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13 Abstract

Urbanisation is an important factor driving species and biodiversity decline. Although habitat 14 alterations can be detrimental for species, studies have shown that many diurnal primates are 15 able to adapt to novel environments. Little is known about the ability of nocturnal primates to 16 survive within the urban environment. To increase our understanding on this topic, we 17 present ad libitum observations on group movement and sociality from urban and rural 18 19 populations of the African lesser bushbaby (Galago moholi) in South Africa from 2014-2018. Our data show considerable changes in the social dynamics within urban bushbaby 20 21 populations. In contrast to rural individuals, which spent the majority of their activity period solitarily or in pairs, urban individuals displayed a larger degree of sociality throughout their 22 active period, forming groups of up to 10 individuals. Furthermore, urban individuals spent 23 24 less time moving around, while increasing social (communication/pair-grooming), foraging and feeding behaviour. Urban individuals fed on a range of different anthropogenic and 25 natural food sources (insects/gum/nectar) compared to their rural counterparts. In summary, 26 27 urban bushbabies showed a large degree of behavioural plasticity, with changes in social dynamics and structure frequently observed. Such alterations in sociality, along with the 28 ability to utilise different feeding resources, may explain the ability of the species to survive 29 within a highly altered environment. 30

Keywords: Urbanisation, nocturnal primates, sociality, anthropogenic, dietary flexibility

33

34 Introduction

A general 'rule-of-thumb' description for primate sociality is based on the diurnal and
nocturnal activity pattern of a species and describes diurnal primates as social, gregarious
animals, often living in medium to large groups. In contrast, nocturnal primates, are often

thought of as lower, primitive species and have historically been defined as 35 solitary and 38 non-gregarious, with limited interaction between conspecifics outside of the reproductive 39 40 season (Crook and Gartlan 1966). This definition of nocturnal primate sociality was not developed through robust, quantitative data, but rather the absence thereof (Sterling and 41 Richard 1995). Although defining these elements for nocturnal primates is difficult, an ever-42 43 growing body of literature actually indicates that the majority of nocturnal primates are semi-44 gregarious, forming complex social networks, share nest sites and even forage together (Bearder 1999; Dammhahn and Kappeler 2005; Génin 2010; Gursky 2000; Müller and Soligo 45 46 2005; Müller and Thalmann 2000; Nowack et al. 2013; Radespiel 2000). Furthermore, indirect interactions, such as vocalisation and home range overlap, offer additional support 47 for a complex social structure in nocturnal primates (Bearder 1999; Sterling and Richard 48 1995). 49

In the rural environment, both food resource availability and habitat size, are primary 50 51 drivers of social structure (Dunbar 1996; Janson 2017; Pinto et al. 1993; Wich et al. 2006). However, the food resource type and availability, along with the size of the available habitat, 52 are drastically altered within urban centres compared to the rural environment. The urban 53 54 land scape is a novel and ever changing environment, which exposes animals to a diverse and constant range of stressors (Atwell et al. 2012; Shochat et al. 2006). In order to survive in 55 such an environment, urban wildlife must adapt physiologically, physically and behaviourally 56 (Lowry et al. 2013; Sol et al. 2013). For example, urban avian populations have turned to 57 anthropogenic food sources to survive within heavily altered environments. Although the use 58 of such sources are often linked to disease transmission, research shows that the use of high 59 60 quality anthropogenic food sources may be advantageous to species survival within the urban environment (Robb et al. 2008). Although the majority of research on urban wildlife has 61 focused on the effect of urbanisation on avian species (Ditchkoff et al. 2006; Miranda et al. 62

2013; Møller 2009; Møller 58 2010; Partecke et al. 2006), there is an increasing number of
studies focussing on diurnal primates. For example, studies on the Rhesus macaque (*Macaca mulatta villosa*, Jaman and Huffman 2013) and the white-footed tamarin, (*Saguinis leucopus*,
Poveda and Sánchez-Palomino 2004) have found a change in social interactions and group
size for populations living in urban environments. However, no study has yet looked at
changes of social behaviour in nocturnal primates within urban environments.

The African lesser bushbaby, Galago moholi, is a small, nocturnal prosimian primate 69 found throughout southern Africa. Two clear mating periods have been described for the 70 71 species, which occur during May and September (Pullen et al. 2000; Scheun et al. 2016). Despite an observed difference in body weight between male and female bushbabies (~20%, 72 Kappeler 1991; Scheun et al. 2015) it is near impossible to differentiate between the sexes as 73 a result of limited sexual dimorphism. Originally defined as food specialists only feeding on 74 small insects and gum the species has now been shown to display a large degree of dietary 75 flexibility, utilising fruits and avian species when its primary food sources (insects, gum) are 76 scarce or unavailable (Engelbrecht 2016; Ray et al. 2016; Scheun et al. 2014). Bushbabies 77 have also been shown to adapt remarkably well to anthropogenic habitats, utilising a range of 78 human food sources (Scheun et al. 2015). Furthermore, the once established solitary social 79 paradigm established for the species (Doyle et al. 1967) has come under scrutiny as 80 behavioural data are published (Bearder 1999; Nowack et al. 2013; Pullen et al. 2000), 81 suggesting a large degree of gregarious behaviour in the species. 82 With anthropogenic activities driving increased land alterations throughout southern 83 Africa, understanding the effects of urbanisation on the social dynamics of nocturnal primates 84

are of utmost importance. Here we report differences in behaviour and sociality between

86 populations of urban and rural bushbabies, which indicate the profound changes urban

87 species undergo in order to survive within the urban environment.

88

89 Material and Methods

To compare the social dynamics of urban and rural bushbabies, we collected behavioural 90 observations on group size and activity patterns from two urban and two rural populations. 91 Rural environments were characterised as habitats with little to no anthropogenic activity and 92 93 natural plant structure including availability of indigenous floral species, particularly gum producing trees. Urban sites were characterised as habitats with fragmented and exotic floral 94 structure and species composition and a high degree of anthropogenic structures and 95 disturbance. The two rural bushbaby populations were studied at Nylsvley Nature Reserve 96 (NNR, S24° 39'.50" – E28° 39'54", Limpopo, 2014-2016) and the Buffelsdrift Conservancy 97 98 (BC, S25°35'.55", E28°19'30", Pretoria, 2014-2016), respectively. Free-ranging urban bushbaby populations were observed at the SANBI National Zoological Garden (NZG, S25° 99 44'18", E28° 11'21", Pretoria, South Africa) and within Onderstepoort, a suburb of Pretoria, 100 South Africa (Onderstepoort: OP, S25° 38'.52" – E28° 10'54" E). At the NZG, animal 101 enclosures (fenced and open) and administration buildings were primary factors resulting in 102 loss of sight once bushbabies entered the premises. Similarly, boundary fences and buildings 103 obstructed follows at OP. To remove the confounding effects reproductive activity may have 104 105 on behaviour and the social organisation of the species, we excluded breeding periods from the analyses (May and September, Scheun et al. 2017; Scheun et al. 2016) and therefore 106 observations were limited to the winter (June – August) periods of 2014 - 2018. Bushbabies 107 were not captured or marked during the study period; as such we were unable to identify 108 specific individuals or sex distribution at each site. 109

Within the four study sites *ad libitum* (Altmann 1974) observations on species
foraging, movement and social interactions was conducted. Specific animal behaviours were
recorded according to an ethogram (Tab. 1). At each site, follows were initiated at dusk

(17h00-18h00) and continued until dawn the following morning (05h00-06h00). Individuals
were located by shining headlamps and locating eye-shine. Behaviours were noted every 20
seconds, with follows continuing until the individual was out of sight for >5 min. Along with
behavioural data, the group composition (alone/pair/group) and food source utilised was also
determined. All statistical analyses were performed in R 3.2.1 (R Core Team 2018) using the
MASS package (Venables and Ripley 2002).

As a number of observers (n=4) assisted in data collection at the different locations, the inter-observer reliability (IOR) was determined. In this regard, the percentage agreement method was used for calculating the IOR score, with the equation: IOR = A/(A +

122 *DS*), where A is the number of agreements and D the number of disagreements (Ostrov and

Hart 2014). The average IOR score between the observers was 95 ± 70 % SD.

All values reported in this study include \pm standard deviation (SD). The total 124 observation time at each site was 39 h at NNR, 35 h at BC, 45 h at OP and 18 h at NZG. The 125 average time spent following one individual was 15.80 ± 8 SD min (NNR: 24.3 ± 5 SD min 126 (N=90), BC:14.25±5.5 SD min (N=80), OP: 19.5±2.80 SD min (N=125), NZG: 5.25±1.7 SD 127 min (N=255)). The frequency of time spent following individuals were approximately evenly 128 distributed prior to and following midnight at OP (55%, 45%), NNR (53%, 47%) and BC 129 (48%, 52%); however, follows at NZG were mainly conducted prior to midnight (63%, 37%). 130 Despite this difference at NZG, a goodness of fit chi-square test found no significant 131 difference between the sites (X_2 (9, N=520) = 11.1, p=0.2) when comparing the number of 132 observations at 3 h intervals (17:00-20:00; 20:00-23:00; 23:00-126 02:00; 02:00-05:00). As 133 such, time of night did not seem to influence the number of observations made at each site. 134 To limit the contact with individuals at both urban and rural sites, observers were never 135 nearer than 5m to an individual. 136

Goodness of fit chi-squared tests were conducted to determine whether the (1)
behaviours observed and (2) food resources used differed between study sites. A goodness of
fit chi-squared test was also conducted to determine whether a significant difference in the
frequency of feeding behaviours, observed at 3 h intervals (17:00-20:00; 20:00-23:00; 23:0002:00; 02:00-05:00) at all sites, occurred.

142

143 **Results**

A goodness of fit chi-squared test showed that the observed behaviours differed significantly 144 145 between study sites ($X_{2(27)} = 43.7$, p = 0.02). Urban bushbabies spent considerably less time 137 moving compared to their rural counterparts (38.6 % (NZG) and 36.4% (OP) vs. 63.1 % 146 (NNR) and 56.0% (BC)). However, the percentage time spent resting was similar between all 147 study sites (NZG: 26.9 %, OP: 30.1 % vs. NNR: 27.1 %, BC: 29.7 %). In contrast to this, 148 urban individuals spent more time foraging and feeding. Within the urban environments 149 bushbabies also spent considerably more time on social activities such as pair-grooming and 150 -playing than their rural counterparts (Fig. 1). Frequent aggressive interactions were 151 observed at OP, with no aggressive interactions at the remaining three sites. We observed no 152 successful predation on bushbabies during the four years at any of the sites although we had 153 multiply observations of known bushbabies predators (rural: owls, genets, mongoose; urban: 154 cats, owls, genets). 155

A goodness of fit chi-square test showed that food resource utilisation was significantly different between study sites ($X_{2(9)} = 500.6$, p < 0.001). At both rural sites, bushbabies fed exclusively on gum and arthropods (F 148 ig. 2). At OP, bushbabies fed predominantly on 149 anthropogenic food sources, while individuals at NZG utilised considerably more natural sources, although frequent nectar feeding from the bird of paradise flower (*Strelitzia nicolai*) was observed here (Fig. 2). Furthermore, feeding behaviour was

distributed equally across the night when comparing 3 h intervals at all four sites, i.e. in rural as well as urban populations ($X_{2(9)} = 11.23$, p=0.44).

Group sizes differed considerably between study sites. Within the rural environment,
bushbabies were seen to move on their own the majority of time, with limited pair
observations (NNR: 10 %, BC: 15 %). In contrast to this, such pair movements were
frequently observed within the urban environment (NZG: 43 %, OP: 30 %, Fig.3).
Furthermore, group sizes exceeding two individuals (range: 3-10 individuals) were only
observed at both urban sites (NZG: 35 %, OP: 20 %, Fig. 3).

171 Discussion

The results of this study clearly highlight the difference in sociality, group dynamics and foodresource utilisation between urban and rural bushbaby populations.

A significant difference in observed behaviours between the populations was found 174 during this study. Urban bushbabies spent less time moving through their home range, while 175 time spent on activities such as foraging, feeding, self- and pair-grooming were considerable 176 elevated. Habitat loss and fragmentation within the urban environment, as a result of 177 anthropogenic activities, considerably limit movement options of urban wildlife species (see 178 Fahrig 2003; Goldingay et al. 2018; Tuomainen and Candolin 2011). As the total area 179 available for movement and foraging is limited in the studied urban environments, time spent 180 on additional behaviours, such as resting and sociality, increased substantially. This change in 181 daily behaviours 171 has for example been observed in chacma baboons (Papio ursinus, 182 Hoffman and O'Riain 2010) and vervet monkeys (Cercopithecus aethiops pygerthrus, Saj et 183 al. 1999; Saj et al. 2001). 184

In contrast to rural bushbabies, which fed exclusively on naturally occurring foodsources (gum/insects), we found that urban individuals supplemented their diet with

anthropogenic food sources and nectar. The results of this study supports our previous 187 anecdotal observations which highlighted the ability of urban bushbabies to exploit a range of 188 189 anthropogenic food sources within the urban environment (Scheun et al. 2015). The loss of endemic floral species has been observed in a number of urban environments (Alvey 2006). 190 Such a decrease in natural flora may lead to a decrease of a species' preferred food source, 191 resulting in an increase in time spent foraging and the utilisation of novel food sources. This 192 193 shift in food resource use in urban environments has been observed in the common marmoset (Callithrix jacchus, Cunha et al. 2006) and the rhesus macaques (Macaca mulatta, Jaman and 194 195 Huffman 2013). Dietary flexibility is generally enhanced in the urban environment, where habitat fragmentation and alterations may limit the availability of naturally occurring food 196 sources, but increase the availability of novel, anthropogenic and exotic sources (Li 2005; 197 Wieczkowski 2005). Furthermore, despite the use of high energy anthropogenic food sources 198 within the urban environment, both urban and rural bushbaby populations continued to feed 199 throughout their active period, which might be explained by the high metabolism inherent 200 189 in small-bodied mammals (Martin 1990). 201

In contrast to rural bushbabies, urban populations readily formed permanent social 202 groups. The availability of anthropogenic food sources within the urban environment may 203 encourage group formation and sociality within the species (Scheun et al. 2015). The 204 influence of food resource availability on social structure has been shown for a number of 205 diurnal species, such as C. a. pygerythrus (Brennan et al. 1985), the savannah 194 baboons 206 (P. cynocephalus, Altmann and Muruthi 1988), olive baboons (P. anubis, van Doorn et al. 207 208 2010), rhesus macaques (Macaca mulatta, Jaman and Huffman 2013), the black-tuffed marmoset (Callithrix penicillata, Teixeira et al. 2015) and saki monkeys (Chiropotes satanas 209 210 chiropotes, Boyle and Smith 2010). Metabolic requirements of urban individuals are usually 211 met considerably quicker than possible in a rural environment, in which individuals need to

forage longer to acquire sufficient resources. This results in a decrease in foraging time, while
allowing for an increase in social activities such as pair-grooming, playing and group
formation.

The pair and group movement observed in this study, along with social activities 215 within both the urban and rural environment, support previous research which indicated the 216 semigregarious nature in prosimians (Bearder and Martin 1979). Additionally, pair 217 218 interactions outside of the mating season have been observed on numerous occasions (Bearder and Martin 1979). Gregarious behaviour of this kind has also been observed in a 219 220 number of other nocturnal prosimian species including the spectral tarsier (Tarsius spectrum, Gursky 2002), as well as the gray (*Microcebus murinus*, Radespiel 2000) and reddish-gray 221 mouse lemur (Microcebus griseorufus, Génin 2010). Despite the similarities with other 222 prosimians, a considerable difference in activity patterns was observed between rural and 223 urban bushbaby populations. 224

225 Conclusion

The transformation of pristine areas into highly altered, fragmented urban environments is 226 occurring at an accelerated rate in southern Africa (Ruhiiga 2013; Kok and Collinson 2006). 227 With the resulting decrease of pristine environments, the presence of bushbabies and other 228 nocturnal primates is set to increase within the urban environment. In order for primates to 229 survive within novel environments (e.g. anthropogenic landscapes/changes due to climate 230 231 change), a large degree of behavioural plasticity and dietary flexibility is required 217 (McKinney 2011; Sih et al. 2011; van Schaik 2013). Bushbabies displayed considerable 232 flexibility in terms of social organisation and resource utilisation, allowing for the species to 233 survive within the urban environment. However, despite this ability to adapt and survive 234 within the urban landscape, little is known of the possible effects that changes in diet, group 235 composition and sociality may have on population fecundity and survivability. Thus, further 236

- research into this topic is urgently required to determine population health and survivability
- 238 of species within the urban environment.
- 239
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Table 1. Ethogram listing the behaviours observed during the study as well as the respective definitions for each behaviour.

Behaviour	Definition		
Moving	The locomotion of an individual, through		
	vegetation or across open ground, by means of		
	jumping or walking.		
Resting	An individual remains stationary in a single		
	location with no other behaviour performed		
Foraging	An individual actively searching for food		
	resources by means of lowering its head,		
	sniffing and locating nutrient sources		
Feeding	The consumption of a nutrient source (defined		
	as anthropogenic or natural)		
Drinking	The consumption of water		
Communicating	Sound emitted by an individual as soft squeaks		
	or loud calls		
Self-grooming	Tooth-combing or licking oneself		
Pair-grooming	One individual "tooth-combing" or licking		
	another's fur		
Pair-playing	The positive interaction of two conspecifics		
	which may include		
	grabbing, rolling, jumping and vocalisation.		
Fighting	The negative interaction between two		
	individuals, which includes		
	chasing, grappling, biting and vocalisation.		
	Often results in one		
	individual being driven from an area.		

Figure 1. Frequency of time spent (mean ± standard deviation) on the defined activities by *Galago moholi* populations in two rural and two urban study sites (NNR: Nylsvley Nature Reserve, BC: Buffelsdrift Conservancy, OP: Onderstepoort, NZG: National Zoological Garden).

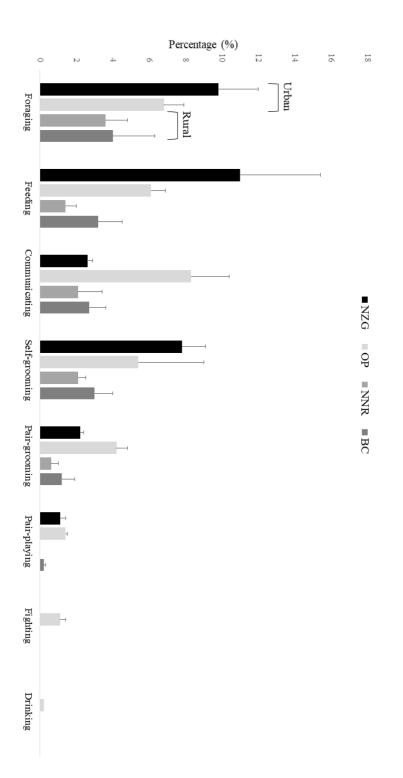


Figure 2. The percentage of food resources utilised by urban and rural populations of *Galago moholi* (NNR: Nylsvley Nature Reserve, BC: Buffelsdrift Conservancy, OP: Onderstepoort, NZG: National Zoological Garden).

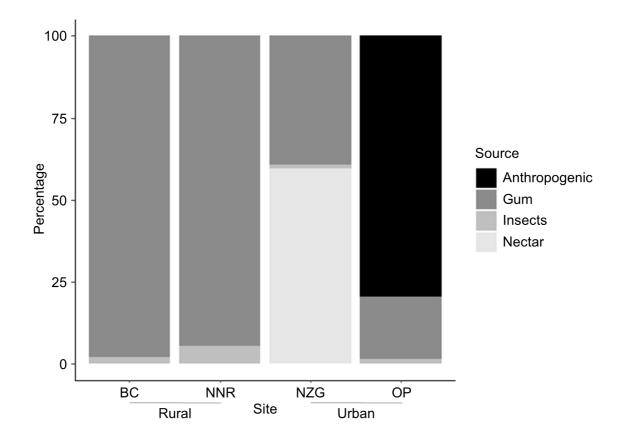


Figure 3. The percentage of time each group size was observed at each study site during the study (NNR: Nylsvley Nature Reserve, BC: Buffelsdrift Conservancy, OP: Onderstepoort, NZG: National Zoological Garden).

