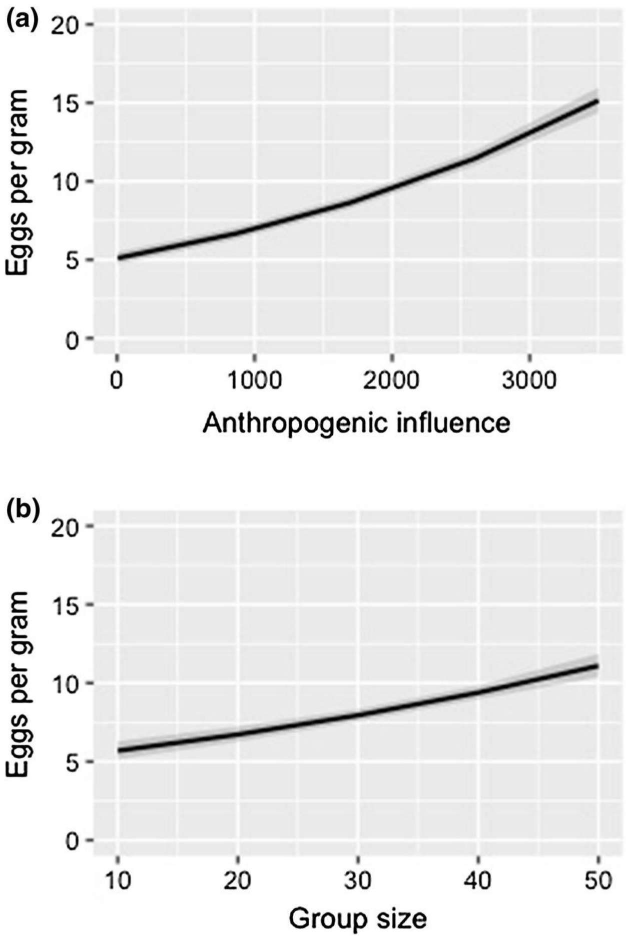

Fig. 1. Eggs per gram obtained from vervet monkey faecal samples collected from four sites representing a gradient of urbanization in KwaZulu-Natal, South Africa, where a shows the positive significant effect of increased anthropogenic influence on eggs per gram of vervet monkeys (p 0.001), and b shows the positive significant effect of troop size on eggs per gram of vervet monkeys ($p = 0.001$).

Table 2. Maximum Model Output from Likelihood Ratio Test on the Eggs per gram of Vervet Monkey Faecal Samples ($n = 286$) Collected Along a Rural–Periurban–Urban Gradient in KwaZulu-Natal, South Africa.

Dependent variables	Fixed effects	Estimate	Standard error	Bootstrapped confidence intervals		Likelihood ratio test	
				Lower	Upper	Deviance	p (chi)
Eggs per gram	Intercept	1.45	1.64				
	Anthropogenic value km^2	2.84	4.51	0.02	0.01	35.83	0.001
	Troop size	6.34	1.93	0.12	0.21	11.17	0.001

Table 3. Maximum Model Output from Likelihood Ratio Test on the Parasite Richness in Vervet Monkey Faecal Samples ($n = 286$) Collected Along a Rural–Periurban–Urban Gradient in KwaZulu-Natal, South Africa.

Dependent variable	Fixed effects	Estimate	Standard error	Bootstrapped confidence intervals		Likelihood ratio test	
				Lower	Upper	Deviance	p (chi)
Species richness	Intercept	- 8.87	2.39				
	Anthropogenic value km^2	2.47	4.34	0.01	0.03	29.96	0.001
	Troop size	1.23	5.38	0.01	0.02	5.27	0.021

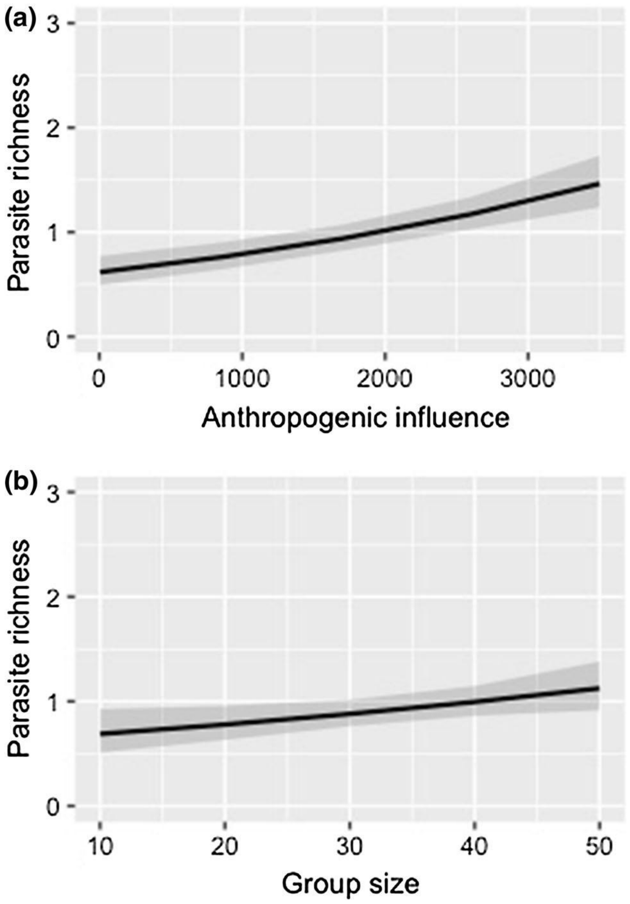

Fig. 2. Parasite richness obtained from vervet monkey faecal samples collected from four sites representing a gradient of urbanization in KwaZulu-Natal, South Africa where a shows the positive significant effect of increased anthropogenic influence on parasite richness of vervet monkeys (p 0.001), and b shows the positive significant effect of troop size on parasite richness of vervet monkeys ($p = 0.021$).

Overall, our findings suggest that increased urbanization increases parasite load in vervet monkeys. Past results into the effects of anthropogenic disturbance on primate parasite load are mixed (Cable et al. 2017), although the majority of studies have compared only disturbed and undisturbed categories (Gillespie and Chapman 2008). Here, we analysed a gradient of urbanization, crucially including a highly human-populated urban area.

Anthropogenic pressures in dense urban environments, such as city centres, can have a negative impact both at an individual level (body condition: Eley 1989; Scheun et al. 2015) and at a group level (group stability: Sinha and Mukhopadhyay 2013). Supporting this, we found that parasite eggs per gram and richness were greater where anthropogenic pressures were higher. Increased anthropogenic influences result in increased contact with humans for wildlife that can facilitate disease transmission (Eley 1989; Hahn et al. 2003; Hegglin et al. 2015). A greater public awareness of the need to minimize food raiding opportunities for vervet monkeys could limit contact and reduce exposure to potential pathogens for both species. This is especially important considering the nature of foods raided. Both provisioned and raided foods generally con-tain a greater starch content which can contribute to in-creased parasite concentrations in host species (Weyher et al. 2006; Becker et al. 2015).

Although the vervet monkey parasite species found in our study were consistent with those found in other studies on urban primates, without genetic analysis we were unable to look at the direct transmission effects of these parasites, particularly as those we found are species specific. A greater understanding of zoonotic transmission would be a valuable asset, both from the perspective of human well-being and ecological biodiversity conservation (Dı´az et al. 2006). Our findings highlight the suitability of the faecal flotation protocol as a relatively low-cost sampling method to monitor host–parasite responses to urbanization in species such as vervet monkeys. Such methodology could be included in urban management plans on a wider scale to assess the relationship between anthropogenic ecological change and wildlife health.

Our study is the first to provide baseline parasite data on vervet monkeys living in relatively highly urbanized areas. The wide range of sites used allowed us to conduct a controlled comparison of the effect of anthropogenic influences across a rural–periurban–urban gradient. Results highlight that increased urbanization is related to both increased eggs per gram and parasite richness in vervet monkeys. The study provides an important foundation for these successful urbanites. As urbanization increases, a greater understanding of urban exploiters' adaptations to ecological changes is important.

The datasets generated during the current study are available from the corresponding author on reasonable request.

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