Urbanisation as an important driver of nocturnal primate sociality

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Abstract

Urbanisation is an important factor driving species and biodiversity decline. Although habitat alterations can be detrimental for species, studies have shown that many diurnal primates are able to adapt to novel environments. Little is known about the ability of nocturnal primates to survive within the urban environment. To increase our understanding on this topic, we present *ad libitum* observations on group movement and sociality from urban and rural 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 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 active period, forming groups of up to 10 individuals. Furthermore, urban individuals spent less time moving around, while increasing social (communication/pair-grooming), foraging and feeding behaviour. Urban individuals fed on a range of different anthropogenic and natural food sources (insects/gum/nectar) compared to their rural counterparts. In summary, 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 ability to utilise different feeding resources, may explain the ability of the species to survive within a highly altered environment.

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

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 non-gregarious, with limited interaction between conspecifics outside of the reproductive 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 Richard 1995). Although defining these elements for nocturnal primates is difficult, an ever-growing body of literature actually indicates that the majority of nocturnal primates are semi-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 2005; Müller and Thalmann 2000; Nowack et al. 2013; Radespiel 2000). Furthermore, indirect interactions, such as vocalisation and home range overlap, offer additional support for a complex social structure in nocturnal primates (Bearder 1999; Sterling and Richard 1995).

In the rural environment, both food resource availability and habitat size, are primary 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, are drastically altered within urban centres compared to the rural environment. The urban 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 such an environment, urban wildlife must adapt physiologically, physically and behaviourally (Lowry et al. 2013; Sol et al. 2013). For example, urban avian populations have turned to anthropogenic food sources to survive within heavily altered environments. Although the use of such sources are often linked to disease transmission, research shows that the use of high 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 focused on the effect of urbanisation on avian species (Ditchkoff et al. 2006; Miranda et al.

2013; Møller 2009; Møller 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 found throughout southern Africa. Two clear mating periods have been described for the 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%, Kappeler 1991; Scheun et al. 2015) it is near impossible to differentiate between the sexes as a result of limited sexual dimorphism. Originally defined as food specialists only feeding on small insects and gum the species has now been shown to display a large degree of dietary flexibility, utilising fruits and avian species when its primary food sources (insects, gum) are scarce or unavailable (Engelbrecht 2016; Ray et al. 2016; Scheun et al. 2014). Bushbabies have also been shown to adapt remarkably well to anthropogenic habitats, utilising a range of human food sources (Scheun et al. 2015). Furthermore, the once established solitary social paradigm established for the species (Doyle et al. 1967) has come under scrutiny as behavioural data are published (Bearder 1999; Nowack et al. 2013; Pullen et al. 2000), suggesting a large degree of gregarious behaviour in the species.

With anthropogenic activities driving increased land alterations throughout southern Africa, understanding the effects of urbanisation on the social dynamics of nocturnal primates are of utmost importance. Here we report differences in behaviour and sociality between populations of urban and rural bushbabies, which indicate the profound changes urban species undergo in order to survive within the urban environment.

Material and Methods

To compare the social dynamics of urban and rural bushbabies, we collected behavioural observations on group size and activity patterns from two urban and two rural populations. Rural environments were characterised as habitats with little to no anthropogenic activity and natural plant structure including availability of indigenous floral species, particularly gum producing trees. Urban sites were characterised as habitats with fragmented and exotic floral structure and species composition and a high degree of anthropogenic structures and disturbance. The two rural bushbaby populations were studied at Nylsvley Nature Reserve (NNR, S24° 39′.50″ – E28° 39′54″, Limpopo, 2014-2016) and the Buffelsdrift Conservancy (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° 44′18″, E28° 11′21″, Pretoria, South Africa) and within Onderstepoort, a suburb of Pretoria, South Africa (Onderstepoort: OP, S25° 38′.52″ – E28° 10′54″ E). At the NZG, animal enclosures (fenced and open) and administration buildings were primary factors resulting in loss of sight once bushbabies entered the premises. Similarly, boundary fences and buildings obstructed follows at OP. To remove the confounding effects reproductive activity may have 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 observations were limited to the winter (June – August) periods of 2014 - 2018. Bushbabies were not captured or marked during the study period; as such we were unable to identify specific individuals or sex distribution at each site.

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 = $A/(A + DS)$, 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 ± standard deviation (SD). The total observation time at each site was 39 h at NNR, 35 h at BC, 45 h at OP and 18 h at NZG. The average time spent following one individual was 15.80 ± 8 SD min (NNR: 24.3±5 SD min (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 min (N=255)). The frequency of time spent following individuals were approximately evenly distributed prior to and following midnight at OP (55%, 45%), NNR (53%, 47%) and BC (48%, 52%); however, follows at NZG were mainly conducted prior to midnight (63%, 37%). Despite this difference at NZG, a goodness of fit chi-square test found no significant difference between the sites ($X_{2\ (9,\ N=520)}$ = 11.1, p=0.2) when comparing the number of observations at 3 h intervals (17:00-20:00; 20:00-23:00; 23:00-126 02:00; 02:00-05:00). As such, time of night did not seem to influence the number of observations made at each site. To limit the contact with individuals at both urban and rural sites, observers were never nearer than 5m to an individual.

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; 23:00-02:00; 02:00-05:00) at all sites, occurred.

Results

A goodness of fit chi-squared test showed that the observed behaviours differed significantly between study sites ($X2_{(27)} = 43.7$, $p = 0.02$). Urban bushbabies spent considerably less time moving compared to their rural counterparts (38.6 % (NZG) and 36.4% (OP) vs. 63.1 % (NNR) and 56.0% (BC)). However, the percentage time spent resting was similar between all study sites (NZG: 26.9 %, OP: 30.1 % vs. NNR: 27.1 %, BC: 29.7 %). In contrast to this, urban individuals spent more time foraging and feeding. Within the urban environments bushbabies also spent considerably more time on social activities such as pair-grooming and –playing than their rural counterparts (Fig. 1). Frequent aggressive interactions were observed at OP, with no aggressive interactions at the remaining three sites. We observed no successful predation on bushbabies during the four years at any of the sites although we had multiply observations of known bushbabies predators (rural: owls, genets, mongoose; urban: cats, owls, genets).

A goodness of fit chi-square test showed that food resource utilisation was significantly different between study sites ($X2_{(9)} = 500.6$, $p < 0.001$). At both rural sites, bushbabies fed exclusively on gum and arthropods (Fig. 2). At OP, bushbabies fed predominantly on 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).

Discussion

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

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

In contrast to rural bushbabies, which fed exclusively on naturally occurring food sources (gum/insects), we found that urban individuals supplemented their diet with anthropogenic food sources and nectar. The results of this study supports our previous anecdotal observations which highlighted the ability of urban bushbabies to exploit a range of 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). Such a decrease in natural flora may lead to a decrease of a species' preferred food source, resulting in an increase in time spent foraging and the utilisation of novel food sources. This 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 Huffman 2013). Dietary flexibility is generally enhanced in the urban environment, where habitat fragmentation and alterations may limit the availability of naturally occurring food sources, but increase the availability of novel, anthropogenic and exotic sources (Li 2005; Wieczkowski 2005). Furthermore, despite the use of high energy anthropogenic food sources within the urban environment, both urban and rural bushbaby populations continued to feed throughout their active period, which might be explained by the high metabolism inherent 189 in small-bodied mammals (Martin 1990).

In contrast to rural bushbabies*,* urban populations readily formed permanent social groups. The availability of anthropogenic food sources within the urban environment may encourage group formation and sociality within the species (Scheun et al. 2015). The influence of food resource availability on social structure has been shown for a number of diurnal species, such as *C. a. pygerythrus* (Brennan et al. 1985), the savannah 194 baboons *(P. cynocephalus,* Altmann and Muruthi 1988*),* olive baboons (*P. anubis*, van Doorn et al. 2010), rhesus macaques (*Macaca mulatta*, Jaman and Huffman 2013), the black-tuffed marmoset (*Callithrix penicillata*, Teixeira et al. 2015) and saki monkeys (*Chiropotes satanas chiropotes*, Boyle and Smith 2010). Metabolic requirements of urban individuals are usually 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 within both the urban and rural environment, support previous research which indicated the semigregarious nature in prosimians (Bearder and Martin 1979). Additionally, pair 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 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 mouse lemur (*Microcebus griseorufus*, Génin 2010). Despite the similarities with other prosimians, a considerable difference in activity patterns was observed between rural and urban bushbaby populations.

Conclusion

The transformation of pristine areas into highly altered, fragmented urban environments is occurring at an accelerated rate in southern Africa (Ruhiiga 2013; Kok and Collinson 2006). With the resulting decrease of pristine environments, the presence of bushbabies and other nocturnal primates is set to increase within the urban environment. In order for primates to survive within novel environments (e.g. anthropogenic landscapes/changes due to climate 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 flexibility in terms of social organisation and resource utilisation, allowing for the species to survive within the urban environment. However, despite this ability to adapt and survive within the urban landscape, little is known of the possible effects that changes in diet, group composition and sociality may have on population fecundity and survivability. Thus, further research into this topic is urgently required to determine population health and survivability of species within the urban environment.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behavior 49: 227 – 267

Altmann J, Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. Am J Primatol 15: 213-221. doi:10.1002/ajp.1350150304

Atwell JW, Cardoso GC, Whittaker DJ, Campbell-Nelson S, Robertson KW, Ketterson ED (2012) Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. Behav Ecol 23: 960-969. doi:10.1093/beheco/ars059

Bearder S (1999) Physical and social diversity among nocturnal primates: A new view based on long term research. Primates 40: 267-282. doi:10.1007/BF02557715

Bearder SK, Martin RD (1979) The social organization of a nocturnal primate revealed by radio tracking. In: Amlaner Jr CJ, MacDonald W (eds) A Handbook on biotelemetry and radio tracking.Pergamon, Oxford, pp 633-648

Boyle SA, Smith AT (2010) Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51: 43

Brennan EJ, Else JG, Altmann J (1985) Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. Afr J Ecol 23: 35-44. doi:10.1111/j.1365-2028.1985.tb00710.x

Cunha AA, Vieira MV, Grelle CE (2006) Preliminary observations on habitat, support use and diet in two non-native primates in an urban Atlantic forest fragment: The capuchin monkey (Cebus sp.) and the common marmoset (*Callithrix jacchus*) in the Tijuca forest, Rio de Janeiro. Urban Ecosyst 9: 351-359

Dammhahn M, Kappeler PM (2005) Social System of Microcebus berthae, the World's Smallest Primate. Int J Primatol 26: 407-435. doi:10.1007/s10764-005-2931-z

Ditchkoff S, Saalfeld S, Gibson C (2006) Animal behavior in urban ecosystems: Modifications due to human-induced stress. Urban Ecosyst 9: 5-12. doi:10.1007/s11252-006-3262-3

Doyle GA, Pelletier A, Bekker T (1967) Reproduction in the lesser bushbaby (*Galago senegalensis moholi*) under semi natural conditions. Folia Primatol 14: 15-22

Dunbar RIM (1996) Determinants of group size in primates: A general model. In: Runciman WG, Smith JM, M. DRI (eds) Evolution of social behaviour patterns in primates and man. Proceedings of The British Academy, Vol. 88. Oxford University Press, New York, pp 33-57

Engelbrecht D (2016) Galagos as avian nest predators in South Africa. Primates 57: 455-458

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487-515. doi:10.2307/30033784

Génin F (2010) Who sleeps with whom? Sleeping association and socio-territoriality in *Microcebus griseorufus*. J Mammal 91: 942-951. doi:10.1644/09-MAMM-A-239.1

Goldingay RL, Taylor BD, Parkyn JL (2018) Use of tall wooden poles by four species of gliding mammal provides further proof of concept for habitat restoration. Australian Mammalogy:

Gursky S (2002) Determinants of gregariousness in the spectral tarsier (Prosimina: *Tarsius spectrum*). Journal of Zoology: 402-410

Gursky SL (2000) Sociality in the spectral tarsiers, *Tarsius spectrum*. Am J Primatol 51: 89-101. doi:10.1002/(SICI)1098-2345(200005)51:1<89::AID-AJP7>3.0.CO;2-7

Hoffman TS, O'Riain MJ (2010) The spatial ecology of chacma baboons (*Papio ursinus*) in a human modified environment. Int J Primatol 32. doi:10.1007/s10764-010-9467-6

Jaman MF, Huffman MA (2013) The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. Primates 54: 49-59. doi:10.1007/s10329-012-0330-6

Janson CH (2017) Evolutionary ecology of primate social structure. In: Smith EA (ed) Evolutionary ecology and human behavior. Routledge, New York, pp 95-130

Kappeler PM (1991) Patterns of sexual dimorphism in body weight among prosimian primates. Folia Primatol 57: 132-146

Li Y (2005) Effects of annual change in group size, human disturbances and weather on daily travel distance of a group in Sichuan snub-nosed monkey (Rhinopithecus roxellana) in Shennongjia Nature Reserve, China. Biodiv Sci 13: 432-438

Lowry H, Lill A, Wong BBM (2013) Behavioural responses of wildlife to urban environments. Biol Rev 88: 537-549. doi:10.1111/brv.12012

Martin RD (1990) Primate origins and evolution: a phylogenetic reconstruction. Princeton University Press, Princeton, New Jersey, pp. 804

McKinney T (2011) The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced Capuchins (Cebus capucinus). Am J Primatol 73: 439-448. doi:10.1002/ajp.20919

Miranda AC, Schielzeth H, Sonntag T, Partecke J (2013) Urbanization and its effects on personality traits:a result of microevolution or phenotypic plasticity? Global Change Biol 19: 2634-2644. doi:doi:10.1111/gcb.12258

Møller AP (2009) Successful City Dwellers: A Comparative Study of the Ecological Characteristics of Urban Birds in the Western Palearctic. Oecologia 159: 849-858. doi:10.2307/40309951

Møller AP (2010) Interspecific variation in fear responses predicts urbanization in birds. Behav Ecol 21:365-371

Müller AE, Soligo C (2005) Primate sociality in evolutionary context. Am J Phys Anthropol 128: 399-414. doi:10.1002/ajpa.20086

Müller AE, Thalmann URS (2000) Origin and evolution of primate social organisation: a reconstruction. Biol Rev 75: 405-435. doi:10.1111/j.1469-185X.2000.tb00050.x

Nowack J, Wippich M, Mzilikazi N, Dausmann KH (2013) Surviving the cold, dry period in Africa: behavioral adjustments as an alternative to heterothermy in the African lesser bushbaby (*Galago moholi*). Int J Primatol 34: 49-64

Ostrov JM, Hart E (2014) Observational methods. In: Little TT (ed) The Oxford handbook of quantitative methods in psychology: foundations, vol 1. Oxford University Press, Oxford, UK, p 286

Partecke J, Schwabl I, Gwinner E (2006) Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecol 87: 1945-1952. doi:10.1890/0012- 302 9658(2006)87[1945:SATCUA]2.0.CO;2

Pinto LPS, Costa CMR, Strier KB, da Fonseca GAB (1993) Habitat, density and group size of primates in a Brazilian tropical forest. Folia Primatol 61: 135-143

Poveda K, Sánchez-Palomino P (2004) Habitat use by the white-footed tamarin, *Saguinus leucopus*: a comparison between a forest-dwelling group and an urban group in Mariquita, Colombia. Neotrop Primates 12: 6-9

Pullen SL, Bearder SK, Dixson AF (2000) Preliminary observations on sexual behavior and the mating system in free-ranging lesser galagos (*Galago moholi*). Am J Primatol 51: 79-88

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Radespiel U (2000) Sociality in the gray mouse lemur (*Microcebus murinus*) in northwestern Madagascar. Am J Primatol 51: 21-40

Ray I, Wren BT, Bowers EJ (2016) Documentation of plant consumption by *Galago moholi* in South Africa. Afr Primates 11: 45-48

Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6: 476-484. doi:10.1890/060152

Saj T, Sicotte P, Paterson JD (1999) Influence of human food consumption on the time budget of vervets. Int J Primatol 20: 977-994. doi:10.1023/A:1020886820759

Saj TL, Sicotte P, Paterson JD (2001) The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. Afr J Ecol 39: 195-199

Scheun J, Bennett N, Ganswindt A, Nowack J (2014) Spicing up the menu: evidence of fruit feeding in *Galago moholi*. Primates 55: 359-363. doi:10.1007/s10329-014-0420-8

Scheun J, Bennett N, Ganswindt A, Nowack J (2015) The hustle and bustle of city life: monitoring the effects of urbanisation in the African lesser bushbaby. Sci Nat 102: 1-11

Scheun J, Bennett NC, Nowack J, Ganswindt A (2017) Reproductive behaviour, testis size and faecal androgen metabolite concentrations in the African lesser bushbaby. J Zool 301: 263-270. doi:10.1111/jzo.12420

Scheun J, Nowack J, Bennett N, Ganswindt A (2016) Female reproductive activity and its endocrine correlates in the African lesser bushbaby, *Galago moholi*. J Comp Physiol B 186: 255-264. doi:10.1007/s00360-015-0947-z

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21: 186-191. doi:10.1016/j.tree.2005.11.019

Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4: 367-387. doi:10.1111/j.1752-4571.2010.00166.x

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85: 1101-1112. doi:https://doi.org/10.1016/j.anbehav.2013.01.023

Sterling EJ, Richard AF (1995) Social organization in the Aye-Aye (*Daubentonia Madagascariensis)* and the perceived distinctiveness of nocturnal primates. In: Alterman L, Doyle GA, Izard MK (eds)

Creatures of the Dark: The Nocturnal Prosimians. Springer US, Boston, MA, pp 439-451. doi:10.1007/978-1-4757-2405-9_26

Teixeira B, Hirsch A, Goulart VDLR, Passos L, Teixeira CP, James P, Young R (2015) Good neighbours: distribution of black-tufted marmoset (*Callithrix penicillata*) in an urban environment. Wildl Res 42: 579-589. doi:10.1071/WR14148

Tuomainen U, Candolin U (2011) Behavioural responses to human-induced environmental change. Biol Rev Camb Philos Soc 86: 640-657. doi:10.1111/j.1469-185X.2010.00164.x

van Doorn AC, O'Riain MJ, Swedell L (2010) The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal chacma baboons (*Papio ursinus*) in the Cape Peninsula of South Africa. Am J Primatol 72: 104-112. doi:10.1002/ajp.20759

van Schaik CP (2013) The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. Phil Trans R Soc B: Biol Sc 368. doi:10.1098/rstb.2012.0339

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

Wich SA, Geurts ML, Mitra T (2006) Influence of fruit availability on Sumatran orangutan sociality and reproduction. Feeding Ecology in Apes and Other Primates 48: 337

Wieczkowski J (2005) Examination of increased annual range of a Tana mangabey (Cercocebus galeritus) group. Am J Phys Anthropol 128: 381-388

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).

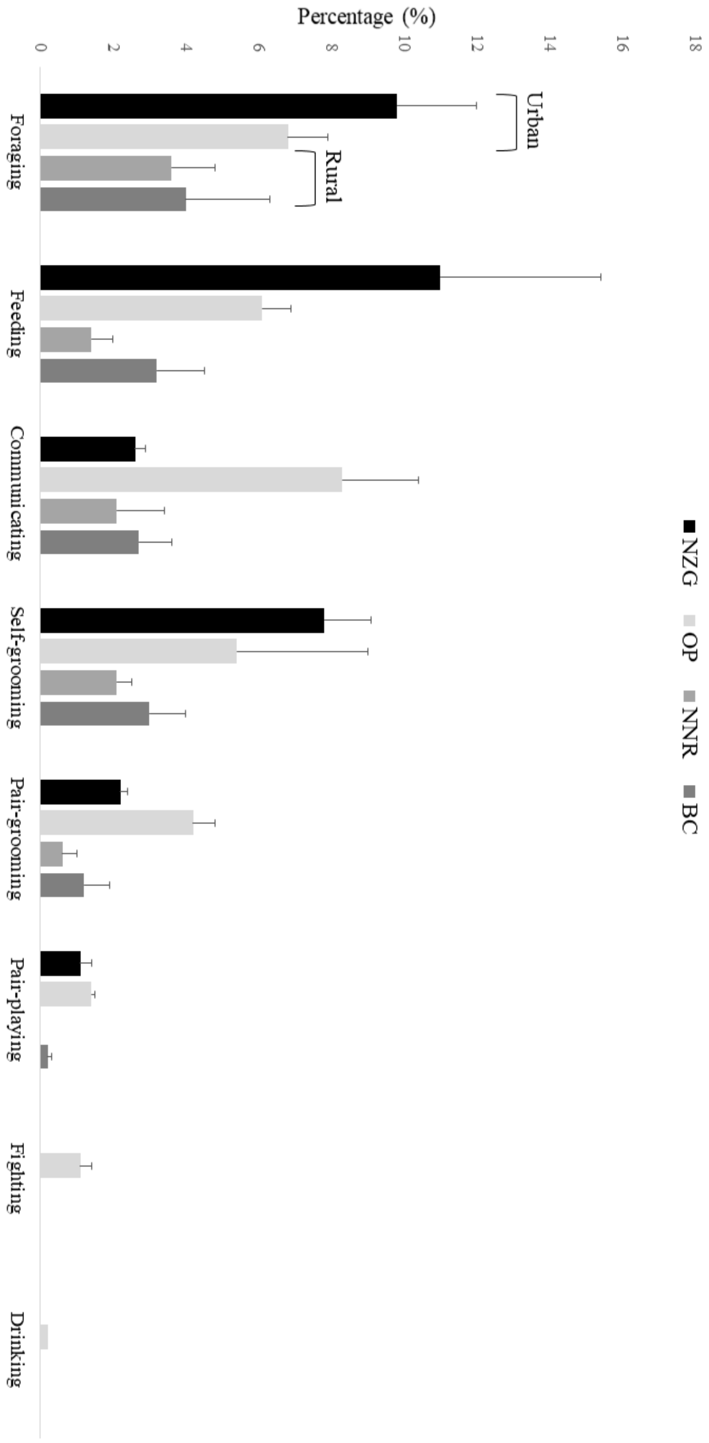

Figure 2. The percentage of food resources utilised by urban and rural populations of *Galago moholi* (NNR: Nylsvley Nature Reserve, BC: Buffelsdrift Conservancy, OP: Onderstepoort, NZG: National Zoological Garden).

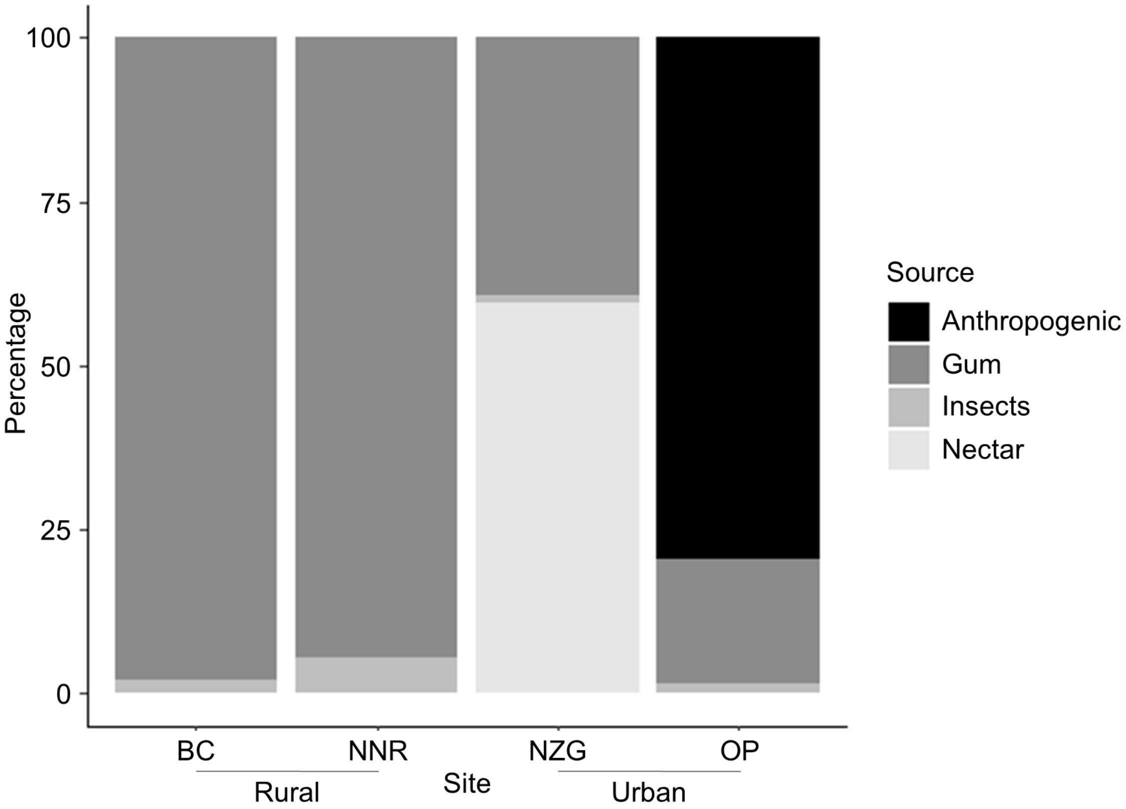

Figure 3. The percentage of time each group size was observed at each study site during the study (NNR: Nylsvley Nature Reserve, BC: Buffelsdrift Conservancy, OP: Onderstepoort, NZG: National Zoological Garden).