Variation in individual and collective behaviours by chacma baboons using urban space in Cape Town, South Africa

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Submitted to Swansea University in collaboration with University of Cape Town in fulfilment of the requirements for the degree of Doctor of Philosophy

Swansea University	University of Cape Town
2022	2022

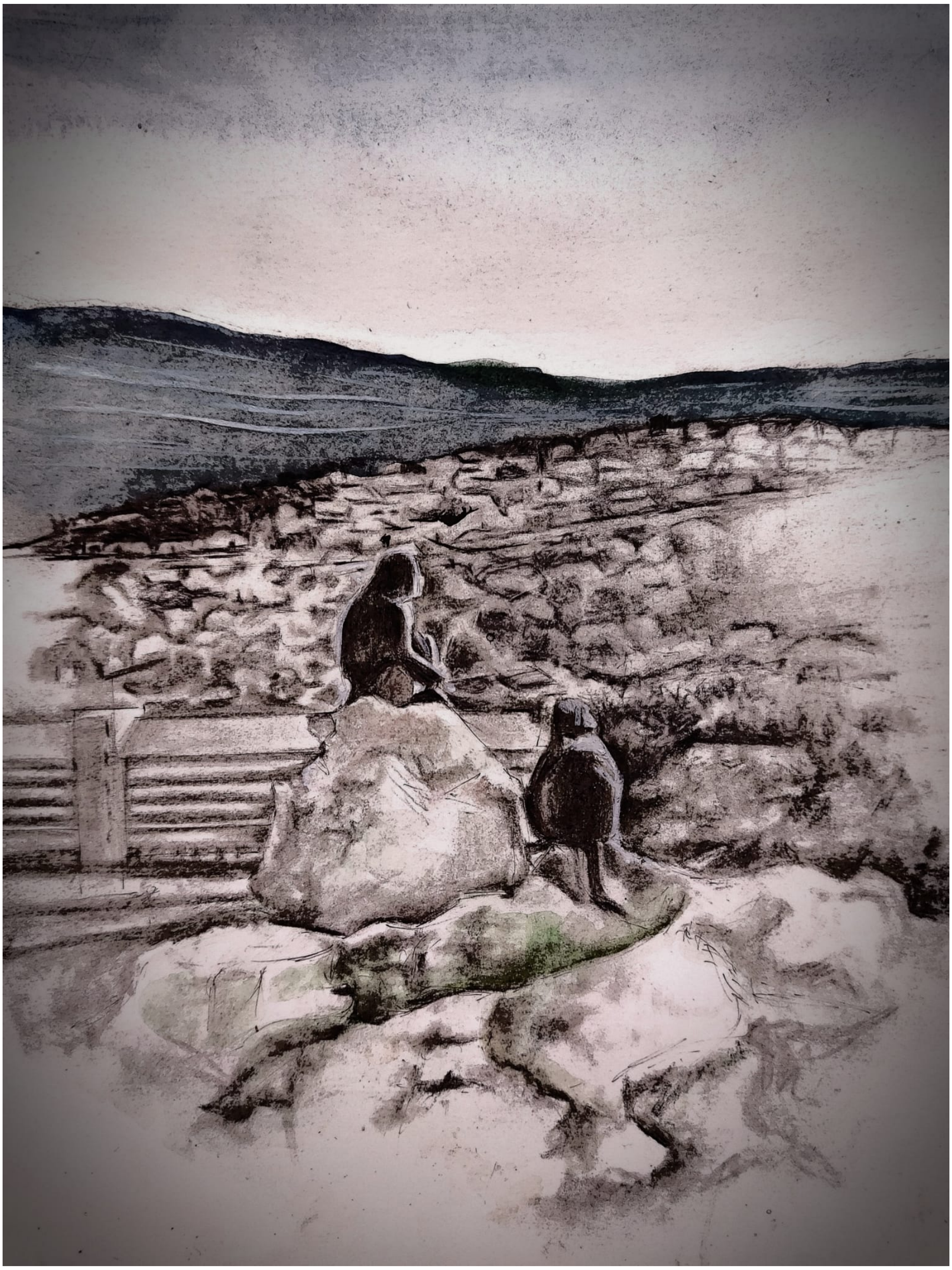

Image by Dora Bracken

To all the powerful women in my life: my gran, my mum, my sister, my friends.

ABSTRACT

As human populations continue to grow, so does the demand for space – with urban centres encroaching into wild animal habitats. Social, generalist species, which show high rates of innovation and behavioural flexibility tend to adapt to and use human-altered landscapes. However, we know less about what factors drive differences among individuals in use of human-altered landscapes, or the repercussions of individual differences for social dynamics in animal groups, which I review in my introductory chapter (Chapter 1). In Chapter 2 I introduce my study system and methods. I study chacma baboons (*Papio ursinus*) in Cape Town, South Africa that frequently have negative interactions with people at the urban edge and are managed by a team of rangers that herd the baboons from urban spaces, using aversive conditioning. Using high-resolution GPS data (recording at 1Hz frequency) combined with behavioural observations, field ranger survey and hormonal data I investigate variation in individual and collective behaviour associated with urban space-use. First, I examine variation in the time individuals spend in urban space, and contrary to expectations, find that females, rather than males, spend most time in urban space, and tend to use urban space with other group members and not with vulnerable offspring (Chapter 3). Second, I examine predictors of variation in urban space-use, and find that socially-peripheral, low-ranking female baboons make the most use of urban space, which is likely as a result of a management focus on adult males (Chapter 4). Further examination of fine-scale movement trajectories revealed both baboon phenotype and personality effect individual-level movement in urban space, where baboons most targeted by management show the greatest flexibility in movement (Chapter 5). Finally, I show that use of urban spaces drastically effects group dynamics, reducing cohesion and coordination of the troop, though high-ranking adults consistently lead the troop both in and out of urban space (Chapter 6). I synthesise these major findings in my final discussion chapter (Chapter 7) and discuss how my results will be important in current and future management of the Cape baboons and provide a basis for future examinations of urban space-use across species and systems.

DECLARATIONS AND STATEMENTS

Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed [redacted]

Date 05/05/2022

Statement 1

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended to this thesis.

Signed [redacted]

Date 05/05/2022

Statement 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Ethical note

Collar deployment

Baboons were fit with tracking collars after being cage trapped and anesthetized by a veterinarian. Cage trapping was organised by Human Wildlife Solutions (the company contracted to manage the baboons in 2018) and conducted according to the Baboon Technical Team's protocols (Hoffman, 2011) as described in the Supplementary Materials of Fehlmann et al., (2017c). Collars were approved by Swansea University's Ethics Committee (IP-1314-5) and weighed a mean of 2.2% of baboon body mass (range 1.2% - 2.6%). Collars were fitted with a drop-off mechanism (version CR-7, Telonics, Inc.) to reduce the need for recapture.

Field ranger surveys

To assess field ranger herding 'strategy', surveys were presented to each field ranger (n = 12) (described in detail in Methods, Chapter 2). Surveys were anonymous and undertaken with permission from both rangers and their employers, and Swansea College of Science Ethics (Approval No: SU-Ethics-Student-051118/1151).

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ACKNOWLEDGEMENTS

I would first like to say a massive thank you to Charlotte Christensen – who has been consistently positive, encouraging and supportive throughout this PhD. We have never failed to have a laugh together, even when times were tough, and I feel extremely lucky to have been able to share this experience with such a good friend, person and scientist.

I would also like to give a huge thank you to my main supervisor, Andrew King, who has such a depth of interest and positivity about the research, as well as being an excellent scientist and an encouraging supervisor. Through Andrew I have learned a huge amount about the scientific process during my PhD. I would also like to thank Ines Fürtbauer for her valuable input on aspects of this thesis, as well as for her hard efforts analysing the hormonal samples which were used in my first data chapter. Thanks to both for the opportunity. Thanks also for the pub lunches/dinners/beers – both virtual and face-to-face!

Similarly, I would like to say a big thank you to Justin O'Riain – for his cheerful kindness, his support and his thoughtful advice, as well as for always putting the results into context for management of baboons on the Cape. I would particularly like to thank Justin for recognising and encouraging my abilities as a scientist. Alongside Justin, thanks to everyone at iCWild, particularly Esme Beamish (who has an inspiring love for the baboons, and also kindly gave me somewhere to stay at the end of the field season) and Joselyn Mormile – for being so open and encouraging, and helpful with her time and baboon expertise. Thanks to the rest of the iCWild lab group for being so friendly and fun.

Thanks go to the rest of the South African contingent; particularly a huge thanks to Human Wildlife Solutions and their rangers, for being open with knowledge of the baboons, as well as providing protection when out in the field. Thanks to Dorothy Breed, the vet, for all her efforts when cage trapping. Particular thanks to Richard Voges, Calford Zodzi, Cath Shutte and Ziggy Rode (RIP), who made the field season go so smoothly. I will always remember

Ziggy as a genuinely warm and kind person, who was incredibly dedicated to the baboons and their welfare.

Additionally, a big thanks to our three field assistants – Charlotte Solman, Lucy Robertson and Francesca Marshall-Stochmal. Their combined efforts helped enormously with the research (as well as being great craic in the field!).

A huge thanks to everyone on the Swansea side, particularly to everyone in the SLAM lab, who were all so friendly and forthcoming with their help. Particular thanks to Mark Holton and Phil Hopkins for their help with collar design and build (and last-minute field questions!). Thanks to Gaëlle Fehlmann – for help with the collar build, and for being another positive, open person – always happy to give her expert advice. Thanks to Alexis Malagnino for helping me understand R – this will be forever appreciated! Thanks too to Baptiste Garde for being another helpful hand in Swansea. Thanks to Will Allen and Kayleigh Rose for constituting my progression panel and offering their guidance.

A big thanks to our little lab group: Amanda Fry, Charlotte Christensen and Charlotte Solman. I was lucky to be surrounded in our office by three excellent friends and scientists. Our cocktail and games evenings were also much needed and appreciated!

Thanks to my family and friends. Thanks to Kyle Walker; his relaxed attitude to life definitely helped with a crazy field season. Thanks to Charlotte's family – particularly her mum Marijntje, for offering a listening ear and lots of hygge times. Thanks to my uncle, Ken, for his advice. A massive thanks to my family for their unconditional support; my parents (Pat and Joan), my brothers (Joe and Timmy), and particularly my sister, Dora, for being such a huge help while I've been working from home due to COVID-19, for the past two-ish (!) years. Thanks to my Gran, who though her memory is fading, still offers me lots of love. Lastly, I would like to (unapologetically) thank my little puppy, Murphy, for unfailingly being able to put a smile on my face.

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Chapter One

Introduction

ENVIRONMENTAL CHANGE

Human activity has altered every ecosystem on planet Earth, transforming between one-third and one-half of the worlds surface (Sterling & Ducharne, 2008; Vitousek et al., 1997). These changes to the world's landscape cause destruction of natural habitats, which is the leading cause of species extinctions (Pimm & Raven, 2000), inducing huge biodiversity losses (Dirzo et al., 2014; McKinney, 2002). This human-caused species and biodiversity loss has been termed the "Anthropocene Defaunation" (Dirzo et al., 2014), with certain taxa more susceptible to human impacts than others (McKinney, 1997; Sih et al., 2011).

Urban development is a major driver of habitat loss and fragmentation (Elmqvist et al., 2016) and, though accounting for only 1 – 6% of the Earth's surface, urban spaces have complex and powerful direct and indirect effects on ecosystems (Alberti et al., 2003), causing a reduction in species diversity (McKinney, 2002). Since urban spaces are drastically different to natural ranges, it is expected that in these areas the tolerance level of many species is exceeded (Sih et al., 2011; Sol et al., 2013). However, certain wildlife has adapted to urban spaces (Lowry et al., 2013), with some species thriving in these habitats and capitalising on the opportunities they present (Sih et al., 2011).

WHAT TRAITS ARE KEY TO WILDLIFE'S SUCCESS IN HUMAN-ALTERED LANDSCAPES?

A key challenge for conservationists is to understand why certain animals thrive and others fail in human-altered landscapes (Fehlmann et al., 2021). Research indicates flexibility in phenotype is necessary for using novel human areas (Bonier et al., 2007; Lowry et al., 2013; Santini et al., 2019), but studies have mainly focused on why certain species are more successful (and flexible) than others (Evans et al., 2010; Kark et al., 2007; Šálek et al., 2015; Slabbekoorn & Peet, 2003). Less is known about within-group variation in flexibility to environmental change (Lowry et al., 2013). However, natural selection occurs at the individual level (Austin et al., 2004), and human-altered landscapes affect individual fitness, influencing reproductive success, fertility, mortality and longevity (Ouyang et al., 2018). Therefore, understanding variation in individual response is necessary to understand the mechanisms behind wildlife's success in human-altered landscapes. Additionally, integrating these individual-level differences into studies of wildlife conservation and management is likely to aid its application, for example, in locating “problem” individuals within human-altered landscapes (Merrick & Koprowski, 2017).

Species-level traits

Generalism

Many species using human-altered landscapes tend to be generalists (species with a wide ecological niche), both in habitat (Bonier et al., 2007; Clergeau et al., 2006; Devictor et al., 2008) and diet (Santini et al., 2019). Generalist species have a broader environmental tolerance (Ducatez et al., 2014; Yusefi et al., 2021), which allows for adaptation to novel environmental conditions (Cassey, 2002) and means that they are less likely to be threatened by extinction (Ducatez et al., 2014). Concurrently, habitat generalist species also tend to have a wide and varied diet, which allows them to opportunistically incorporate novel food items (Ducatez et al., 2015) making them more successful in human-altered landscapes (Franzén et al., 2020; Palacio, 2020). Urbanisation causes the homogenization of wildlife (Lockwood & McKinney, 2001) as these areas are built to meet the needs of only one species: humans (McKinney, 2006). More specialist species therefore tend to decrease in these areas (Sorace & Gustin, 2009).

Innovation

Innovation - the development of new behaviours (Kark et al., 2007; Navarrete et al., 2016) - is regarded as important for species that colonise novel environments (Griffin et al., 2017; Sinha & Vijayakrishnan, 2017; Sol et al., 2005). Animals inhabiting human-altered landscapes tend to exhibit greater learning and problem-solving skills (Griffin et al., 2017), as well as incorporating new food items in their diet ("feeding innovation": Ducatez et al., 2015). Innovative behaviours are often used as a measure of the behavioural flexibility of a species (Kark et al., 2007; Lowry et al., 2013), for example, the behaviour of singing at a higher pitch by great tits (*Parus major*) in urban spaces is referred to as behavioural plasticity (Slabbekoorn & Peet, 2003). Innovation is the first step in social learning (Hoppitt & Laland, 2008), which is of great importance for social species in human-altered landscapes where "problem" behaviours can be generated and rapidly transmitted through a population (Donaldson et al., 2012; Morehouse et al., 2016; Whitehead, 2010).

Sociality

Many species which use human-altered landscapes form social groups (Chiyo et al., 2012; Fehlmann et al., 2017b; Kark et al., 2007; Stillfried et al., 2017). Living in a group buffers against risk as well as providing better efficiency in seeking food resources (Krause & Ruxton, 2002; Sueur et al., 2011a). Both of these aid animals living in human-altered landscapes, which typically have high-quality food rewards, as well as increased risks (Fehlmann et al., 2021). However, there are other more solitary species which use these environments (e.g. some carnivore species), but evidence suggests that even these have plastic social systems (Bateman & Fleming, 2012). For example, red foxes (*Vulpes vulpes*) living in a desert region in Saudi Arabia change their social structure in response to food distribution; exhibiting increased tolerance to other foxes around food-rich sites associated with human activity (Macdonald et al., 1999). Since some species reach greater densities in human-altered landscapes (Fischer et al., 2012; Møller, 2009; Møller et al., 2012; Parker &

Nilon, 2008; Prange et al., 2003), having a plastic social system is likely to aid living in these environments.

Individual-level traits

Behavioural flexibility

Behavioural flexibility (the ability to alter behaviour in response to environmental change) is considered to be a key determinant for species in colonising novel human-altered landscapes (Carrete & Tella, 2011; Sol et al., 2013; Sol et al., 2002). However, behavioural flexibility is determined at the individual level and individuals modify their behavioural phenotype to adapt to environmental changes within their lifetime (Dingemanse et al., 2010), with some more responsive to environmental change (Koolhaas et al., 1999; Réale et al., 2007). This can be seen across different phenotypes within a group (Killen et al., 2013), where factors such as age and sex (Baker et al., 2007; Chiyo et al., 2012; Maibeche et al., 2015) can predispose certain individuals to respond flexibly to human-altered landscapes (Lowry et al., 2013; Santini et al., 2019). Species' social systems and life-history strategies can also drive phenotypic differences in flexibility to human-altered landscapes (Baranga et al., 2012; Kark et al., 2007; Williams et al., 2010). For example, phenotypic differences in energy requirements and fitness expectations may predispose certain age-sex classes to risk-taking behaviour (Wolf et al., 2007). Adult males are often noted for being more risk-prone (Sukumar, 1991) and, in many species, show increased use of human-altered landscapes (Chiyo et al., 2012; Fehlmann et al., 2017b; Maibeche et al., 2015; Merkle et al., 2013; Srinivasaiah et al., 2019). This is seen in Barbary macaques (*Macaca sylvanus*) which show variability in dietary flexibility across individuals; adult males eat more human foods than females or juveniles (Maibeche et al., 2015). Female black bears (*Ursinus americanus*) use urban space less than males, which may be due to a risk of infanticide from males or because males have a higher probability of encountering urban space as they have larger home ranges (Merkle et al., 2013).

Personality

Other research has highlighted that consistent individual differences (where each individual does not express the full range of behavioural traits in a population) underlie and modulate the expression of behaviour (McDougall et al., 2006). These are consistent over time and context with some individuals having a higher average “behavioural expression” than others (Bailey et al., 2021; Hertel et al., 2020; Réale et al., 2007). This average behavioural expression (or “behavioural type”, “temperament” or “personality”: Fürtbauer et al., 2015; Koolhaas et al., 1999; Réale et al., 2007; Sih et al., 2004) can influence how individuals respond to changes in their environment (Dingemanse et al., 2010), where certain individuals are better able to cope with stressors (Dingemanse & Wolf, 2013; Koolhaas et al., 1999; Réale et al., 2007). For example, temperaments that are bolder in response to risk, are more exploratory and/or are more aggressive to conspecifics are predicted to be better predisposed to invading novel urban spaces (Atwell et al., 2012; Phillips & Suarez, 2015; Sol et al., 2013) and adapting to human presence (Evans et al., 2010). This has been exhibited in population comparisons of urban and rural birds (Atwell et al., 2012; Evans et al., 2010; Lowry et al., 2011; Møller, 2008); for example, urban individual song sparrows (*Melospiza melodia*) were found to be bolder towards humans and showed higher levels of territorial aggression than their rural counterparts (Evans et al., 2010). Personality may also affect individual plasticity to environmental change (Dingemanse et al., 2010); for example, in great tits, exploratory individuals were more responsive to changes in predation risk (Quinn et al., 2012).

Less is known about the way in which differences in individual personalities within a group respond to human-altered landscapes (Lowry et al., 2013). Boldness (Found & Clair, 2016) and exploratory behaviour (Wat et al., 2020) have been linked to individual urban space-use, and it may be the case that personality is expressed more strongly under extreme conditions (Réale et al., 2007). Individual personality is increasingly recognised as imperative information to incorporate into conservation efforts (McDougall et al., 2006; Merrick & Koprowski, 2017). It is predicted to help in multiple wildlife conservation areas, from detection probability to translocation, as well as in the design of efficient management strategies and in individual response to urbanisation (Merrick & Koprowski, 2017).

WHAT IS THE IMPACT OF USING HUMAN-ALTERED LANDSCAPES ON SOCIAL PROCESSES WITHIN AN ANIMAL GROUP?

The use of human-altered landscapes can have large consequences for species (described in detail in Fehlmann et al., 2021). It alters foraging (Branco et al., 2019; Hill, 2018; Merkle et al., 2013), movement (Fahrig, 2007; Lewis et al., 2011; Walton et al., 2017) and social (Morrow et al., 2019) ecology, which results in changed life-history traits (Beck & Heinsohn, 2006; Chace & Walsh, 2006; Šálek et al., 2015) and population dynamics (Barbosa et al., 2020; Bateman & Fleming, 2012; Rodewald & Gehrt, 2014). Evidence suggests that animal groups adapt their social systems to human presence (Hockings et al., 2012; Macdonald et al., 1999; Morrow et al., 2019; Srinivasaiah et al., 2019) as a result of high-quality food rewards and increased risk (Fehlmann et al., 2021). For example, Asian elephants (*Elephas maximus*) which are typically solitary or associate in mixed-sex groups, form novel, stable, long-term all-male groups in human-altered landscapes (Srinivasaiah et al., 2019). Understanding the functioning and stability of social groupings under change will be vital information in conservation and management efforts (King et al., 2018). However, this remains understudied due to a lack of simultaneous information on multiple individuals in these landscapes (Hughey et al., 2018; King et al., 2018).

For social species, remaining as a cohesive unit provides decreased individual risk (Sueur et al., 2011a), and coordination in movement and behaviour between individuals promotes food-searching efficiency (Fernández-Juricic et al., 2007; King & Cowlishaw, 2007; King & Cowlishaw, 2009a). When individuals differ in their propensity to use human-altered landscapes, however, (for the reasons highlighted above) this can result in conflicts of interest between group members (Conradt et al., 2009; Merkle et al., 2015; Sueur et al., 2011b) and difficulties for the group to remain as a cohesive, synchronous unit (Jolles et al., 2019; King & Cowlishaw, 2009a). In some species and environments, the high risk associated with human-altered landscapes can result in increased party cohesiveness (e.g. crop-foraging chimpanzees (*Pan troglodytes*) in Bossou, New Guinea: Hockings et al., 2012). For others, human influence can cause increased inter-neighbour distances and reduced cohesion: e.g. moor macaques (*Macaca maura*), which use a provisioned road in South Sulawesi, Indonesia (Morrow et al., 2019) and Atlantic croaker (*Micropogonias undulatus*), when exposed to oil (Armstrong et al., 2019).

Fission-fusion dynamics

Patchy high-quality food resources, coupled with heightened spatial risks (typical of human-altered landscapes: Fehlmann et al., 2021), can cause conflicts of interests between group members (Conradt et al., 2009; Kaplan et al., 2011), particularly in groups with large individual heterogeneity (i.e. in social roles: Farine et al., 2015). This can result in greater consensus costs for certain individuals (Fehlmann et al., 2021; Kaplan et al., 2011; King et al., 2008). In human-altered landscapes, individuals may be more motivated by environmental rather than social factors, which can lead to certain individuals having a disproportionate influence on group movement and group fragmentation (Conradt et al., 2009). Fission into subgroups has been previously observed in animals using human-altered landscapes (i.e. crop-foraging baboon (*Papio anubis*) parties in West Africa: Warren, 2009; urban rhesus macaque (*Macaca mulatta*) groups in India: Southwick & Siddiqi, 1994; and lion-tailed macaques (*Macaca silenus*) in a forest fragment in India: Sakthivelou & Kumar, 1998). Increased fission-fusion dynamics within an animal group may lead to permanent group fission (Sueur et al., 2011a) creating two groups where there was originally one, which creates a greater challenge for management of groups (see later). Permanent fission may also change the social organisation of these groupings (e.g. in dominance hierarchy position: van Horn et al., 2007), with certain phenotypes more likely to move between groups (Jolles et al., 2019). This could affect individual use of human-altered landscapes.

Keystone roles

Within a collective group there may be individuals that play “keystone” roles – i.e. they have a large effect on group members’ behaviour or group dynamics (Modlmeier et al., 2014). If these individuals are preferentially exploited, harvested or killed, this can potentially destabilise social structures and affect fitness (King et al., 2018; Leclerc et al., 2017a; Swan et al., 2017; Williams & Lusseau, 2006). Additionally, loss of specific individuals may inadvertently put selective pressure on other traits in a population (Biro & Post, 2008; Leclerc et al., 2017b; Swan et al., 2017), which could drive the use of human-altered landscapes by other group members. However, understanding the influence of these individuals can also aid in more targeted management strategies (Fehlmann et al., 2017a). For example it has been proposed that selectively culling bolder individuals, in order to select for shyer individuals in groups using human-altered landscapes, may help to reduce human-wildlife conflict (Honda et al., 2018).

EFFECT OF MANAGEMENT ON WILD ANIMAL GROUPS

Animal groups that use human-altered landscapes inevitably come into increased contact with humans (Soulsbury & White, 2016; Thirgood et al., 2005) which can result in negative interactions. Common impacts of wildlife in human-altered landscapes include huge economic losses through crop and livestock damage (Hill, 2000), damage to property and pets (Soulsbury & White, 2016), disease transmission (Daszak et al., 2000; Drewe et al., 2012) and even attacks on humans (Baker & Timm, 2017; Bargali et al., 2005). Retaliation killings or lethal control of conflict animals is a common response

(Dickman, 2010), contributing to species' decline. Species that forage on human foods are frequently chased, attacked or killed (Ahlering et al., 2011; Bargali et al., 2005; Hill, 2000). Nevertheless, human-altered landscapes provide energy-rich, easily-accessible human food sources, which provides huge motivation for animal groups to use these landscapes (Fehlmann et al., 2021).

Management strategies used to deter wildlife in contact with humans are diverse, both across the environments in which they occur (Nyhus, 2016) and with the species in question (Thapa, 2010). Common strategies include imposing structural barriers to the landscape (e.g. implementing fences between human settlements and species habitats: Kesch et al., 2015; Otto & Roloff, 2015) or physically chasing animals from human-altered landscapes (Fehlmann et al., 2017b; Findlay & Hill, 2021b; Hill, 2000).

Fences are used in mitigating human-wildlife conflicts across the world (Geisser & Reyer, 2004; Pekor et al., 2019; Proctor et al., 2018) mainly in preventing depredation of crops and livestock (Lesilau et al.; Nyirenda et al., 2011; Sekhar, 1998), but also to safeguard endangered species in protected areas (Hayward & Kerley, 2009). Physical fences generally have a high success rate, particularly electric fences (Hayward & Kerley, 2009; Kistler et al., 2013), but require ongoing maintenance; they also frequently exclude non-targeted species (Jachowski et al., 2014). More recently, 'virtual' or 'metaphorical' fences (non-physical barriers, often achieved through sensory deterrents, e.g. sound, smoke, smell: Hayward & Kerley, 2009; Jachowski et al., 2014) have been introduced in a number of human-wildlife conflict situations (Chelliah et al., 2010; King et al., 2007; Sitati & Walpole, 2006). For example, playbacks of disturbed African honeybees (*Apis mellifera scutellata*) successfully prevent elephants (*Loxodonta africana*) from foraging on crops (King et al., 2007), and deployment of 'alarm' collars, which send out a sensory shock (electric or auditory) when the animal crosses a predefined barrier, deters wild wolves (*Canis lupus*) from baited areas (Rossler et al., 2012).

Virtual fencing is becoming an increasingly popular management tool, as it is relatively inexpensive, easy to initiate and has a reduced impact on non-targeted species (Jachowski et al., 2014).

Guarding, or physically chasing animals away from, an area (Fehlmann et al., 2017b; Findlay & Hill, 2021b; Thapa, 2010) is another common wildlife deterrent method; particularly used by subsistence farmers in keeping wildlife away from crops (Hill, 1997, 2000; Mackenzie et al., 2015; Naughton-Treves, 1998). Guards employed by farmers stay present at crop fields and chase animals away when they enter fields to forage (Findlay & Hill, 2021b), through, for example, banging drums, shouting and throwing objects (Osborn & Parker, 2003; Thapa, 2010). Though it requires low financial investment (Wang et al., 2006), it is an intensive process (Thapa, 2010), which varies in success (Findlay & Hill, 2021b; Linkie et al., 2007; Thapa, 2010). It also has social implications; for example, boys attending primary schools in villages surrounding Kibale National Park, Uganda, were preferentially held back from school to guard crops, and were less likely to complete primary education (Mackenzie et al., 2015). In urbanised areas, similar approaches to guarding have been adopted (Fehlmann et al., 2017b); for example, ‘baboon rangers’ in Cape Town, South Africa physically herd baboons from urban spaces (Kaplan et al., 2011; van Doorn & O'Riain, 2020). Many wildlife groups are deterred using such guarding methods (Linkie et al., 2007; Osborn & Parker, 2003; Thapa, 2010), but primates are particularly difficult to manage in this way (Hill, 2000) due to their intelligence and adaptability (Else, 1991; Findlay & Hill, 2021b; Webber et al., 2007).

Other non-lethal deterrent methods employed by management include diversionary feeding (Amar et al., 2004; Kaplan et al., 2011; Kubasiewicz et al., 2016), physical handicapping (Mutinda et al., 2014) or aversive conditioning (Mazur, 2010; van Doorn & O'Riain, 2020). Diversionary feeding involves drawing animals away from problem activities or locations using food rewards (Kubasiewicz et al., 2016). It has been successful in reducing predation of game species – red grouse (*Lagopus lagopus*) – by hen harriers (*Circus cyaneus*) (Redpath et al., 2001) and in deterring black bears from damaging trees in commercial forests (Ziegltrum, 2008), but less so in preventing baboons from using urban spaces (Kaplan et al., 2011). Physical handicapping of animals, for example removing the tusks of elephants (*Loxodonta africana*) (Mutinda et al., 2014) or the horns from black rhinos (*Diceros bicornis*) (Milner-Gulland et al., 1992), has been used cautiously in an effort to reduce human-wildlife conflict (i.e. to increase effectiveness of electric fencing for elephants, which use their tusks as 'fence-breakers', or to reduce rhino poaching for their valuable horns). Lastly, aversive conditioning or 'hazing' (a form of operant conditioning: Dugatkin, 2008) uses a stimulus which causes an animal pain, avoidance or irritation so that the animal will associate humans, or a problem behaviour, with a negative response (Mazur, 2010). This is seen in the use of shock collars on wolves (Rossler et al., 2012; described above), the use of slingshots, rubber slugs and pepper spray on bears (Mazur, 2010), and the use of paint-ball marker guns on baboons (Fehlmann et al., 2017b). Aversive conditioning often has only a temporary effect (Honda et al., 2019).

More recently, there has been a move towards selective wildlife management, which focuses on deterring or removing 'problem' individuals (i.e. through lethal removal: Swan et al., 2017, or translocation: Massei et al., 2010) rather than targeting the whole group or population. In many wildlife groups in contact with humans, conflict can often be ascribed to the behaviour of individuals rather than the group (Baranga et al., 2012; Swan et al., 2017), such as certain age-sex classes (Maibeche et al., 2015; Marty et al., 2019; Merkle et al., 2013) or social groups (Baranga et al., 2012). Certain selective management techniques can be socially contentious, however (Swan et al., 2017), which leads to specific individual animals gaining international fame, such as 'Bruno' the bear in Germany, before and after his lethal removal (Münchhausen & Herrmann, 2008), and the translocation of 'Kataza' the baboon in Cape Town, South Africa (Jordan, 2021; Magill, 2020; Viljioen, 2021).

Effect of management focus on individuals

Selective management programmes can disproportionately focus on certain ‘problem’ phenotypes or individuals within a group (such as those of a certain size, sex or social position) (Swan et al., 2017); for example, males tend to be the focus of management efforts and lethal removal in Cape baboons (Beamish, 2009; Fehlmann et al., 2017a), large feral cats (*Felis catus*) (Moseby et al., 2015), and, inadvertently, in Baltic grey seals (*Halichoerus grypus*), as male seals tend to spend more time near fishing gear (Kauhala et al., 2015). As has been highlighted above, focusing efforts on specific individuals can aid management (e.g. if individuals are “keystone” in collective dynamics: King et al., 2018, or by culling ‘bolder’ individuals from a population: Honda et al., 2018). However, this may have unintended consequences for social structures within the group (Alberts et al., 2002; Leclerc et al., 2017a; Sogbohossou et al., 2014). For example, focusing efforts on adult males may skew natural sex ratios (Beamish, 2009); when males are preferentially hunted, this potentially increases infanticide and sexual conflict (Gosselin et al., 2017; Swenson et al., 1997), thereby affecting population dynamics (Gosselin et al., 2015; Rankin & Kokko, 2007). Removal of individuals can also cause alterations in space-use and social contacts. For example, in a population of white deer (*Odocoileus virginianus*), removal of group members caused adult females to reduce contacts with neighbouring groups, but caused juveniles to increase contacts and join neighbours; this has implications for disease transmission (Tosa et al., 2017). Understanding how group members respond to certain individuals being targeted in human-altered landscapes will be important for the successful management of whole groups.

STUDYING INDIVIDUAL-LEVEL DIFFERENCES IN WILD ANIMAL GROUPS

An overview of individual-level differences in response to human-altered landscapes in the wild has been lacking, as collecting whole-system data on wild groups can be very challenging (King et al., 2018). Therefore, studies can have a disproportionate amount of information on certain ‘conspicuous’ individuals, leading to sampling bias (Biro, 2013; Carter et al., 2012b) and overlooking more cryptic individuals (Merrick & Koprowski, 2017). Bio-logging offers a solution to this, allowing researchers to collect information on multiple individuals simultaneously (Hughey et al., 2018).

Tracking collars

Bio-loggers are devices that can be attached externally to, or implanted in, an animal (Fehlmann & King, 2016). They are an important tool for gathering remote information about an animal from a completely new perspective (Urbano et al., 2010), allowing researchers to study aspects of wild animal physiology, behaviour and ecology previously only possible in captive settings (Wilmers et al., 2015). On-board sensors include GPS, accelerometers, magnetometers, pressure sensors and acoustic recorders, amongst others (Hughey et al., 2018). Bio-loggers may be particularly important in studying animals that are in conflict with people. Since these species are sensitive to human proximity, their behaviours could be altered by traditional behavioural sampling methods (Wilson et al., 2008). The Global Positioning System (GPS) provides longitude and latitude (*x*,*y*) data on an individual animal, pinpointing its location in space and time (Joo et al., 2020; Wilmers et al., 2015). This can be particularly useful for understanding individual-level differences in response to human-altered landscapes, as long as positional data can be gathered from many individuals simultaneously.

GPS data can be used to uncover a wealth of information, such as resource selection (Gustine et al., 2006; Rode et al., 2006; Watson et al., 2014), movement (Cagnacci et al., 2010), foraging behaviour (Evans et al., 2013; Lesmerises et al., 2015; Zhang et al., 2019), social networks (Farine & Whitehead, 2015; Robitaille et al., 2019) and group dynamics (Farine et al., 2016; Strandburg-Peshkin et al., 2015). As spatial tracking datasets are increasing, so too is the development of sophisticated tools to process, visualise and analyse this data (Joo et al., 2020). Spatial data is often used in conservation efforts, for example in understanding movement and space-use of animals using human-altered landscapes (Fehlmann et al., 2017a; Merkle et al., 2013; Odden et al., 2014). This is important information for the management of wild groups (Bartoń et al., 2019; Fehlmann et al., 2017a; Schieltz et al., 2017; Schofield et al., 2007; Weber et al., 2015). The field of movement ecology therefore holds great promise for animal conservation and management (Allen & Singh, 2016; Fraser et al., 2018).

A MODEL SYSTEM FOR UNDERSTANDING INDIVIDUAL AND SOCIAL RESPONSES TO HUMAN-ALTERED LANDSCAPES: BABOONS

Baboons are Old World primates, belonging to the genus *Papio*, which consists of six baboon species (though different morphological types occur): the Guinea baboon (*Papio papio*), the hamadryas baboon (*Papio hamadryas*), the olive baboon (*Papio anubis*), the yellow baboon (*Papio cynocephalus*), the Kinda baboon (*Papio kindae*) and the chacma baboon (*Papio ursinus*) (). They mainly occur in Africa, but their range also extends to Arabia.

Baboons are an extremely generalist species, showing great flexibility in behaviour (Barrett & Henzi, 2008). This is particularly seen in their diverse range across Africa: they have colonised almost all of Africa's landscapes, from deserts in Namibia (Cowlishaw, 1997) and tropical forests in Uganda (Okecha & Newton-Fisher, 2006), to highlands in Ethiopia (Abie et al., 2017), the seashore (Lewis, 2015) and urban spaces (Hoffman & O'Riain, 2011) on the Cape Peninsula. These habitats are subject to frequent short-term, as well as long-term, change (Alberts & Altmann, 2006). This adaptability is shown in the average distance different troops across the genus' range travel each day; ecological conditions (e.g. rainfall, temperature, anthropogenic disturbance) predict differences in day path lengths (Johnson et al., 2015). Baboons also have great dietary flexibility. They have a 'selective generalist' diet, being omnivorous (eating plants, invertebrates and small vertebrates), but selective with the plant species and parts that they consume (Barton & Whiten, 1994). Foraging behaviour and dietary composition varies greatly across different populations, as vegetation structure and food availability differs with changing climatic parameters (Hill & Dunbar, 2002).

Baboons are long-lived (Archie et al., 2014a) and highly social (Alberts, 2019; Silk et al., 2009). Baboon mating systems, social organization and social structure vary across species (Fischer & Zinner, 2011; Kappeler & van Schaik, 2002; Swedell, 2011) and are responsive to differing environmental pressures (Cheney & Seyfarth, 2008). Typically, olive, yellow, kinda and chacma baboons live in mixed male/female groups of up to 100 individuals, in which natal females spend their lives (‘female philopatry’), while natal males emigrate (male dispersal) (Henzi & Barrett, 2003; Clarke et al., 2008). These groups are ‘female-bonded’; female success depends on the ability of individuals to form strong, grooming-mediated bonds with other females (Silk et al., 2003; Silk et al., 2010b), particularly when local resources are scarce (Barton & Whiten, 1993). Males join and leave these female units. Mating success, and therefore reproductive skew, is largely predicted by male rank, and male-female associations vary with female reproductive state; during consortships, males and oestrus females remain in close proximity and, whilst lactating with dependent offspring, females maintain ‘friendships’ with males (Palombit et al., 1997; Swedell, 2011). Contrastingly, hamadryas and guinea baboons have principal units of singular ‘leader’ males (one-male units) with several females (regardless of reproductive state) and their offspring (Henzi & Barrett, 2003; Goffe et al., 2016; Montanari et al., 2021), and display female-biased dispersal (Kopp et al., 2015). Two to three of these units congregate into a ‘clan’; clans come together to form ‘bands’, and bands can gather into a troop (Galat-Luong et al., 2006).

Baboons have complex social systems, exhibiting high heterogeneity between individual phenotypes (Barrett & Henzi, 2008). They exhibit large physical differences between sexes (Barrett & Henzi, 2008; Smith, 2012) and ages (Altmann et al., 1981), and individual differences in social rank (Johnson, 2003) and inter-individual social affiliation (Silk et al., 2010a). Baboons tend to associate with similar phenotypes (Carter et al., 2015). These large phenotypic differences influence access to foraging patches (King et al., 2009a) and grooming partnerships (Silk et al., 2010b), affecting reproductive output (Alberts, 2019; Silk et al., 2003) and fitness (McLean et al., 2019; Silk et al., 2010b).

Baboons are innovative (Kummer & Goodall, 1985) and show high flexibility to novel situations and environments (Bergman & Kitchen, 2009; Dubay, 2018; Hoffman, 2011), for example, they rapidly learn the locations of food items (Noser & Byrne, 2015). Due to living in highly social systems (Alberts, 2019; Barrett & Henzi, 2008), baboons learn socially (Carter et al., 2014; Whiten, 2000), and transmission of novel behaviour is fast in baboon groups (Cambefort, 1981). Baboon individuals differ in how much they ‘innovate’ or learn from others (seen as ‘producing’ or ‘scrounging’ information: King et al., 2009a).

Human-baboon conflict

Primates, and in particular baboons, pose a huge challenge in their conflict with humans (Hill, 2000; Hoffman & O'Riain, 2012c). Almost all primate families have been seen to forage on crops, which results in disproportionate costs to local communities (Dickman, 2012; Hill, 2018). It is due in part to their intelligence, adaptability and sometimes intimidating nature (Hill, 2000; Webber et al., 2007). The same traits result in mitigation techniques being only temporarily effective. In the Budongo Forest Reserve in western Uganda, baboons caused extensive damage to field crops, with farms closer to the forest edge being hit the worst (Hill, 2000). Crop-foraging activity of baboons poses a significant threat to farmers’ livelihoods because of the degree of destruction and the unpredictability of the timing of raids. Due to this pattern of behaviour, people living alongside baboons often harbour negative perceptions of them (Hill & Webber, 2010; Mormile & Hill, 2017).

THE CASE OF THE CAPE PENINSULA BABOONS

One of the most high-profile cases of human-baboon conflict occurs in the Cape Peninsula, South Africa (Hoffman & O'Riain, 2012c; Kaplan et al., 2011; van Doorn & O'Riain, 2020). Here, due to human population growth and encroachment of humans into natural areas, there is increased overlap between humans and baboons (Hoffman & O'Riain, 2012b), which causes negative interactions.

Baboons regularly use urban spaces to forage from rubbish bins, open food waste, fruits and vegetables in residential gardens and, occasionally, to enter properties for food rewards (Kaplan et al., 2011; van Doorn & O'Riain, 2020). Fruiting trees (e.g. guava: *Psidium guajava*, *Pinus* spp.) and exotic species also tend to occur in urban spaces, attracting baboons to these areas (Fehlmann et al., 2017*a*; Hoffman & O'Riain, 2011).

Humans experience damage to property, economic losses (when troops have access to commercial vineyards) and physical harassment by baboons for food (Fehlmann et al., 2017a; Kaplan et al., 2011; van Doorn & O'Riain, 2020). Consequently, residents harbour negative attitudes towards baboons (Mormile & Hill, 2017), and baboons experience high levels of human-induced mortality and injury (Beamish, 2009).

As a result of the negative repercussions of baboon urban-foraging, the “baboon management team” (BMT) was set up on the Cape, composed of local authorities (Table Mountain National Park, Cape Nature and the City of Cape Town), resident representatives, and biologists, and together developed a ‘baboon management strategy’ (van Doorn & O'Riain, 2020). The baboon management strategy includes a number of methods, from education to waste management and electric fencing. Most notably, the BMT introduced baboon rangers to physically prevent the baboons from using human-altered landscapes (Kaplan et al., 2011). (These are akin to guards, employed to chase baboons elsewhere in the species’ range: Hill, 2000; Warren, 2009).

Between 2012 – 2020, the service provider contracted to manage the baboons, “Human Wildlife Solutions” (Human Wildlife Solutions, 2021), employed around 60 field rangers across 10 baboon troops to prevent baboons from entering urban spaces, largely through the use of pain aversion (i.e. paintball marker guns: Fehlmann et al., 2017b). They also produced monthly reports on each troop, including information on levels of human-baboon conflict (Richardson, 2018a, 2018b). The service provider changed in 2020, when NCC Environmental Services was appointed to manage the baboon population (the “Urban Baboon Programme”: NCC Environmental Services, 2021); however, the use of baboon rangers remains the same. By and large, the use of baboon rangers has greatly reduced baboon group urban-foraging (van Doorn, 2009; van Doorn & O'Riain, 2020), although individual baboons still use urban spaces (Fehlmann et al., 2017a).

Research aimed at mitigating human-baboon conflict on the Cape has mainly focused on predictors of baboon spatial ecology (Hoffman & O'Riain, 2012b; Hoffman & O'Riain, 2012c; Fehlmann et al., 2017b; Hoffman & O’Riain, 2011) and the efficacy of current management techniques (Fehlmann et al., 2017b; van Doorn & O'Riain, 2020), as well as testing novel mitigation strategies (i.e. experimental diversionary food patches: Kaplan et al., 2011). Cape baboon urban-foraging has mainly been ascribed to adult males, who use a “sit-and-wait strategy”, spending a large amount of time on the urban edge (using areas where management are uncertain in how best to herd the baboons) and then making high-activity forays into urban spaces (Fehlmann et al., 2017a; Fehlmann et al., 2017b). However, management monthly reports indicate that females also use urban space (Richardson, 2018a, 2018b), and therefore a complete understanding of how all individuals in a group use urban spaces is lacking. Additionally, little is understood about the way in which individual urban space-use impacts individual movement and group social structures, which may have implications for management strategies aiming to cohesively herd troops.

THESIS AIMS

My thesis aims to provide a comprehensive overview of the individual drivers and individual- and group-level consequences of urban space-use by (1) identifying which phenotypes use urban space (both in temporal and spatial aspects), (2) identifying how underlying ‘personalities’ differ, both between individuals and in their plasticity to urban space and (3) by examining the impacts of urban space-use on group-level properties. This work is organised as follows: an introduction (the current chapter), a methodological chapter (Chapter 2), four empirical data chapters (Chapters 3-6), and a discussion chapter (Chapter 7). In Chapter 2 (methods), I give an overview of all data collection undertaken in the field. In Chapter 3, I explore individual differences in time spent in urban spaces, and the predictors of this. In Chapter 4, I examine individual predictors of space-use by baboons – both at a whole range level, and within the urban space. In Chapter 5, I look at the consequences of urban space-use on individual-level movement: first, quantifying consistent differences between individuals in movement (i.e. “personalities”) and then examining how these change with environment. In Chapter 6, I again investigate the consequences of urban space-use, but at a whole group level, exploring how collective dynamics (cohesion, coordination, leadership) are altered in urban spaces. In Chapter 7, I discuss how these results may be used within current management strategies for the Cape baboon population and how the results might be applied in the management of other species and populations. In this final chapter, I also consider the limitations of the study and the possibilities for future research. The data gathered by myself and the project team members has also contributed to several other manuscripts (reprints are included at the end of this thesis) on topics covering the effect of GPS sampling interval on baboon daily travel distances (McCann et al., 2021, Publication 3), the drivers of faecal and urinary glucocorticoid levels in baboons (Christensen et al., 2022, Publication 4) and the predictors of c-peptide levels in baboons (Fürtbauer et al., 2020, Publication 5).

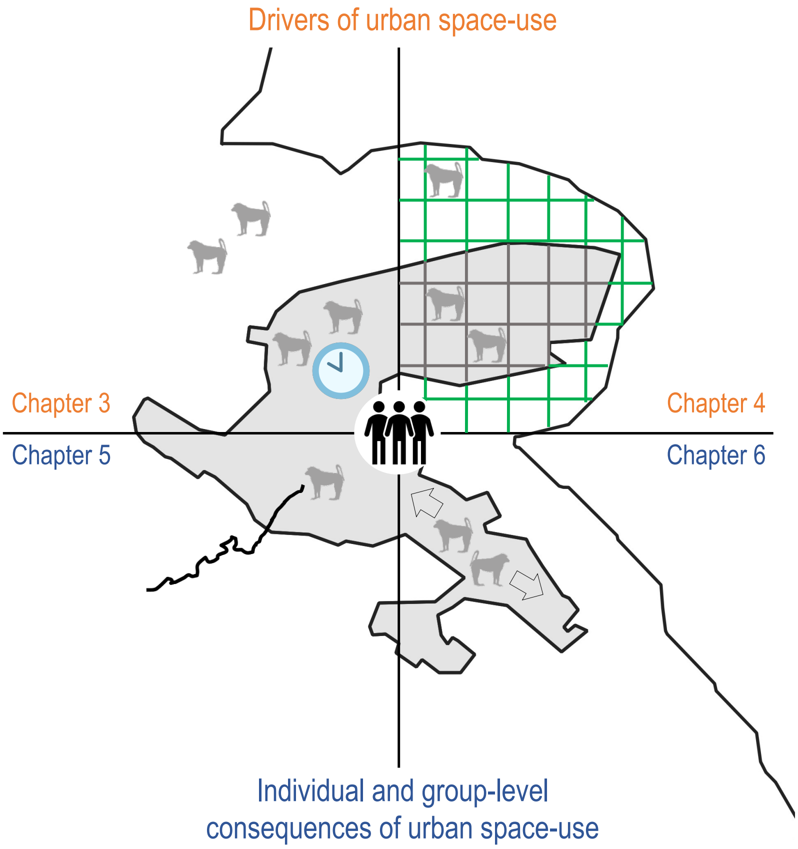

Figure I-1. Schematic of thesis data chapters. Chapter 3 (top left) examines the individual drivers of time spent in urban space; Chapter 4 (top right) examines both the drivers of whole troop space-use, and individual urban space-use; Chapter 5 (bottom left) examines the consequences of urban space-use on individual movement; Chapter 6 (bottom right) examines the consequences of urban space-use on whole group movement. Baboon rangers are a constant environmental factor for the baboons and are represented as human icons in the centre of the schematic.

Chapter Two

Methods

GENERAL OVERVIEW

In order to study the drivers and consequences of individual level urban space-use in a group of baboons, I used high-resolution GPS data from n = 13 tracking collars and *ad libitum* behavioural observations for the calculation of dominance ranks (Fig. II-1). Additionally, in Chapter 4, I used ranger survey data to quantify risk across the baboons' home range, and C-peptide hormonal data in Chapter 3 to investigate whether internal energetic state influenced individual time in urban space. The data streams used in the current thesis were only a subsection of the overall dataset gathered, which contributed to a larger research programme and research outputs (Fig. II-1). Therefore, in this chapter I give a brief overview of all data collected.

Data stream		**Chp 3**	**Chp 4**	**Chp 5**	**Chp 6**	**Publ. 1**	**Publ. 2**	**Publ. 3**	**Publ. 4**	**Publ. 5**
Collar	GPS	✓	✓	✓	✓	✓	✓	✓		
	Daily Diary									
Observational	Scan									
	Focal									
	Ad lib	✓	✓	✓	✓	✓	✓		✓	✓
Environmental	Ranger survey		✓							
	Habitat									
Hormonal	C-peptide	✓								✓
	Urinary GC								✓	
	Fecal GC								✓	

Figure II-1. Overview of the data streams used in this thesis, and other research outputs from the whole collected dataset. Daily diaries collect several data types including acceleration data, which has been used previously to quantify Cape baboon behaviour (Fehlmann et al., 2017c). "GC" stands for "glucocorticoid", and measures were extracted from both urine and faeces. "Publ." stands for "Publication", and reprints are included at the end of the thesis.

Overview of 2018 field season

I conducted my PhD in tandem with another PhD student, Charlotte Christensen, as part of a collaborative project between Swansea University and University of Cape Town. Charlotte is investigating the link between individual grooming budgets and physiological stress levels in the same baboon troop. Charlotte and I led the field season, with the data that we collected contributing to both PhD projects, to collaborative work between the two of us, and to the larger research programme. During the field season, we had help from three research assistants: Charlotte Solman and Lucy Robertson in July and August, and Francesca Marshall-Stochmal in September.

The field season occurred between June and November 2018 (Fig. II-2). This constitutes the winter season on the Cape, in which baboons are known to use urban spaces more frequently (van Doorn et al., 2010). The period between June and the end of July was mainly used to select an appropriate study troop collectively to answer our research questions – i.e. a troop that used urban spaces, had a terrain that allowed daily follows on foot, and were well enough habituated to humans to allow close video recording of individuals (used for the validation of the acceleration dataset: Fehlmann et al., 2017c) and to facilitate frequent faecal and urine collection.

During the first part of the field season we met with the management team (Human Wildlife Solutions) and familiarised ourselves with individual baboons, baboon behaviour, and baboon home range. Baboon collaring (detailed below) was carried out at the end of July and the first week of August, after which we focused intensive efforts on data collection (during the time that collars were recording data). This included video recording, behavioural observations and hormonal collection. Collars contained drop-off mechanisms (version CR-7, Telonics, Inc.) and were programmed to release on 16th October 2018 (78-83 days after deployment, depending on the individual baboons' trapping dates). Of the 16 collars deployed, 11 collars dropped at the scheduled date, three at a later date and two, not at all (these individuals were re-trapped to retrieve the collars). We organised a collar search for the three missing collars, but did not locate them at this time, as the area to cover was extensive. Two of these collars were subsequently found by the management team when out monitoring the baboons, and one was never retrieved. We also collected ranger survey data and habitat data (described below). Faecal samples were freeze-dried at University of Cape Town, and both faecal and urine samples were exported to Swansea University at the end of November.

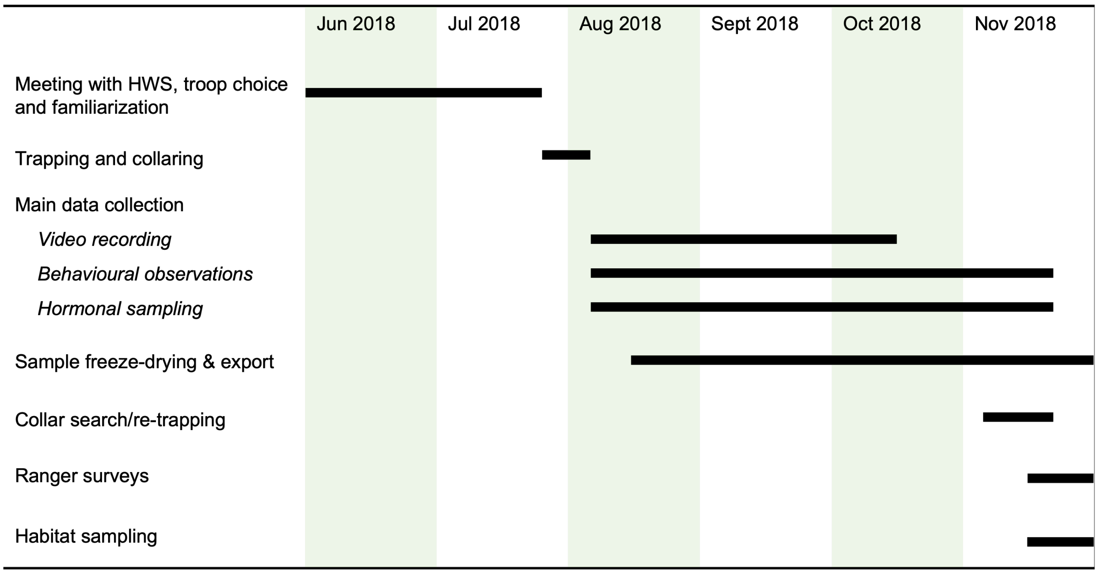

Figure II-2. Timeline of field season.

STUDY AREA AND SUBJECTS

Today, there are 16 baboon troops on the Cape Peninsula, nine of which are managed by the current service provider (Urban Baboon Programme, NCC), one of which is only monitored on road, and five of which are unmanaged (the latter troops are located in Cape Point Nature Reserve) (Justin O’Riain, personal communication). In 2018 (when the field season was conducted), the then contracted service provider for management of the baboons (Human Wildlife Solutions) reported a total population of 463 baboons (mean ± SD individuals/troop: 46 ± 28, Fig. II-3) in 11 managed troops on the Cape Peninsula (two of which were a result of a fission of a larger troop) (Richardson, 2018a, 2018b). Though all baboons come into contact with humans, the frequency with which they do this differs across troops, with some inhabiting residential areas and others more tourist-dominated areas (Hoffman & O'Riain, 2011). I studied the "Da Gama Troop" (-34.161, 18.403) which inhabits urban space and comes into daily contact with humans (the troop frequently sleeps in the urban space on top of a block of flats: Fig. II-4c). The Da Gama troop were chosen as they were habituated to close observation (historically, the troop were used to take the public on 'walking tours' with baboons: Thomas, 2011), allowing direct behavioural observations and reducing the potential for any adverse effects of observer presence (since habituation of primates by field researchers can lead to increased human-primate conflict with local communities: Bezanson & McNamara, 2019; Riley & Bezanson, 2018). Moreover, Human Wildlife Solutions put forward the Da Gama troop as having the highest probable success rate for collaring multiple individuals, which was important as we wanted to deploy tracking collars on as many adults as possible to get a representation of whole troop movement. The Da Gama troop also frequently used urban space, which was important for the questions I wanted to address in my PhD. Additionally, on a practical note, the terrain across the baboon's home range was accessible and safe to traverse (unlike other Cape Peninsula troops) and encompassed large flat rocky outcrops which facilitated sample collection; in particular of urine samples which easily pooled into rock hollows. Frequent sample collection was important to address questions regarding changes in hormonal state, which were primarily used by the other PhD student on the project (Charlotte Christensen), but were also used in my first data chapter.

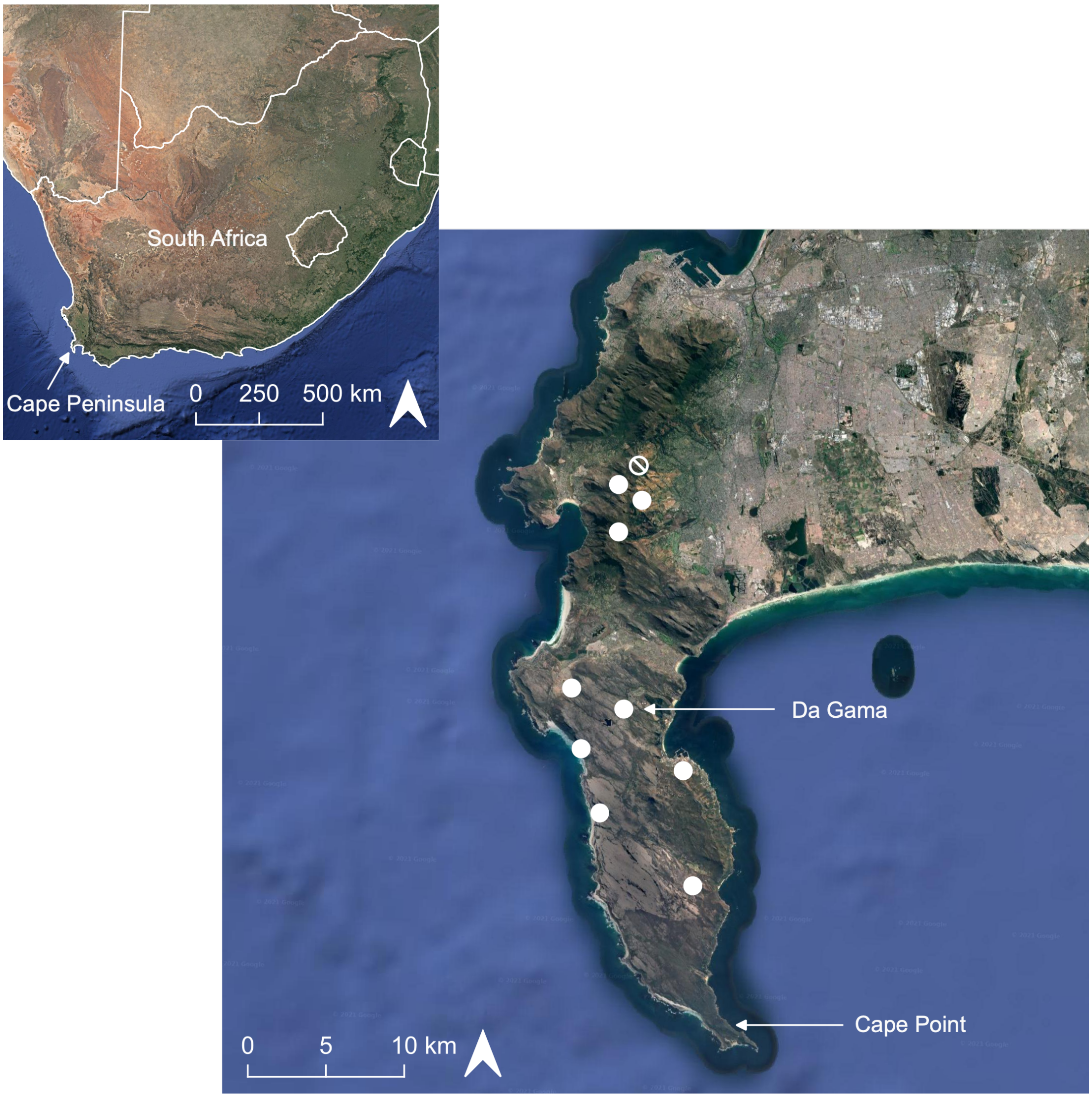

Figure II-3. Location of managed baboon troops (as of 2018) on the Cape Peninsula. The studied troop (Da Gama) is indicated. The circle with a dashed line indicates a troop that fissioned into two (the Constantia troop). Inset: the location of the Cape Peninsula in South Africa (-34.161, 18.403).

The Da Gama troop comprised 2 adult males, 19 adult females, 2 sub adult males, 3 sub adult females and approximately 25 juveniles of both sexes. During the study period, the beta male (M2) was competing for alpha status. This resulted in frequent chases and fights between both males, and several (sometimes successful) infanticide attempts. The troop ranges over both urban and natural spaces. The urban space covers the suburbs of Da Gama Park and Welcome Glen on the Cape Peninsula, which differ considerably in their social demographic: Da Gama Park comprises a complex of low-income housing for naval officers, whilst Welcome Glen is a middle-to-high-income suburb. Additionally, the town of Da Gama is split between the main housing matrix and an area of high-rise flats, on top of which the troop has a main sleeping site (Fig. II-4c). The Da Gama troop natural space is bordered on all sides by urban areas and is dissected partially by a main tarmacked road (Fig II-4b). It encompasses two dams, a water-works facility, and private homes, and is a popular spot for hikers, containing a variety of walking trails. The Da Gama troop's home range has a distinctive border between urban and natural space, facilitating analyses in this study.

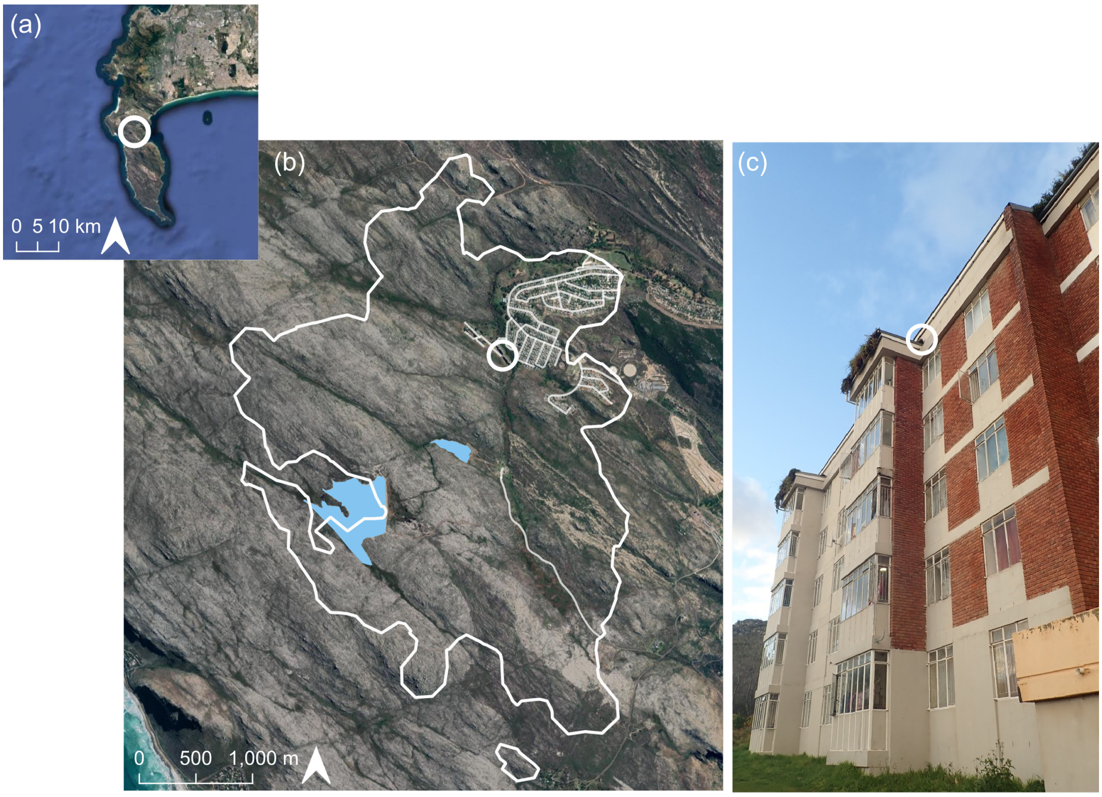

Figure II-4. Da Gama troop home range. (a) Position of home range (circled) on the Cape Peninsula; (b) 95% troop home range (outer white line) and position of the residential sleep-site (circled); (c) image of the troop's residential sleep-site (with a baboon circled on the roof). Main tarmacked roads are indicated by fine white lines in (b).

BABOON MANAGEMENT

The Da Gama troop was continually herded throughout its range by a team of up to six rangers from the City of Cape Town’s service provider in 2018: Human Wildlife Solutions. The remit of the rangers is to keep the baboons out of urban spaces and away from human activity. They do this using a variety of methods, from shouts, claps and whistles to the use of paintball marker guns (van Doorn & O'Riain, 2020). The team arrives at the baboon sleep-site before dawn and leaves at dusk; in the winter this is between approximately 7am to 5pm. The team alternates every four days with another team of six rangers and, unlike other troops on the Cape (which are designated an area manager according to ‘region’, so that a single area manager oversees the management of several troops), there is a single person dedicated to overseeing the management of the Da Gama troop. This is most likely because of the high levels of contact that the troop has with humans; along with being continually managed, the troop is often in the vicinity of people.

BABOON COLLARING

Collar development and deployment

GPS data from individual tracking collars constituted the underlying dataset in this thesis. 20 tracking collars were developed in-house in Swansea University and were a more recent model of those developed by Fehlmann et al., (2017c). I built the tracking collars with Charlotte Christensen, Gaëlle Fehlmann and Phil Hopkins, with help from Mark Holton, and overseen by Andrew King and Ines Fürtbauer. Francesca Marshall-Stochmal documented the collar-build process.

Tracking collars contained two main sensors: GPS units (Gipsy-5, Technosmart) and daily diary tags (Wildbyte Technologies, Swansea University). GPS units sat in a 3-D printed housing at the top of each collar (located on the back of the baboons’ necks to facilitate connectivity to satellites) and the daily diary was in a 3-D printed housing at the bottom of the collar, alongside a single D-cell battery (Fig. II-5). This battery powered both units, connected through a switch and wires running up the length of the collar. All circuit units (GPS, daily diary, battery and switch) were encased in heat-shrink plastic to reduce water infiltration. Collars also included a drop-off mechanism (CR-7, Telonics Inc.) to reduce the need for recapture. Leather straps were constructed by a local saddler (Gwenda Kesans) and had an inner layer of soft leather to protect the wiring leading to the GPS unit, as well as enhancing comfort for the baboons. To secure the leather in place and to create an additional waterproof layer the collars were taped using Gorilla tape. Different colour combinations of electrical tape were used to individually ID each baboon. Tracking collars weighed less than 2.5% of the body mass of all baboons and were approved for use by Swansea University Ethics Committee (Swansea University IP-1314-S), local authorities and the Baboon Technical Team (BTT, in Cape Town).

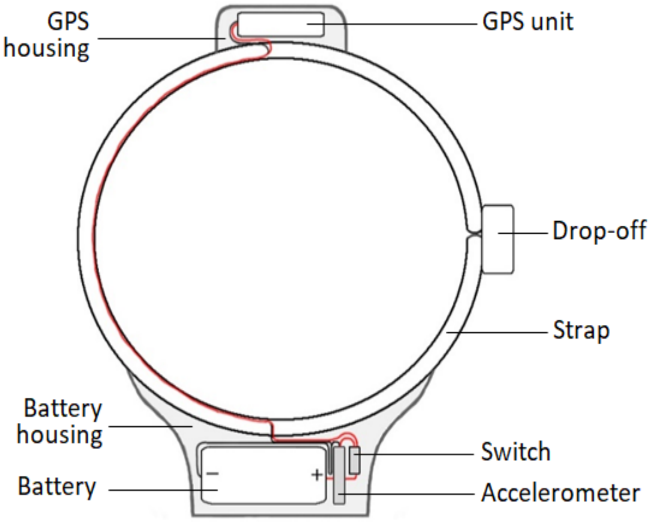

Figure II-5. Schematic of a SHOAL group F2HKv3 collar. As published in McCann et al., (2021). The circuit of the collar consists of a battery unit, switch, accelerometer (Daily Diary, Wildbyte Technologies) and GPS unit (Gipsy-5, Technosmart), connected together by red (positive) and black (negative) wires. Main components (battery, switch, accelerometer and GPS-unit) and soldered wire connections are encased in plastic heat-shrink (with a shrink ratio of 4:1 and adhesive lining on inner surface) to reduce water infiltration. Main components are held in 3D printed plastic housings, which are attached to a leather strap; wires run up the collar under a soft inner leather lining (which is sewn and glued to the main leather strap, encasing the wires). Collars are fitted to size for each baboon, and open collar ends are secured with a drop-off mechanism (CR-7, Telonics Inc.), programmed to release automatically on 16th October 2018.

Prior to deployment, the troop was provisioned with fruit, vegetables and corn in the baboons' home range to attract them to an area and to accustom them to cages. After capture, baboons were anesthetised by a local veterinarian and collars were fitted. We aimed to collar the maximum number of adult baboons in the troop. However, females with young infants were not collared and one adult female that was trapped was considered too small for the collars. Therefore, of the 20 tracking collars built, 16 were deployed on adult baboons

(2 males, 14 females). Of these, 13 recorded GPS and 13 recorded daily diary data (10 of which recorded both). Tri-axial accelerometers and magnetometers in daily diary tags recorded baboon speed, behaviour and cardinal direction continuously at 40Hz. Collars were calibrated in the field before deployment to give a reference point for this data. The acceleration dataset has been used by Charlotte Christensen to identify baboon grooming behaviour (Christensen, 2022). GPS units recorded position at 1 fix/second between 08:00 – 20:00 local time (06:00 – 18:00 UTC). The GPS dataset used in this thesis is presented in Fig. II-6.

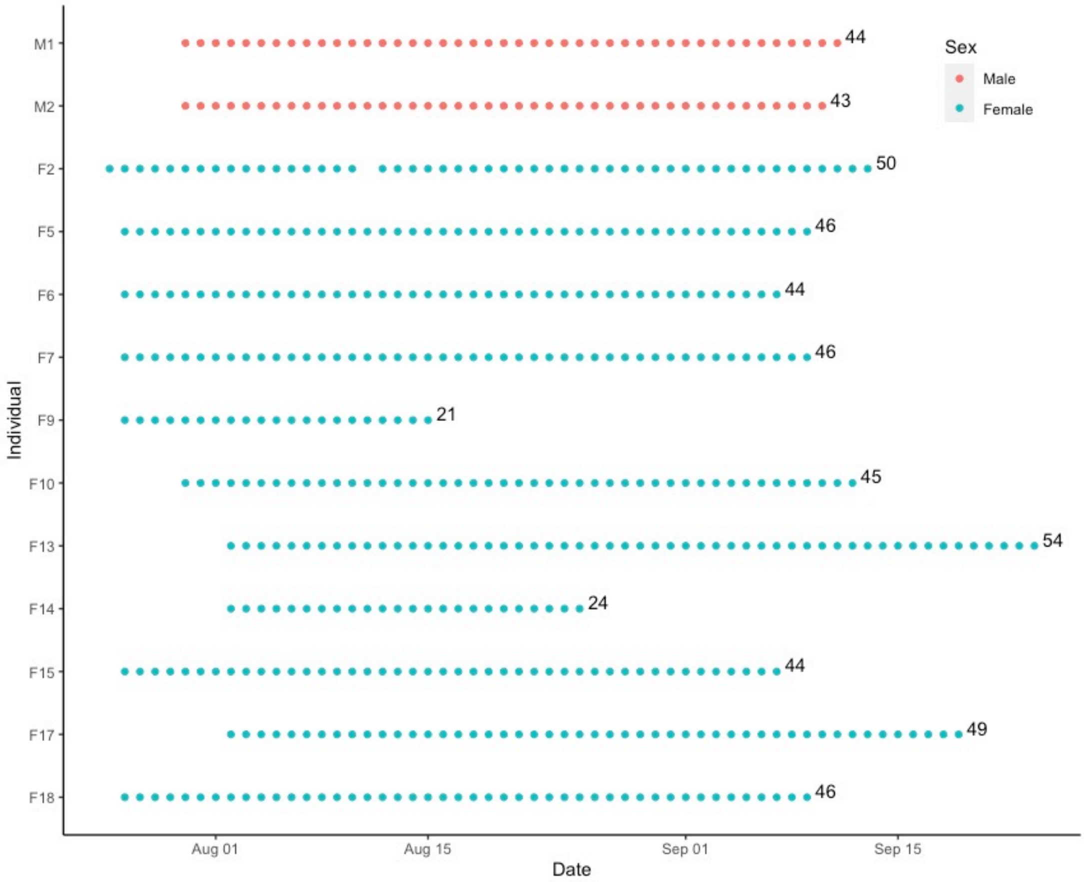

Figure II-6. Length of time GPS was recording for each individual baboon (n = 13). Males are indicated in red, and females in blue. Number of recorded days are included to the right of each individual's recording period. F2 missed GPS data for one day in August.

Since GPS units were programmed to turn off each day at 20:00 pm local time, the last two hours of recorded GPS data (18:00 – 20:00) for each day were mainly taken when the troop were at their urban sleep-site (for 52/61 days, the baboons slept within the urban space, often on top of an apartment block: Fig. II-4c). This resulted in a large proportion of urban space GPS fixes being taken during these “inactive” times (Fig. II-7). Therefore, analyses in this thesis are conducted using a reduced dataset (between 08:00 – 18:00 local time), so as to get a clear representation of urban space-use during active “daytime” hours.

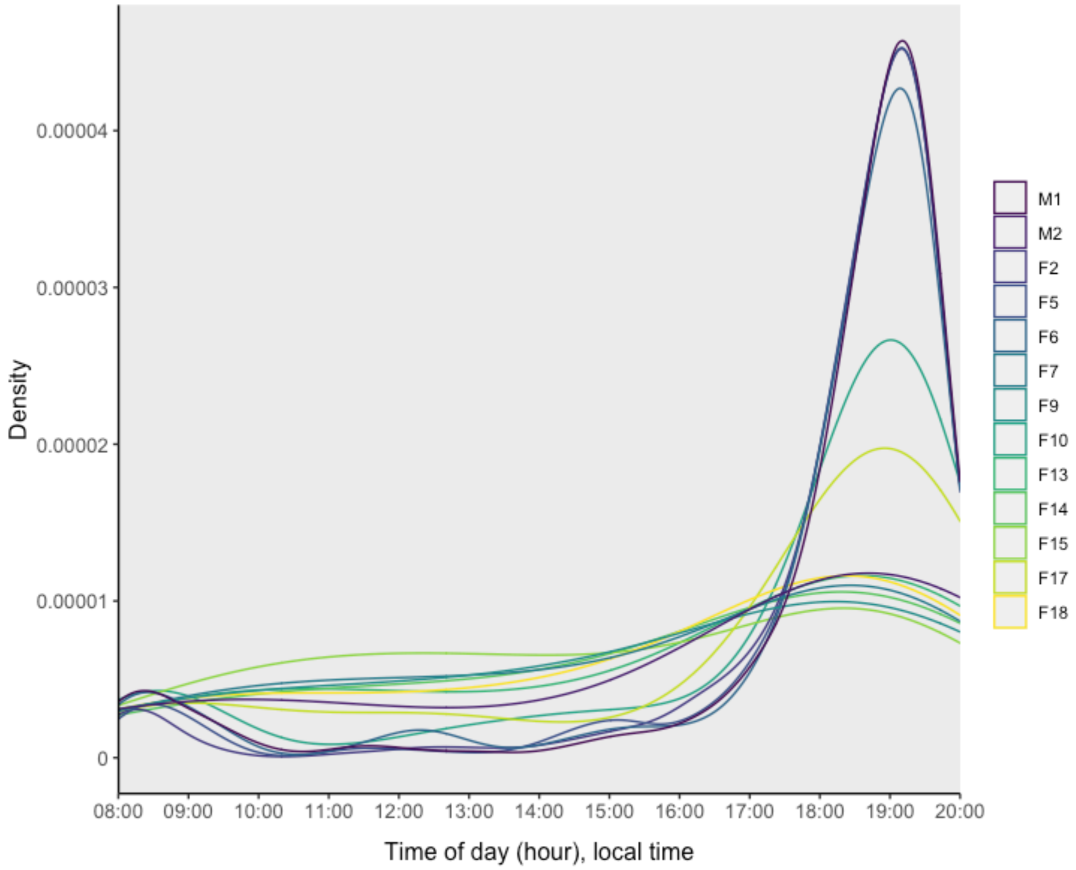

Figure II-7. Density histogram showing the time spent by the baboons within the defined urban polygon (See Fig. III-2, Chapter 3), for n = 13 collared individuals.

BEHAVIOURAL OBSERVATIONS

Baboons were habituated to close human observation and could be followed on foot by up to 4 human observers without any visible effect on their behaviour or movement (Fig. II-8). The troop were followed for 6 days each week, resulting in 78 days of troop follows. Observational sampling consisted of a combination of scan, focal, social ad lib, herding and video-recording data. Scan samples were taken at 30-min intervals, in which activity and proximity to other individuals (within 5 m) were recorded for each adult baboon, as well as ranger presence and behaviour, and habitat type. Troop location was recorded using handheld GPS units (eTrex 10, Garmin Ltd, Olathe, Kansas, USA) with every scan.

To generate activity budgets and interaction data, 30-min focal observations were conducted for each of the 16 collared baboons (focal minutes: n = 14277, mean ± SD per baboon = 892.3 ± 134.3). Instantaneous behaviour was recorded at one-minute intervals (classified as resting, social, feeding, foraging or traveling) as well as continuous data on social interactions, proximity to other baboons (at 5-min intervals) and ranger behaviour (at 5-min intervals). Social data was recorded *ad libitum* when aggressive, socio-positive and displacement activities were observed. Urban-foraging behaviour was recorded *ad libitum* when an event was observed, and included information on risks (threats from residents, dogs, management) and rewards (location and food item) and was stamped with a GPS location. Additionally, in order to capture herding tactics and efficiency, data was recorded *ad libitum* when the rangers started herding the baboons and included information on number of rangers and the method used. *Ad libitum* observations of aggressive interactions (displacements, chases and aggressive displays) were used in this thesis to calculate the dominance hierarchy.

Figure II-8. Direct behavioural observations.

ENVIRONMENTAL DATA

Field ranger survey data

Information on ranger ‘strategy’ was collected using surveys, mirroring the method used in Fehlmann et al., (2017b), in which ‘strategy’ was assessed as the likelihood of herding baboons from a specific area. Two maps were presented to each field ranger (n = 12) of the troops’ 1) entire home range (Fig II-9a) and 2) the urban space (Fig. II-9b). Maps were constructed in QGIS (QGIS.org, 2020). Rangers were given three coloured highlighters and were asked to colour in the areas in which the baboons were allowed to stay: 1) at any time (green), 2) some of the time (orange) and 3) never (red). Surveys were anonymous and were undertaken with permission from both the rangers and their employers, and the Swansea College of Science Ethics Committee.

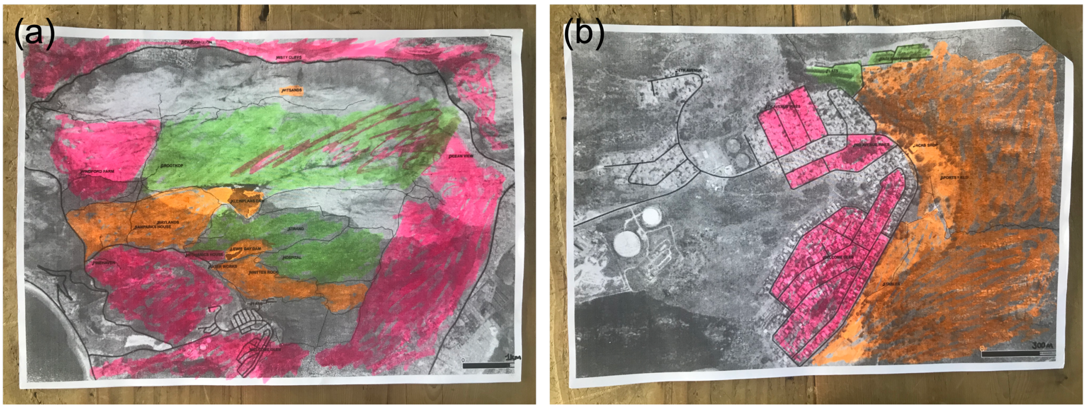

Figure II-9: Example of a coloured ranger map for: (a) home range and (b) urban space.

Habitat data

In order to map food availability and potential energy returns, a survey of the vegetation was taken using 85 random quadrats of 1 m² (n = 255) (Fig. II-10) for each of three habitat types, across an area of 25 km². The area sampled was estimated using a minimum convex polygon method, which was calculated in QGIS using handheld GPS locations recorded throughout the main study period. The three habitat types ('urban', 'mixed' and 'fynbos') were defined from maps constructed in QGIS and from observer knowledge of the study site. In each quadrat, we reported the presence of each baboon food type (plant species that the baboons had been observed eating), distribution of this species across the quadrat, and its abundance.

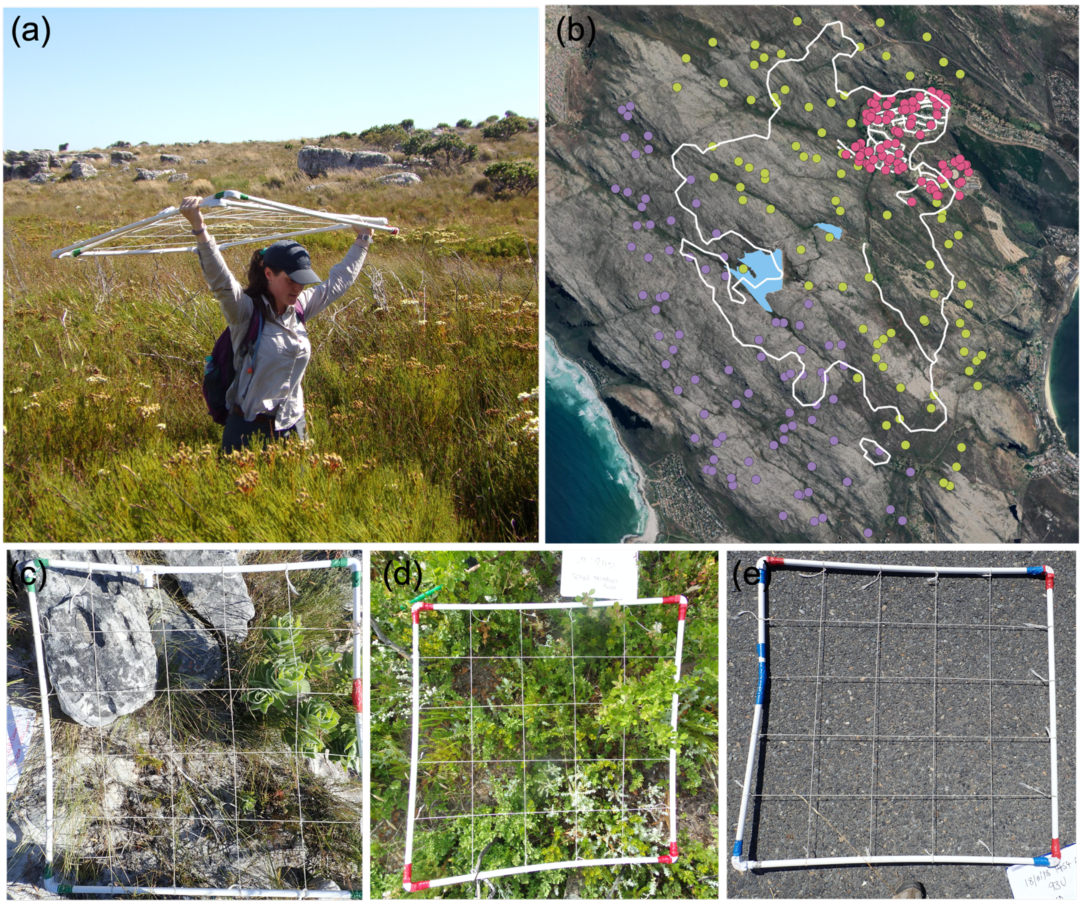

Figure II-10: Habitat sampling. (a) Carrying a quadrat through dense vegetation; (b) representation of 85 sampling points in each of 'fynbos' (purple), 'mixed' (yellow) and 'urban' (pink) habitats (c) quadrat taken in 'fynbos' habitat; (d) quadrat taken in 'mixed' habitat; (e) quadrat taken in 'urban' habitat.

HORMONAL DATA

In order to investigate individual energetic state and physiological stress levels, faecal (n = 318) and urine (n = 385) samples were collected opportunistically (Fig. II-11) when following the study troop. Faecal and urine samples both contain excreted glucocorticoids, but these show up at different time lags (Chen et al., 2017), with cortisol showing up between 24-48 hours in faeces and up to 24 hours in urine. C-peptide concentration of urine was also measured, which is a marker of insulin and indicative of individual energetic state (Thompson et al., 2009). Faecal samples were homogenised in the field, put into secure lock pots, labelled and kept on ice for the remainder of the field day. Urine was collected either by pipetting the sample directly from the substrate or by using ‘Salivette’ cotton swabs. A refractometer reading (measuring urine concentration) was taken if the sample was large enough.

Samples were processed at the research house at the end of each field day. Faecal samples were re-labelled with freeze-proof labels and sample information was recorded. Urine samples were split, if the sample was large enough, and pipetted into two separate Eppendorf tubes to use for both cortisol and c-peptide analysis and labelled accordingly. Both sample types were then frozen at -20°C at the research house until further processing. Faecal samples were freeze-dried at University of Cape Town before samples were exported back to Swansea University. Further information on faecal and urine cortisol analysis is included in Christensen et al., (2022) and urine c-peptide analysis in Fürtbauer et al., (2020).

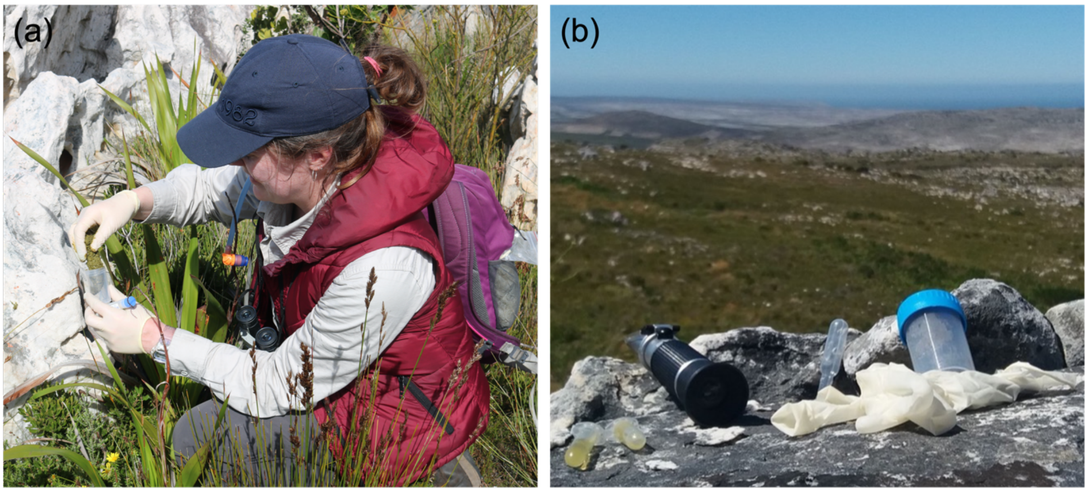

Figure II-11: Sample collection. (a) Collection of a faecal sample; (b) left to right: urine samples, refractometer, pipette, protective gloves and faecal sample.

Chapter Three

Sociality and risk shape inter-individual variation in urban space-use by chacma baboons

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Statement of contributions:

AB and AJK designed the study. AB and CC conducted and led the field work. IF analysed hormonal samples in the lab. AB compiled data and conducted analyses with advice from AJK and IF. AB wrote the chapter with advice from AJK and IF.

Parts of this work formed the following publication:

Bracken, A. M., Christensen, C., O'Riain, M. J., Fehlmann, G., Holton, M. D., Hopkins, P. W., Fürtbauer, I. & King, A. J. 2021. Socioecology explains individual variation in urban space use in response to management in Cape chacma baboons (*Papio ursinus*). *International Journal of Primatology*, 1-18

A reprint of the publication is available at the end of the thesis

ABSTRACT

As human populations expand, so does the demand for space, with urban centres sprawling into natural habitats. In response, a number of animal species are using urban spaces, which increases human-wildlife contacts; often with negative consequences. Understanding the predictors of urban space-use by animals is therefore important; however, though much work has identified the species-level traits common to urban-dwellers, less research has looked at commonalities at an individual level. I investigated the individual-level predictors of time spent in urban space for n = 13 baboons (*Papio ursinus*) living on the urban edge in Cape Town, South Africa, using high resolution tracking collars (recording 1Hz GPS), behavioural observations and hormonal data. Here, I show that all adults use the urban space, but that it is a risky strategy, with female baboons tending to not use urban spaces when they have vulnerable offspring and using urban spaces with close affiliates (perhaps to buffer the associated risk). I discuss the implications of these results in the context of current and future management practices of the Cape baboons.

INTRODUCTION

With increasing expansion of human populations around the globe, wildlife species must adapt to human-altered landscapes or risk going extinct (Lowry et al., 2013). Human activities have transformed the physical landscape through deforestation, the conversion of wild land to agriculture, and through urbanisation (Sih et al., 2011). This transformation reduces and fragments habitats and is the primary driving force of biological diversity loss worldwide (Vitousek et al., 1997). Urban areas are growing in size and structure (Alberti et al., 2003), are built solely for humans, and attract the same "urban-adaptable" wildlife species, therefore becoming biologically and ecologically homogenous (McKinney, 2006).

Key to the success of urban species is their ability to adapt their behaviour to human-altered landscapes (Chapman et al., 2012; Lowry et al., 2013; Sih et al., 2011). Since modification of behaviours can potentially improve an organism's prospects of surviving and reproducing in a changing world (Lima, 2009), flexibility in behaviour allows species to occupy a wider niche and to have greater success in colonising novel environments (Sol et al., 2002). For example, stone martens (*Martes foina*) have adjusted to urban habitats by denning in inhabited buildings, using insulation material for nesting (Herr et al., 2010) and common European bird species have adapted flight distances to road speed limits – maximising foraging time whilst reducing risk of collision and vehicle-induced mortality (Legagneux & Ducatez, 2013). Chacma baboons living on the urban edge adaptively modify their space-use, minimizing their distances to refuges and potential food rewards, to reduce human-baboon conflicts and maximise opportunities for acquiring high calorie human food and food waste (Fehlmann et al., 2017a; Fehlmann et al., 2017b). Improved nutrition derived from human foods can result in higher reproductive rates, potentially increasing population sizes substantially (Ditchkoff et al., 2006).

Given the increasing number of species that are living in urban spaces (Poveda and Sánchez-Palomino, 2004, Strohbach et al., 2009, Saunders et al., 1993) understanding the commonalities between these urban-adapted species is important for their conservation and management in the wild. Much research has identified the species-level traits that are common to these urban-dwellers (Kark et al., 2007). Urban species tend to be social (Kark et al., 2007), have a wide habitat tolerance (Bonier et al., 2007; Ducatez et al., 2015) and generalist diet (McKinney, 2002), are intelligent (Sol et al., 2005) and are adaptable (or 'behaviourally flexible': Lowry et al., 2013). In the case of sociality, being in a group allows easy communication of food sources in a patchy environment, provides a buffer against predators, and improves competition with other species for food (Kark et al., 2007). Tolerance to a variety of habitats and diets makes it easier for urban-dwellers to exploit novel human resources (Kristan III et al., 2004, Bateman and Fleming, 2012). In terms of intelligence, larger brain sizes have been associated with successful invasion of urban spaces by bird species (Sol et al., 2005), and with higher rates of behavioural flexibility, tool use and innovation in primate species (Reader & Laland, 2002). Finally, behavioural flexibility (an animal's ability to respond and adjust behaviour to changing environmental conditions (Papp et al., 2015) has been identified as an important modification for urban space-use (Proppe et al., 2011, Lowry et al., 2013). Adopting new feeding techniques and feeding on novel food items (Kark et al., 2007), as well as demonstrating greater problem-solving skills in new environments (Lowry et al., 2013), allows species to adjust to new conditions.

As well as adapting to changing landscapes, intelligent, social, and behaviourally flexible generalist species also tend to be better able to cope with variability in environmental risk (Fehlmann et al., 2017a; Sih et al., 2011; Slabbekoorn & Peet, 2003). Risk is an important selective pressure that constrains the life history and reproductive success of species (Ricklefs & Wikelski, 2002), commonly seen through predation, but more frequently as a result of human influence (van Kleunen & Richardson, 2007). For example, cougars (*Puma concolor*) use of human-altered landscapes substantially increases mortality risk, with every 10% increase in housing density increasing cougar mortality risk by 6.5% due to a combination of vehicle collisions, hunting and direct removal (Moss et al., 2016). However, high risks associated with frequenting urban space can be offset by the high-quality food rewards that are usually the attractants to human-altered landscapes (Kaplan et al., 2011), which can improve physical condition (Otali & Gilchrist, 2004; Strum, 1994), reduce inter-birth intervals (Strum, 2010), and reduce levels of stress hormones (Dantzer et al., 2011, Stabach et al., 2015, Pokharel et al., 2018). Individuals choosing to exploit urban space will therefore do so (via selection not rational decision-making) when the benefits outweigh the risks.

The way in which the risks and rewards associated with urban space shapes the decision-making and behaviour at the level of the individual has received much less study. However, it is expected that risks and rewards of foraging in urban space will vary according to an individual's phenotype (Lowry et al., 2013; Merrick & Koprowski, 2017). For example, due to differences in energy requirements and fitness expectations, certain individuals may be predisposed to take more risks for greater rewards (Wolf et al., 2007) and such "risk-taking" behaviour can be viewed as a "high-cost, high-return" strategy (Habig et al., 2017). Sex differences are a good example of this, with males more commonly observed to use human-altered landscapes, and display high-risk but potentially high-return behaviours compared to females (Merkle et al., 2013; Riley et al., 2003). This is especially the case in sexually dimorphic species with high levels of male-male competition for resources and reproduction (Chiyo et al., 2011). For instance, male elephants (*Loxodonta africana*) experience a peak in reproduction at 45 years of age, resulting in increased mate-guarding behaviour which in turn requires more energy and results in increased crop-foraging behaviour (Chiyo et al., 2012). There can therefore be considerable fitness benefits associated with high levels of exploratory behaviour and achieving greater than average foraging success in such systems (Sol et al., 2013), since males tend to experience greater variance in reproductive success than females (Breuer et al., 2010; Setchell et al., 2005). However, assessing inter-individual variability in urban space-use is challenging since it requires researchers to track the behaviour and movements of many individuals simultaneously (King et al., 2018), and this is made harder by the ‘cryptic’ behaviours individuals adopt in urban space (Fitzgibbon et al., 2011).

With the advent of bio-logging technologies (Fehlmann & King, 2016) it is now possible for scientists to track the position and behaviours of multiple individuals synchronously (Hughey et al., 2018; Stanley et al., 2012). This affords an opportunity to address fundamental questions about wild animals, to understand cryptic behaviour or to test new theories (Wilmers et al., 2015). For example, miniature tracking devices can record an individual’s GPS location to within a 5 m accuracy (Wilmers et al., 2015), uncovering indirect information on an animal’s behaviour, ecology and social interactions (Rutz & Hays, 2009). In urban species, the ability to record an animal’s location and behaviour can open many doors in understanding responses to human-altered landscapes (Fehlmann et al., 2017b; Merkle et al., 2013). For example the use of GPS loggers has shown both habitat connectivity and quality affect the movement of European hedgehogs (*Erinaceus europaeus*) in fragmented urban spaces (Braaker et al., 2014), and that baboons adaptively use their space to enhance the rewards and minimise the risks of urban foraging (Fehlmann et al., 2017b). Here, we attempt to explain inter-individual variation in urban space-use by a troop of baboons living at the urban edge in Cape Town, South Africa.

In Cape Town, ten troops of baboons live in spatial overlap with humans (Fehlmann et al., 2017b; Hoffman & O'Riain, 2012a). The lack of a buffer area between Table Mountain National Park and the city of Cape Town, and an absence of by-laws to effectively police people’s behaviour, has resulted in baboons exploiting urban space: foraging from rubbish bins, fruiting trees, residential and commercial properties, and even taking food from people

(Fehlmann et al., 2017b; Kaplan et al., 2011; van Doorn & O'Riain, 2020). Indeed, baboons possess all the necessary attributes to make them adept at urban-foraging behaviour: fast learning ability, dexterity, behavioural, social and dietary flexibility, terrestriality, and broad habitat tolerance (Hoffman & O'Riain, 2012c; Warren, 2009). In two related studies on the Cape Peninsula “Constantia troop”, adult male urban-foraging baboons adopted a “sit-and-wait strategy”, spending almost all of their time at the urban edge and then undertaking fast, high-activity forays into the urban space (Fehlmann et al., 2017a; Fehlmann et al., 2017b). These “sit-and-wait” tactics are adopted in order to mitigate risk – the urban space is more energetically demanding to move through (Nickel et al., 2021), increases the likelihood of being deterred by humans (Fehlmann et al., 2017a; Kaplan et al., 2011), and results in direct negative interactions between humans and baboons (Beamish, 2009). Indeed, 15% of the Cape baboon population that overlap with residential areas have permanent disabilities, such as loss of a limb, caused by human-induced injuries (e.g., shootings, domestic dog bites, vehicle accidents, electrocution: Beamish & O’Riain, 2014). But the reward for baboon urban-foraging is great: baboons foraging in urban space can gain access to foods that have a potential energy intake ~ 10 times greater than in natural environments (Fehlmann et al., 2017a), and elsewhere in the species range crop-foraging baboons potentially damage up to 2774m² of crops per event (Naughton-Treves, 1998), with crops comprising up to 58% of their diet in some areas (Strum, 2010).

Given that (i) previous work on the Cape baboons has shown that not all individuals use the urban space equally (Fehlmann et al., 2017a), and (ii) the risks and rewards of foraging in urban space is expected to vary according to an individual’s phenotype (Maibeche et al., 2015; Marty et al., 2019; Merkle et al., 2013) I hypothesised that inter-individual variation in urban space-use in chacma baboons living at the urban edge in Cape Town should be explained by the variation in potential risk and rewards for different baboon phenotypes. First, I predicted that males would spend more time in the urban space than females (prediction 1) since males are more likely to take risks (Reader &

Laland, 2001), and urban space-use has been attributed to them in a number of species (Chiyo et al., 2012; Merkle et al., 2013). However, management reports at the time (Richardson, 2018a, 2018b) and preliminary observations made it clear that both males and females frequented the urban space – in subgroups that vary in size and composition, and which temporarily fission from the main troop. This was unexpected but may be explained by a lack of natural predators on the Cape Peninsula (Skead, 1980) and therefore reduced risk for females when fissioning from the main troop. I therefore tested further predictions regarding variation in urban space-use related to risk in females, and the effect of social ties within the troop.

In the case of female risk, I predicted that low-ranking females would use the urban space more frequently than high-ranking females (prediction 2) on the basis that they are more likely to engage in "innovative" and risky behaviours (Reader & Laland, 2001), are more likely to "produce" foraging information (King et al., 2009a) and have been shown to experience lower average daily food intakes than high-ranking females, ultimately having lower reproductive success (Barton & Whiten, 1993). I also predicted that females without infants would use the urban space more frequently (prediction 3). I made this prediction since female baboons invest heavily in parental care (Johnson, 2003), and infants require protection from predation and infanticide (Cheney et al., 2006; Engh et al., 2006). It therefore follows that female baboons would protect infants from risks associated with fissioning from the troop to use urban space.

Regarding the social aspects of urban space-use, baboons have directed social networks, with certain individuals (usually higher-ranking) being more socially integrated in the troop (Silk et al., 2010b). These socially integrated, high-ranked individuals are more likely to initiate group movements to high-quality food resources (King et al. 2008) and attract a more enthusiastic following from troop members (King et al., 2011b). I therefore expected that baboons would be more likely to spend time in urban space if their close affiliates do so (prediction 4). Conversely, less socially-integrated individuals in the network may be more likely to fission (Furuya, 1969), which could give these peripheral individuals incentive to use the urban space (i.e. less pull to the troop, more pull towards the urban resources) and so I also tested whether individuals with a low centrality in the troop's social network would spend more time in the urban space (prediction 5).

In addition, I aimed to identify the underlying physiological mechanisms driving urban space-use, namely identifying how energetic state differs between individuals. Energetic state is a key driver of an individual's behaviour, physiology and life history, and has been shown to differ between individuals (Emery Thompson & Knott, 2008). It can be measured regularly and non-invasively (Emery Thompson and Knott, 2008) through the use of urinary C-peptide (UCP), which is a biomarker for insulin production (that regulates glucose levels) (Thompson et al., 2009). UCP is produced on an equimolar basis to insulin, and therefore provides a reliable estimate of insulin levels. Having access to superior foods may result in higher reproductive outputs (Lodge et al., 2013; Thompson et al., 2007). Also, in baboon troops, foraging opportunities are not balanced equally between individuals (King et al., 2009a). Therefore, I predicted that individuals with a lower energetic state (lower C-peptide levels) may be more inclined to spend time in the urban space (prediction 6), as the draw for high energy food resources to mediate energetic stress would be greater.

METHODS

Study Site and Subjects

I studied the 'Da Gama troop', named after the town 'Da Gama Park' area of Cape Town (Fig. III-1). The troop was comprised of 2 adult males, 19 adult females, 2 subadult males, 3 subadult females and approximately 25 juveniles of both sexes. The troop's range spans from urban space to natural space, mostly made up of a mix of fynbos and alien vegetation (Hoffman, 2011; van

Doorn & O'Riain, 2020; van Doorn et al., 2010). The urban space encompasses two residential suburbs: Da Gama and Welcome Glen. The town of Da Gama is split between the main housing matrix and an area of high-rise flats, on top of which the troop have a main sleeping site (Fig. II-4, Methods). I studied the troop from July to November 2018, which covered the winter season in Cape Town, when the Cape baboons are known to use urban space more often (van Doorn et al., 2010).

To test my predictions, I first determined basic descriptive statistics of the urban space-use of each baboon and quantified the individual-level traits of the baboons. To do this I used data from 13 custom-built tracking collars, direct observations, and hormonal measures. The methods for each are described below.

Figure III-1. Location of Da Gama Park (-34.161, 18.403) on the Cape Peninsula, South Africa.

Baboon collaring

To obtain information on urban space-use patterns I fitted n = 16 individuals (Table III-1) with GPS-enabled (GiPSy 5 tags, TechnoSmArt, Italy) tracking collars (Fehlmann et al., 2017c). GPS was recorded at 1 fix/ second between 06:00 am - 18:00 pm UTC (08:00 am - 20:00 pm local time). I use a reduced subset of baboon “daytime” hours (08:00 – 18:00 pm local time; Fig. II-7, Methods). Data from 15 collars were retrieved. One collar was not found after release (Collar No. 3; Table III-1) and two collars GPS failed to record data, providing GPS trajectories for n = 13 baboons for a mean average of 42.77 ± 9.92 days, range = 21 - 54 days (Table III-1; Fig. II-6, Methods). GPS receivers used in this study calculate standalone horizontal position to a few meters, but in practice this error depends on 1) satellites available, 2) how the collar was positioned on the baboon at any time point, and 3) the immediate environment surrounding the collared individual. Ad-hoc checks of the GPS data from a known landmark (Fehlmann et al., 2017a, both at the field site in Cape Town and from test walks conducted in Swansea, UK) indicate positional accuracy as within 5 m. Data from n = 13 baboons represented 61% of all adults in the troop.

Table III-1. Details of the collar recording period for each individual.

Col No.	Individual	GPS Start	GPS End	Total duration (days)
1	M1	30-07-2018	11-09-2018	44
2	M2	30-07-2018	10-09-2018	43
3	F1			
4	F2	25-07-2018	13-09-2018	50
5	F4			
6	F5	26-07-2018	09-09-2018	46
7	F6	26-07-2018	07-09-2018	44
8	F7	26-07-2018	09-09-2018	46
9	F9	26-07-2018	15-08-2018	21
10	F10	30-07-2018	12-09-2018	45
11	F13	02-08-2018	24-09-2018	54
12	F14	02-08-2018	25-08-2018	24
13	F15	26-07-2018	07-09-2018	44
14	F17	02-08-2018	19-09-2018	49
15	F18	26-07-2018	09-09-2018	46
16	F19			

GPS data and processing

All processing and analysis of GPS data was undertaken in R (version 3.6). Extreme outliers were removed by restricting the coordinates to within that of the study site (Latitude: > -34.20°, < -30.00°; Longitude: > 18.00°, < 18.45°), resulting in a median average 0.01% of GPS fixes being removed (range 0.00% - 0.1%; Table III-2). Next, the data were searched to identify successive time points which it would have been impossible for the baboons to travel between, i.e. they would have travelled too quickly or made an especially large turn that would not be possible over successive 1-second GPS fixes. I used two functions as described in Bjørneraas et al., (2010) for this purpose.

The first function identifies outliers as being above a pre-determined distance threshold to the x and y coordinates of the mean and median in a moving window of 10 GPS fixes (here mean and median were set at 250 m), and the second function looks for "spikes" caused by a high outgoing and/or incoming speed (here threshold set at 10 m/s) and sharp turning angle (sharper than a predefined threshold: here cosine of turning angle set at $\theta = -0.95$). The second function is contingent on both the speed and turning angle being over the pre-set parameters, and so I implemented additional criteria just looking at the speed: specifying the removal of points in which the outgoing and incoming speed to the next and from the previous point was above 20 m/s (a conservative estimate, as it is impossible a baboon will travel 20 m within a second). This resulted in the removal of a median average 0.01% of GPS fixes for each baboon (range 0.00% - 0.02%; Table III-2).

Finally, the raw GPS files also contained missing values, due to the GPS device temporarily losing satellite signal, and this was more common towards the end of the collar battery life. These missing values (and those removed by the first two stages, above) were then replaced by NA or interpolated using the "swaRm" package, R (Garnier, 2016). NA was inserted where data were not available for a given individual for a given second, using the "fixMissing" function. When a sequence of missing values occurred that was less than or equal to 10 seconds long, the "fixLocNA" function in the "swaRm" package was used to linearly interpolate the missing values, resulting in a median average of 252 interpolated points per collar, or median average 0.02% of the final file (range 0.00% - 0.07%; Table III-2). Sequences of missing values longer than 10 seconds were not interpolated following O'Bryan et al., (2019).

Overall, this resulted in a range of 578-165092 seconds of missing data (NA) per collar (Table III-2). Four collars had a disproportionate number of missing values towards the end of the collar deployment (missing data days: 6 ± 1.41 days, range: 4-7 days per collar). I confirmed these collars/days contained the majority of outliers (entire trajectory for n = 4 collars: median average of 1386.5 ± 741.70, range 692-2461 outliers per collar; reduced trajectory (missing data removed) for n = 4 collars: 130.5 ± 36.59, range 85-171 outliers per collar).

Table III-2. GPS screening descriptives for n = 13 baboons.

		Outliers removed			Final file		
Col No.	Ind	Cape coords	Bjørneraas et al., 2010 function	20m/s criteria	No. data points (s)	Interpolated points	NAs
1	M1	2	114	70	1839542	315	9642
2	M2	27	206	93	1801070	716	165092
3	F1						
4	F2	87	297	130	2054655	1372	159284
5	F4						
6	F5	3	126	12	1923079	252	3569
7	F6	4	111	17	1818437	110	578
8	F7	3	76	32	1908662	171	9140
9	F9	0	13	17	836200	140	7235
10	F10	19	103	30	1869581	392	3519
11	F13	36	208	107	2190456	1076	128665
12	F14	2	32	2	989142	6	2362
13	F15	0	86	46	1825903	175	19063
14	F17	30	170	66	2037078	758	67131
15	F18	8	90	65	1900305	240	8452
16	F19						

Urban space-use statistics

All analyses were done in R (version 3.6). The package “Recurse” (Bracis et al., 2018) was used to obtain descriptive statistics (e.g. frequency of visits and duration of visits) of recursions to urban space for each baboon. The urban space was delineated in QGIS (version 2.18) by manually creating a polygon shapefile layer over an ESRI raster satellite image. This polygon is consistent with the space defined by baboon management (Human Wildlife Solutions) and was defined as the area dominated by residential buildings, surfaced roads and people. The urban polygon covered the areas of Welcome Glen, Da Gama and the flats (Fig. III-2).

To obtain statistics on entrance into, exit out of and time spent inside the urban space polygon, I used the function “getRecursionsInPolygon”, “Recurse”. On a number of instances exit times were calculated at times after the GPS had switched off (likely due to the GPS switching on the following day outside the polygon, as the baboons had already left the polygon). These exit times were relabelled to 18:00 pm local time (16:00 pm UTC) on the day of entry, and time inside was recalculated from this. Since this function works on a ‘recursion’ basis – i.e. there may be multiple ‘recursions’ per day, I calculated further statistics for each day of GPS data for each baboon, including daily time inside the polygon, proportion of the day in the polygon and the daily frequency of visits to the polygon, for different urban group sizes.

Figure III-2. Urban polygon (white outline) with areas of Welcome Glen, Da Gama and the flats highlighted.

Individual-level traits of baboons

To test my six predictions I needed to quantify baboon: 1) sex 2) rank 3) presence/absence of an infant 4) eigenvector centrality measure in the social network 5) closest affiliate and 6) c-peptide level. The procedure for these is outlined below (with the exception of sex, which is easy to identify in adult baboons as they show high body dimorphism between the sexes, sex-differences in ischial callosities, prominent canine teeth in males and sexual swellings in the ovulatory females: Smith, 2012).

Baboon hierarchy

Baboon dominance hierarchies were obtained from aggressive interactions (displacement, chases and aggressive displays; Table III-3) that were recorded *ad libitum* during 78 all-day troop follows. Female rank order was determined using the packages “AniDom” and “Compete” in R (Sánchez-Tójar et al., 2018; Schmid & de Vries, 2013), from 634 observed interactions (median = 96, range 11 – 129). Due to a high sampling effort (ratio of interactions to individuals: 33.4, recommended: 10-20), and low sparseness of the data (observed proportion of known dyads: 0.82, which is above that estimated under a Poisson process: mean = 0.57, 2.5% and 97.5% quantiles: 0.40, 0.74), I determined the hierarchy to be very steep (using the randomized Elo-rating method). Additionally, the hierarchy was repeatable (calculated using the function “estimate_uncertainty_by_repeatability” from “aniDom”: score of 0.984) and highly linear (using triangle transitivity to assess ‘orderliness’: McDonald & Shizuka, 2012). The hierarchy was also found to be truly transitive (Ttri = 1, p-value=0), package “Compete” (Schmid & de Vries, 2013). For these reasons I proceeded to determine hierarchy using the I&SI method (which minimizes the number of inconsistencies (I) in a dominance matrix and subsequently minimises the strength of those inconsistences (SI): Schmid & de Vries, 2013). This finds the “best order” of rank which deviates least from linearity and is most appropriate for very steep hierarchies.

Male baboons go through periods of rank instability (Engh et al., 2006) and the two males in the troop were competing with each other for dominance during the study (*pers. obs.*). Based on 75 observations of male-male interactions, male M1 won 28 interactions (37%), male M2 won 16 interactions (21%), with 31 interactions undecided (41%). M1 was therefore ranked first between the two males. All adult males out-rank adult females in chacma baboon troops (Engh et al., 2009; Kitchen et al., 2009). Ranks were standardised between 0 and 1 (with 1 being the highest and 0 the lowest ranking individuals) using the function “rescale” from the “scales” package in R (Wickham, 2014). M1 and

M2 were assigned the same standardised rank as F1 and F2 respectively, to reduce collinearity with between sex and rank in models.

Table III-3. Behaviours used to construct the dominance hierarchy.

Behaviour	Description	Outcome	
Displacement	Spatial or social disruption of a conspecific from an area	Actor is the winner if receiver moves off	Palombit et al., (2001); Ron et al., (1996).
Chase	Running after a conspecific in an aggressive way	Actor is the winner	Kitchen et al., (2003).
Aggressive display	Eyeflash threat, lunging, slapping the ground, ‘openmouth’ display, threat vocalizations	Actor is the winner if receiver moves off	Beehner et al., (2005)

Presence/absence of an infant

To identify females with and without vulnerable offspring, I used observational data collected *ad libitum*. I recorded any female that had an infant come and suckle from her in the study period as “with infant” and those that never had an infant attach as “without infant”.

Eigenvector centrality

To create the troops social network and calculate a centrality score for each baboon based on associations/proximity to group-mates (Farine, 2015; Farine & Whitehead, 2015; Sosa et al., 2020), I used the package “Spatsoc” (Robitaille et al., 2019). I chose to calculate centrality measures based on proximity networks since spatial periphery is a predictor of human interaction in macaque groups (Balasubramaniam et al., 2020) and previous work has shown that baboon individuals maintain close proximity to affiliates during movement (King et al., 2008). Additionally, proximity networks have been correlated with affiliative (i.e., grooming) networks (Cheney et al., 2006; Silk et al., 2003) and therefore also estimate social integration. I restricted GPS data to times during which all baboons were outside the urban polygon (as proximity to humans is predicted to alter social networks: Morrow et al., 2019). This resulted in 307977 minutes in total; mean: 23690, range: 9743 – 29683 per individual. Data was grouped temporally at 1-minute intervals using the function “group_times” and spatially, within 5 m, using the function “group_pts”. This latter function uses the “chain rule” (Castles et al., 2014), where each GPS fix was buffered by 5 m, and two or more individuals were considered in the same group if they shared a common buffer, even if some of those individuals were not within 5 m of one another (Peignier et al., 2019; Robitaille et al., 2019). I then generated a group by individual matrix from the data (using the function “get_gbi”, “Spatsoc”), and built a proximity-based social network using the package “asnipe”, R (Farine, 2013). Strength of associations between baboon dyads (network ‘edges’) were defined using the simple ratio index (SRI). From this proximity-based network, eigenvector centrality (a baboon’s importance in the network given the importance of its neighbours: Farine & Whitehead, 2015) for each individual was extracted. Because collars recorded for different lengths of time (Table III-1; Fig. II-6, Methods), I created networks and calculated eigenvector centrality scores for periods of time during which different numbers of collars (1 – 13) were recording. I decided to calculate networks from 40 days of synchronous GPS data, for a time period when > 10 collars were active (> 75% of the collared individuals). These criteria were chosen following a sensitivity analysis (Fig. III-S1).

Close affiliate

To quantify each baboon’s closest social partner (close affiliate) I calculated each baboons nearest neighbour using GPS data for 13/19 adult individuals. I chose nearest neighbour data to represent close affiliates, since baboons tend to associate with and follow closely bonded individuals (Farine et al., 2016;

King et al., 2008). All analyses were conducted in R using the package “Spatsoc” (Robitaille et al., 2019). I used 40 days of synchronous GPS data for when 10 or more collars were working, following the sensitivity analysis conducted for eigenvector centrality (above) (Fig. III-S1), and for times the baboons were outside of the urban polygon, as proximity to humans is predicted to alter inter-neighbour distances (Morrow et al., 2019). Data were then grouped temporally (at 1-minute intervals) using the “group_times” function, and each baboons nearest neighbour was calculated within a spatial threshold of 5 m, using the function “edge_nn”. This provided a total of 56871 observed nearest neighbours within 5 m (mean ± SD per baboon: 4374 ± 1467). Using these data the group member that was most frequently observed within 5m of a focal baboon was determined to be the closest affiliate. This provided me with information on each baboon’s ‘group mate that is most frequently observed within 5m’.

C-peptide measurements

To investigate the energetic status of each baboon the urinary C-peptide concentration of individual urine samples was measured. C-peptide is a marker of insulin production (Girard-Buttoz et al., 2011) and has been used previously to investigate food availability and intake (Emery Thompson & Knott, 2008; Fürtbauer et al., 2020; Thompson et al., 2009), energetic costs (i.e. through illness: Thompson et al., 2009), as well as highlighting inter-individual differences in energetics, i.e. in dominance rank (Higham et al., 2011b; Lodge, 2012; Thompson et al., 2009) and female reproductive state (Fürtbauer et al., 2020; Lodge, 2012; McCabe et al., 2013).

Urine samples were collected opportunistically when following the study troop, either by pipetting the sample directly from the substrate into 2.0 ml Eppendorf Safe-Lock microcentrifuge tubes, or by using a synthetic ‘Salivette’ swab (Sarstedt Salivette Cortisol code blue, order number 51.1543.500: as recommended in Danish et al., 2015). Salivettes were centrifuged at the research house in the evening and the sample pipetted into 2.0ml Eppendorf

Safe-Lock microcentrifuge tubes. All urine samples were placed into a freezer at -20C until the end of the data collection period when they were exported to Swansea University on dry ice. N = 107 samples were collected while GPS loggers were recording (median: 9 per individual, range: 2 - 14). To account for differences in urine concentration, C-peptide values were adjusted to urinary specific gravity, which was taken using a refractometer in the field if the sample was large enough, and otherwise in the lab. C-peptide concentrations were measured using a commercial C-Peptide ELISA Kit (IBL International GmbH, Hamburg, Germany; Art. No. RE 53011), which has been previously used in other primate studies (Girard-Buttoz et al., 2014; Girard-Buttoz et al., 2011; Higham et al., 2011a). Further information on sample collection, storage, export and analysis are provided in Fürtbauer et al., (2020).

C-peptide measurements were averaged per week for each individual (median: 4 samples/individual; range 3 - 7) and scaled, to give a weekly scaled ‘energetic state’. Averaging c-peptide has been done previously by month and season in order to investigate seasonal and individual variation in energy balance (Thompson et al., 2009).

Statistical Analysis

First, I used the “ICC” package, R (Wolak et al., 2012) to identify whether individuals repeatedly differed in proportion of time (“ICCest” function) spent in urban space. To obtain confidence intervals around the repeatability estimates, I bootstrapped all models over 1000 iterations. Then, in order to investigate inter-individual differences in the time baboons spend in urban space, I modelled the proportion (time) of each day that the baboons spent in urban space as my response variable using a generalised linear mixed effects model with a beta family and a zero-inflation extension (function “glmmTMB” in “glmmTMB” package, R: Brooks et al., 2017), allowing me to model the proportional data in which I had lots of low values for proportion of time in town. Fixed effects included sex (male, female), rank (dominance rank), presence/absence of an infant (yes or no), the proportion of time a baboon’s closest affiliate spent in urban space on the same day (0-1), focal baboon centrality measure in the social network (0-1) and c-peptide level (average level per week, scaled). I also calculated the mean proportion of the day all baboons spent in the urban space for each day, minus the focal individual, and the sleeping site location (in or out of urban space) which were included as fixed effects. The time the whole troop was in urban space confirms that any effect a close affiliate has on a focal baboons' time in urban space is due to the close affiliates urban space-use, rather than it being influenced by the whole troop. However, proportion of time a close affiliate spent in urban space was correlated with proportion of time the troop spent in urban space (Spearman's rho = 0.66, $p < 0.001$, n = 221 days) and therefore they were tested in a separate models and their respective effects compared using Akaike Information Critera (described below). Sleeping site controls for the fact that the baboons will spend more time in urban space when they sleep within this space (rather than outside it). I also fitted "individual ID" as a random effect in the model, to allow for different intercepts (i.e. inter-individual differences) with respect to the proportion of the day spent in urban space.

Dominance rank was correlated with eigenvector centrality (Spearman's rank correlation: rho = 0.48, $p = 0.09$, n = 13 individuals) and therefore their effects were tested in separate models, as follows. In the first model, I tested the effect of sex, dominance rank, the daily proportion of time a close affiliate spent in urban space and weekly average c-peptide level, whilst controlling for sleepsite (m1). In the second model, I tested the effect of sex, eigenvector centrality, the daily proportion of time a close affiliate spent in urban space and weekly average c-peptide level, whilst controlling for sleepsite (m2). I compared models using Akaike Information Criteria (AIC).

Since the daily proportion of time a close affiliate spent in urban space was correlated with the daily proportion of time the whole troop spent in urban space (above), I tested their effects in separate models, and compared them using AIC. Each individuals GPS started and ended recording on different days (Table III-1; Fig. II-6, Methods) and therefore the focal individuals proportion of the day spent in urban space did not always have a matching value with a close affiliate's proportion of the day spent in urban space. Therefore, I used a reduced dataset (n = 221 days), to allow for model comparison. Due to convergence issues, I dropped all non-significant fixed effects from models. Therefore, I tested the effect of proportion of the day a close affiliate spends in urban space (m3) and proportion of the day the whole troop spends in urban space (m4) on proportion of an individuals day spent in urban space and compared them using AIC.

In order to examine the effect of presence/absence of an infant on proportion of time females spent in urban space I used a reduced dataset that didn't include the males (of which n = 5 had an infant, n = 5 did not have an infant, and one female gave birth during the collaring period, and thus changed from without infant to with infant: Fig III-6). High-ranking, socially-connected female baboons tended to be individuals which had infants (Fig. III-S2) and therefore I tested the effect of presence/absence of an infant (m5) in a separate model to dominance rank (m6) and eigenvector centrality (m7), and compared models using AIC. I controlled for daily proportion of time a close affiliate spent in urban space. Full model results are presented in Table III-S3, Appendix. Model fit was checked using diagnostic plots of model residuals against fitted values.

RESULTS

Urban space-use

During daytime hours (08:00 – 18:00 pm), baboons went into urban space a median average of 3 (range 1 - 40) times per day and spent on average 288 seconds (range 1 – 35819 seconds) in urban space before leaving, with a median average of 7 other collared individuals (range 1 – 12) (Fig. III-4bd). This resulted in individuals spending a mean daily proportion of 0.11 (11%) of their day in the urban space (range 0 – 1) (see Fig. III-3). Some of the observed variation in the proportion of time baboons spend in urban space across days (n = 274 days) could be attributed to variation among individuals (ICC = 0.191; CI = [0.086, 0.424]).

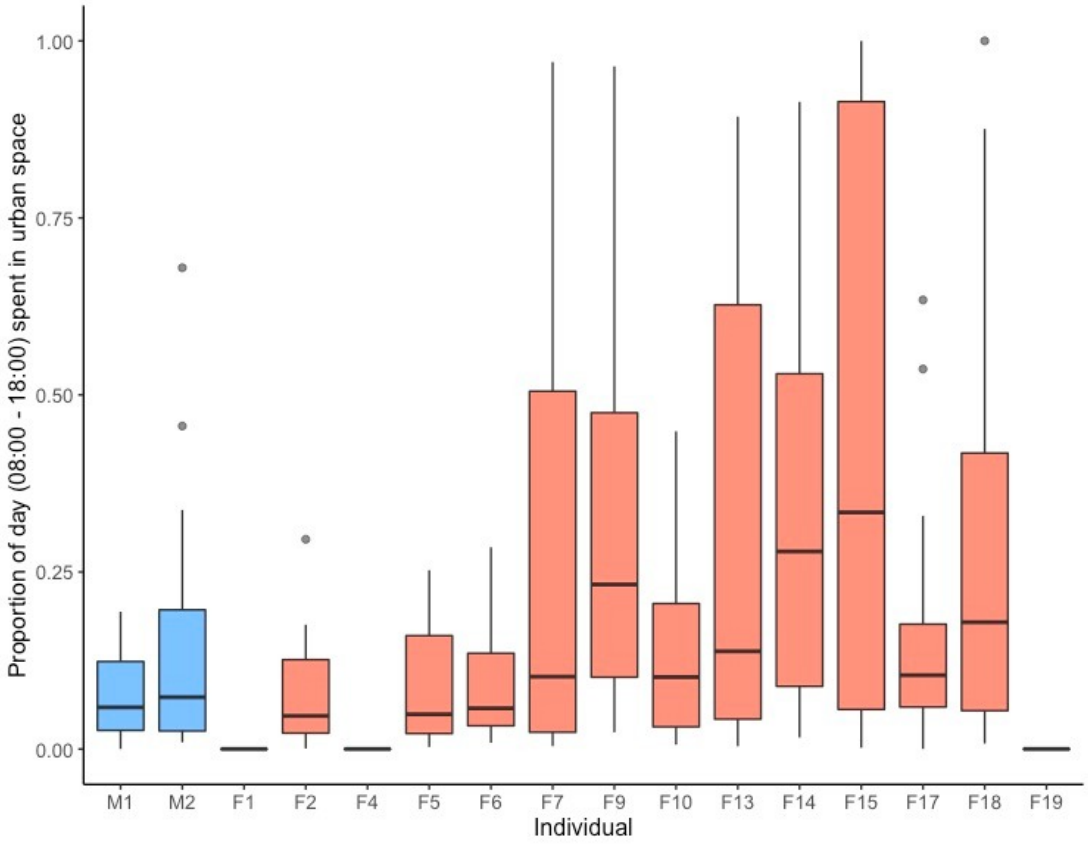

Figure III-3. Proportion of the day (between 08:00 – 18:00 pm) spent in urban space across collared individuals (n = 16). Left to right: high dominance rank to low dominance rank. Males indicated in blue and females in red. Collared females without GPS (F1, F4 and F19) are also indicated.

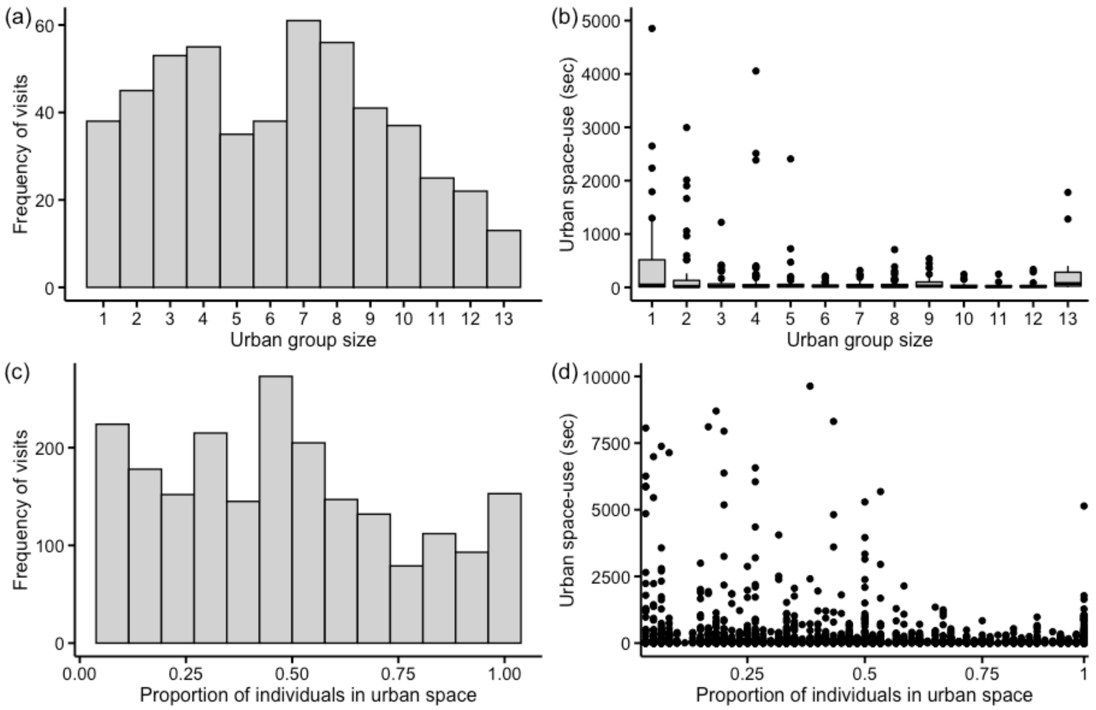

Figure III-4. Urban space-use. (a) Frequency of visits to the urban space and (b) seconds spent in urban space for different group sizes. (c) Frequency of visits and (d) seconds spent in the urban space as a function of the proportion of collared individuals observed in urban space. Panels (a) and (b) are based on times when all tracking collars were recording GPS (n = 13). Panels (c) and (d) are based on all available GPS data, as collars recorded for differing lengths of time.

Predictors of inter-individual variation urban space-use

The first prediction that males would spend more time in urban space than females was not supported (glmmTMB: estimate: -0.193, p = 0.392 (m2); Table III-S1), since both males and females used the urban space (Fig. III-3). When tested using the full dataset (including males), dominance rank (prediction 2) did not predict the proportion of an individual's day spent in urban space (glmmTMB: estimate: -0.613, p = 0.053, Table III-S1). However, on a reduced dataset (just females) dominance rank was a significant predictor (glmmTMB: estimate: -1.087, p = 0.001, Table III-S3), though this accounted for less variance than presence/absence of an infant or eigenvector centrality (AIC:

rank: -242.481; infant: -239.643; centrality: -237.385). Presence/absence of an infant (prediction 3) was a significant predictor of a female's daily proportion of time spent in urban space (glmmTMB: estimate: -0.557, p = 0.030, Table III-S3), though it accounted for less variance than eigenvector centrality (AIC: infant: -239.643; centrality: -237.385). Anecdotal evidence for a single female that gave birth during the study period supports this, with the time she spent in urban space being significantly reduced after birth, whilst her general activity levels were maintained (Fig III-6b). Social factors were important predictors of time spent in urban space: proportion of the day spent by a close affiliate in urban space predicted time spent by a focal individual in urban space (glmmTMB: estimate: 1.048, p = 0.004; Fig. III-5c; Table III-S2) (supporting prediction 4) as did proportion of the day spent by the rest of the troop in urban space (glmmTMB: estimate: 2.622, p < 0.001; Fig. III-5d; Table III-S2), though proportion of the day spent in urban space by a close affiliate accounted for more variance (AIC: close affiliate: -237.216; whole troop: -253.981; Table III-S2). Eigenvector centrality (prediction 5) did not predict proportion of the day a focal individual spent in urban space, on either the full dataset (including males) (glmmTMB: estimate: -0.709, p = 0.145; Table III-S1) or the reduced dataset (just females) (glmmTMB: estimate: -1.028, p = 0.125; Table III-S3), though models with eigenvector centrality included accounted for more variance than other models for both full and reduced datasets (Table III-S1, Table III-S3). Weekly average c-peptide levels did not predict an individual's daily proportion of time in urban space (glmmTMB: estimate: 0.005, p = 0.335 (m2); Table III-S1) and therefore I found no support for the final prediction (prediction 6) regarding individual physiology and proportion of the day spent in urban space.

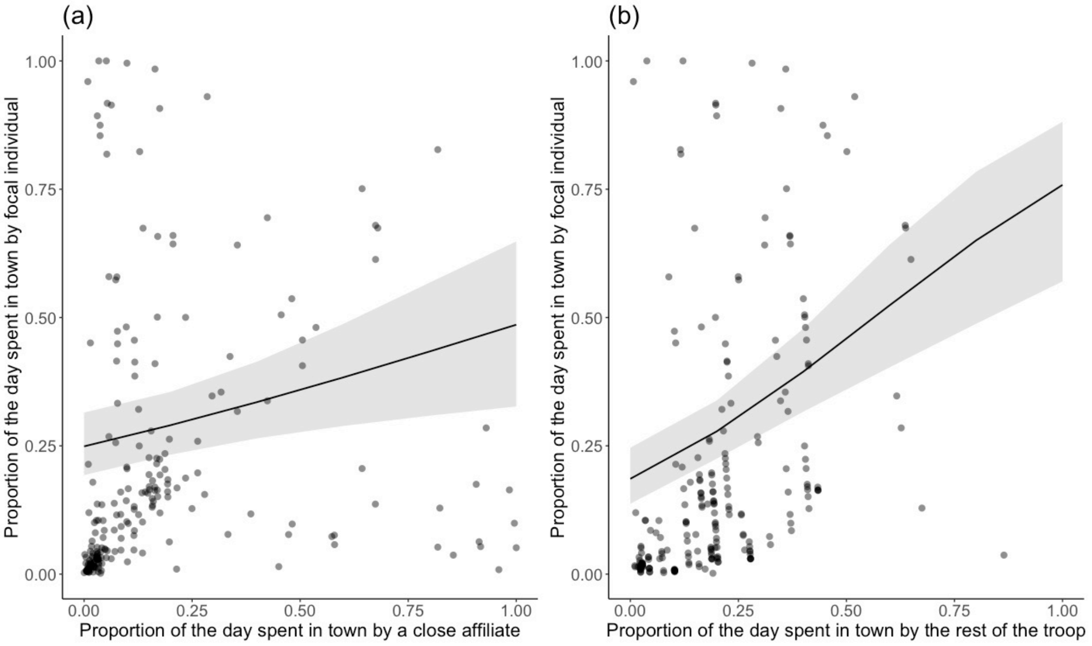

Figure III-5. Social factors predict proportion of the day spent in the urban space. (a) Proportion of the day spent in the urban space as a function of a close affiliates proportion of the day in the urban space. (b) Proportion of the day spent in the urban space as a function of the mean proportion of the troop's day in the urban space. Raw data are plotted in both (a) and (b) and the lines represent predicted values, and the shaded areas represent confidence intervals from the glmmTMB model.

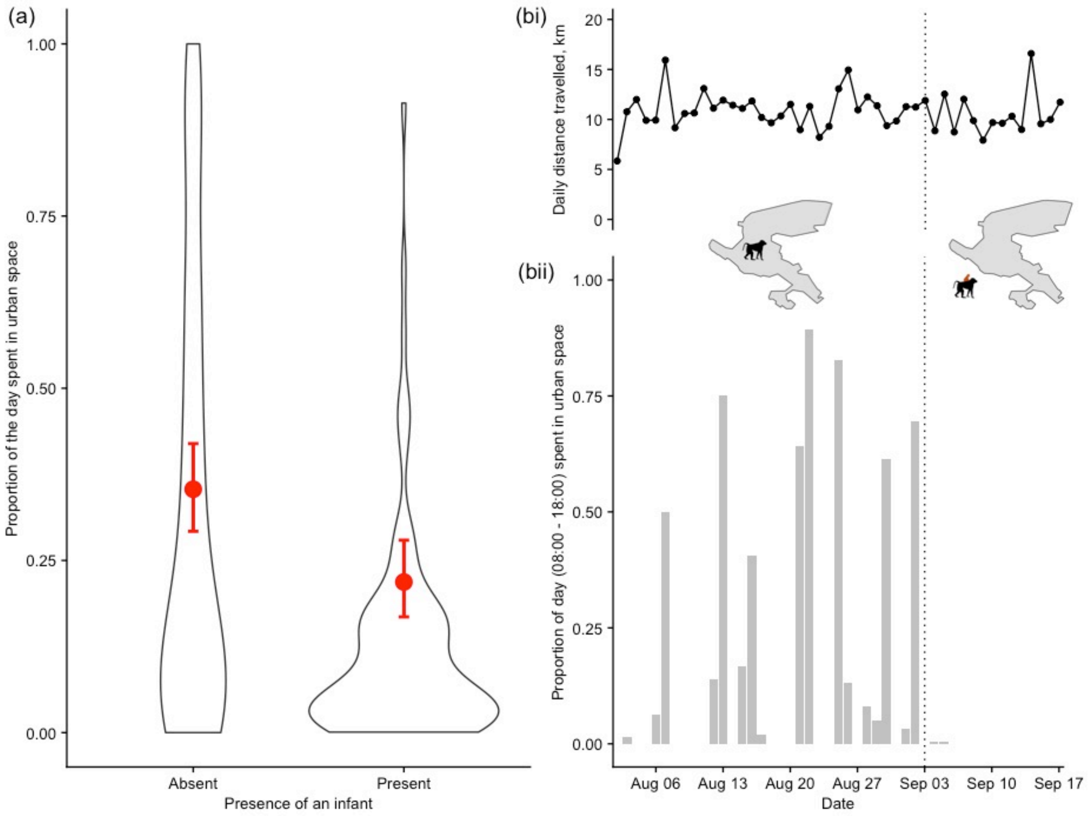

Figure III-6. Presence of an infant reduces daily proportion of time spent in urban space. (a) Predicted proportion of the day spent in the urban space for individuals with (present) and without (absent) an infant, plotted over the raw data (presented as violin plots). The red dots represent predicted values and error bars represent the confidence intervals, from the glmmTMB model. Of 11 females, n = 5 had an infant (present), n = 5 did not have an infant (absent) and one has data represented in both categories (as she gave birth during the study period). (bi) daily distance travelled for a single female baboon and (bii) Proportion of the day (08:00 – 18:00) spent in town for the same baboon, before and after she gave birth (on 03-09-2018, represented by the vertical dashed line).

DISCUSSION

Urban space-use is a risky strategy across many taxa (Bateman & Fleming, 2012; French et al., 2018; Salmón et al., 2016). This is the case for the Cape baboons, where risk of human-induced injury and mortality is high (Beamish, 2009; Hoffman & O'Riain, 2012c). The baboons on the Cape have previously been seen to mitigate this risk by adaptively using their space, and by flexibly responding to management risk (Fehlmann et al., 2017b). I wanted to understand the important predictors of this risk-taking behaviour between individual baboons, as there is relatively little previous work that investigates inter-individual variation in response to urban space. Previous research has highlighted certain primate phenotypes are more likely to exhibit “innovative” or “risk-taking” behaviours (Reader & Laland, 2001), which could aid in adjusting to human-altered landscapes (Kark et al., 2007). I provide evidence that certain behavioural and social traits are important predictors of urban space-use and response to management risk, for a troop living at the urban edge in Cape Town, South Africa.

In contrast to previous work (Chiyo et al., 2012; Fehlmann et al., 2017a; Merkle et al., 2013), I found that females are just as likely as males to use the urban space. Though the average proportion of time in town did not differ strongly between individuals (ICC = 0.191; CI = [0.086, 0.424]), certain females had a much larger range of values than other individuals, with one spending an entire day in urban space (Fig. III-3). In agricultural areas, both sexes have been seen to crop-forage (Strum, 2010; Wallace & Hill, 2012), and benefits to females include faster reproduction and shorter inter-birth intervals, and an earlier first reproduction (Strum, 2010). Male and female baboons have very different life histories – with males dispersing as they reach adulthood and females remaining in their natal troop for life (Altmann & Alberts, 2003). On the Cape, unsuccessful dispersal can result in males entering deep into urban space and developing a taste for human foods, which perhaps is why they are most noted for urban-foraging. For this reason, and because adult males tend to have a large sway in group movement (Kaplan et al., 2011; King et al., 2008; Montanari et al., 2021; Stueckle & Zinner, 2008; Sueur, 2011), baboon management on the Cape tend to focus on adult males when baboon groups use urban space. This focus is perhaps the reason males spend relatively less time in urban space than females (Fig. III-3).

Interestingly, dominance rank did not predict proportion of the day spent in urban space for the full dataset (including males). In males, high dominance rank has previously been shown to be an important predictor of crop-foraging in elephants (Chiyo et al., 2012,) and urban-foraging in baboons (Fehlmann et al., 2017a). However, dominance rank became important on a reduced dataset (just females), though this explained less variation than eigenvector centrality and presence of an infant (Table III-S3). Low-ranking females may use urban space more, as they are less influenced by management (which focus on adult males), enticed by food rewards, and therefore more likely to fission from the troop (Barton & Whiten, 1993; Dittus, 1988). Indeed, subordinate wild toque macaques (*Macaca sinica*) were more likely to fission from groups (Dittus, 1988).

Female baboons were also less likely to use the urban space when they had an infant. Baboon infant survival and reproductive success is dependent on extensive parental care (Altmann & Alberts, 2003; Cheney et al., 2006). During the field season, the beta male attacked a number of infants (attacking four, one of which later died; three other females were additionally recorded carrying dead babies). High infant mortality caused by infanticide is consistent with other baboon troops (Cheney et al., 2006; Palombit, 2003; van Doorn et al., 2010) and is a stressful time, corresponding to increased glucocorticoid levels in lactating female baboons (Engh et al., 2006). Male baboons will defend infants from attacks by other males when the probability of paternity is high (Cowlishaw, 1999), and is perhaps why post-partum females choose to remain in the troop. Certainly, in black bears females may avoid the urban space due to risk of infanticide from males (Merkle et al., 2013). The result gives weight to the hypothesis that leaving the troop to use the urban space is highly risky, and that buffering this risk by remaining in a social group is important to protect against infanticide (Cheney et al., 2006). Previous research has found a reduction in activity levels in the first few months of lactation (Barrett et al., 2006), which may also be the reason for lower levels of urban space-use. However, in the study troop a single female gave birth whilst her GPS was recording data; the change in her reproductive state (pregnant to lactating) made a big difference to the time she subsequently spent in urban space (Fig. III-6bii) but had little effect on her daily distance travelled (Fig. III-6bi). In addition, there were two more females that gave birth during the study period, each spending a lot of time in urban space before giving birth, and then drastically reducing their time in urban space afterwards (*pers. obs.*).

I found that urban space-use seems to be a predominantly social strategy, with a close affiliate's daily proportion of time in urban space and the troop's average daily proportion of time in urban space strongly predicting an individual's daily proportion of time in urban space. Fig. III-4 supports this finding, with common urban-foraging group sizes of 7 individuals. Previous work by Fehlmann et al., (2017b) with predominantly male urban-foragers, found that it tended to be a solitary behaviour with males making lone trips to the urban space. As has been highlighted above, male and female life histories are very different, with females forming long-term bonds with other females in a troop (Silk et al., 2003). This may be an explanation for the finding regarding social groups using the urban space; since females are not known to disperse, and stay in the same group for life, it would be less common for them to make the solitary trips as males do. Females may also be more risk averse than males (Reader & Laland, 2001), and therefore may buffer the dangers of the urban space by remaining as a unit. Additionally, as the natural predators of baboons are absent from the Cape (Skead, 1980), this may have relieved some of the pressures of group-living and therefore the rewards of urban space-use outweigh the costs of fissioning from the troop.

Eigenvector centrality in the spatial network was also not a strong predictor of the proportion of the day an individual spent in urban space. Female baboons with high strength in social networks have been shown to experience enhanced infant survival (Silk et al., 2003) and high rank and strong social bonds increase female baboon longevity (Silk et al., 2010b). In a system devoid of predators (Skead, 1980), it would seem that females on the periphery of the network (that benefit less from sociality) would be more likely to use urban space. However, I did not find such a relationship.

C-peptide levels did not predict daily proportion of time spent in urban space using a weekly average. Since C-peptide has been used as a measure of energetic balance between individuals in previous studies (Thompson et al., 2009), I predicted that it would be lower in individuals that use the urban space more often, as having a lower energetic balance would draw them into town. Since I did not detect any difference, it may be assumed that the baboons are successfully balancing their energy intake with expenditure. However, C-peptide is responsive to periods of high glucose intake (Emery Thompson & Knott, 2008), as occurs in a patchy environment when there is an abundance of fruit. This is not seen in fynbos vegetation, which characteristically has a low nutritional content (Kaplan et al., 2011). Indeed, in the current study troop, C-peptide levels were positively correlated with food provisioning, which occurred over a 10-day period (to facilitate collar deployment: Fürtbauer et al., 2020). The baboons' intake of a large amount of high-calorie human foods over the study period was typically restricted to certain times of the week (i.e. refuse collection day), or intermittently when the baboons foraged from a house, garden or compost heap. This very short time-window is not comparable to animals in patchy areas that periodically experience high fruit availability, or to obtaining high-quality food for over 10 days. Therefore, I may not have had a large enough frequency of samples within the correct time-window to capture these events. Additionally, since C-peptide has previously been shown to vary by season (Emery Thompson & Knott, 2008; Grueter et al., 2014; Thompson et al., 2009) and energy balance differs between female reproductive states (Lodge et al., 2013), it may be that to capture fine-scale variation I would need more frequent and consistent samples (which is often, as in this case, not feasible when studying wild animals).

Future research and management decisions, particularly on the Cape, should take into consideration the current study when developing approaches to keeping baboons out of urban space. In order to restrict troop numbers on the Cape, contraception for female baboons has previously been discussed as a potential future management tool. This strategy is commonly used in captive settings to restrict group numbers from outgrowing the available space (Plowman et al., 2005). However, since I have found that females tend to use the urban space more often without infants, there may be negative repercussions as a result of this decision. The results of the current study may also be important when deciding which individuals are suitable for lethal removal; since completion of the field season, the beta male was removed from the troop in this manner. As it is clear that all individuals in the troop urban-forage, often in groups, removing the beta male may not be a long-term solution to restricting human-baboon conflict in Da Gama (however, male baboons are considered to cause more problems in urban spaces: Beamish, 2009, and therefore it may be necessary to remove a problem individual in this manner).

In summary, I have shown that social factors are important to baboons when balancing the risks and rewards associated with the urban space. Baboons buffer the risks of urban space through remaining in social groups and avoiding urban space when caring for vulnerable offspring. Since baboon gestation is typically six months, followed by approximately 12 months of lactation (Archie et al., 2014a) it is essential for baboon females to allocate much time and energy to parental care (Johnson, 2003). However, capitalising on food opportunities when the risk is low (i.e. for baboons without an infant) is an adaptive response to their environment. I hope this work will contribute to building a framework for managing urban species in future decisions and add to the growing body of work on the Cape baboons.

APPENDIX

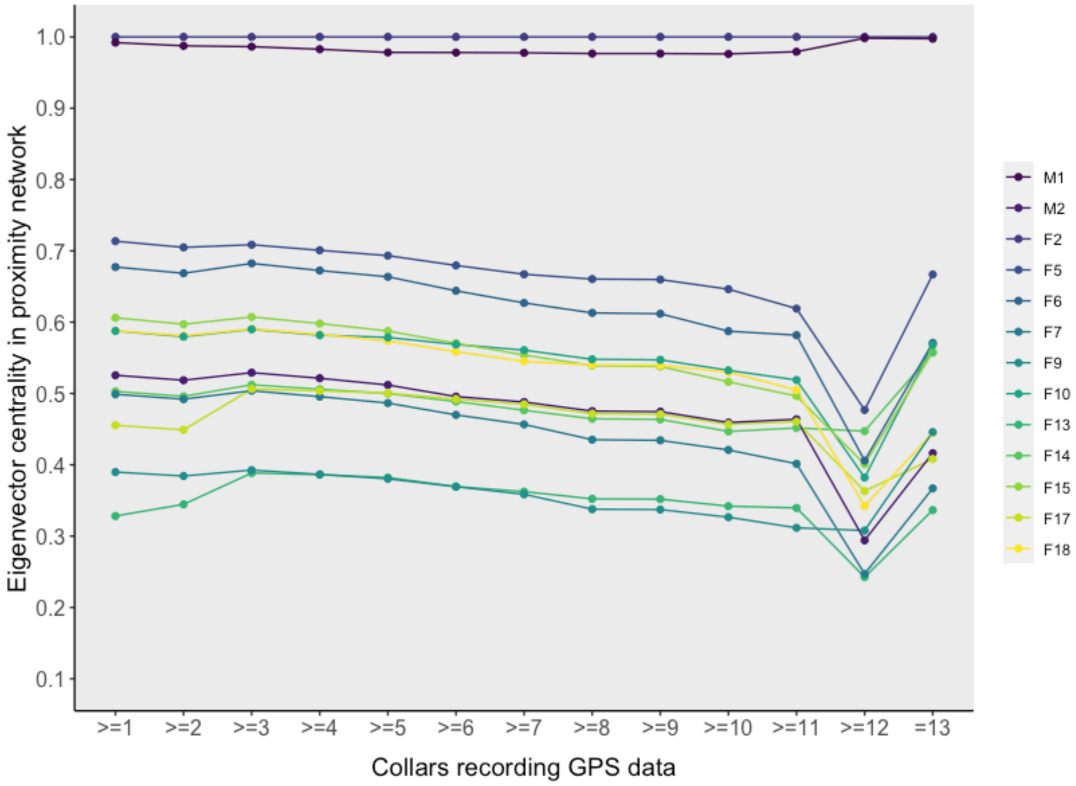

Figure III-S1. Network centrality measures (proximity data) calculated using different numbers of collars recording GPS data. '>=1' provides centrality scores calculated for periods where one or more collars were recording GPS data, and '=13' provides the calculated centrality scores for periods only when all 13 collars were actively recording GPS data.

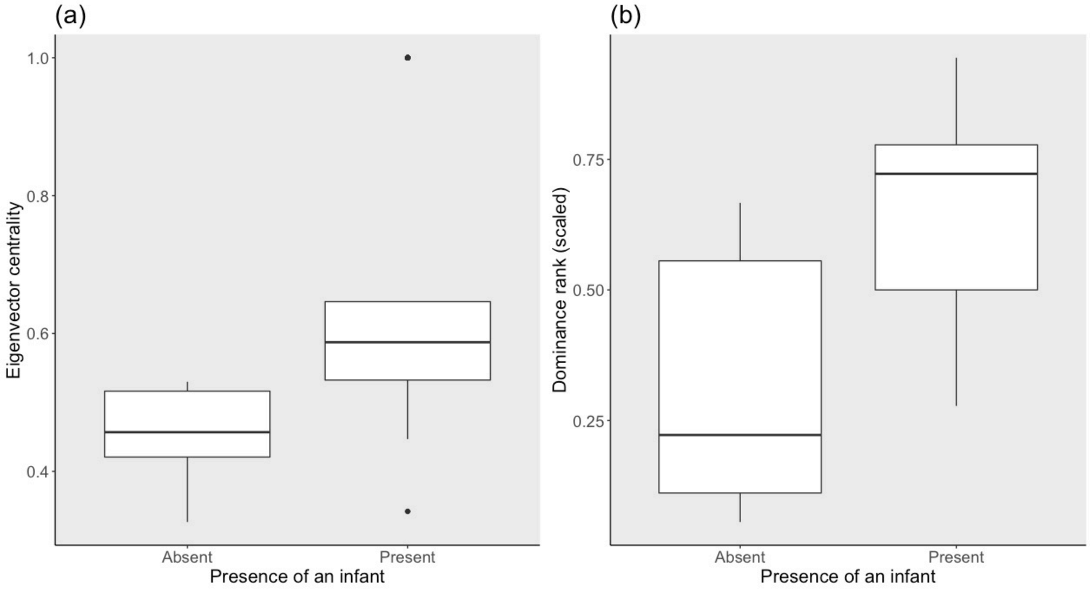

Figure III-S2. Presence/absence of an infant, for n = 11 female baboons. (a) Females with an infant tend to have high eigenvector centrality in the proximity network and (b) high dominance rank. Of 11 females, n = 5 had an infant (present), n = 5 did not have an infant (absent) and one has data represented in both categories (as she gave birth during the study period).

Table III-S1. Results of linear mixed models with zero-inflation, estimated using the glmmTMB model, for the effect of sex, dominance rank ('Rank': m1), eigenvector centrality ('Centrality': m2), weekly c-peptide level ('C-pep'), proportion of the day an affiliate spent in urban space ('Prop. affiliate') and sleepsite on the proportion of the day spent in the urban space by individual baboons in a group living on the urban edge in Cape Town, South Africa.

Model	Term	Estimate	SE	z	p	AIC
m1	Sex	-0.015	0.262	-0.058	0.953	-214.381
m1	Rank	-0.613	0.320	-1.916	0.053	
m1	C-pep	0.008	0.005	1.726	0.084	
m1	Prop. affiliate	1.063	0.373	2.848	0.004	
m1	Sleepsite	0.566	0.319	1.770	0.076	
m2	Sex	-0.193	0.225	-0.856	0.392	-212.910
m2	Centrality	-0.709	0.487	-1.457	0.145	
m2	C-pep	0.005	0.005	0.963	0.335	
m2	Prop. affiliate	1.033	0.377	2.738	0.006	
m2	Sleepsite	0.568	0.320	1.773	0.076	

Table III-S2. Results of linear mixed models with zero-inflation, estimated using the glmmTMB model, for the effect of proportion of the day an affiliate spent in urban space ('Prop. affiliate': m3) and proportion of the day the whole troop spent in urban space ('Prop. troop': m4) on the proportion of the day spent in the urban space by individual baboons in a group living on the urban edge in Cape Town, South Africa.

Model	Term	Estimate	SE	z	p	AIC
m3	Prop. affiliate	1.048	0.370	2.827	0.004	-237.216
m4	Prop. troop	2.622	0.525	4.988	< 0.001	- 253.981

Table III-S3. Results of linear mixed models with zero-inflation, estimated using the glmmTMB model, for the effect of presence/absence of an infant ('Infant': m1), dominance rank ('Rank': m2), eigenvector centrality ('Centrality: m3) and proportion of the day an affiliate spent in urban space ('Prop. affiliate') on the proportion of the day spent in the urban space by individual baboons in a group living on the urban edge in Cape Town, South Africa.

Model	Term	Estimate	SE	z	p	AIC
m5	Infant	-0.557	0.257	-2.166	0.030	-239.643
m5	Prop. affiliate	0.979	0.367	2.663	0.007	
m6	Rank	-1.087	0.333	-3.258	0.001	-242.481
m6	Prop. affiliate	0.878	0.369	2.376	0.017	
m7	Centrality	-1.028	0.671	-1.533	0.125	-237.385
m7	Prop. affiliate	0.956	0.376	2.542	0.011	

Chapter Four

Socioecology and management practices drive inter-individual variation in urban space-use by Cape Town’s chacma baboons

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Statement of contributions:

AB and AJK designed the study. AB and CC conducted and led the field work. AB compiled data and conducted analyses with advice from AJK. AB wrote the chapter with advice from AJK and all contributors.

Parts of this work formed the following publication:

Bracken, A. M., Christensen, C., O’Riain, M. J., Fehlmann, G., Holton, M. D., Hopkins, P. W., Fürtbauer, I. & King, A. J. 2021. Socioecology explains individual variation in urban space use in response to management in Cape chacma baboons (*Papio ursinus*). *International Journal of Primatology*, 1-18

A reprint of the publication is available at the end of the thesis

ABSTRACT

Urban space can offer substantial attractants to species through easy access to high calorie human foods, which can lead to smaller home ranges, greater overlap with neighbours and higher population densities. Additionally, the propensity to use urban space can vary among individual phenotypes within a group. For example, different age-sex classes can exhibit varying responses to urban space-use; in many species adult males most frequently use urban space. Cape chacma baboons are well known for their high overlap with humans and as a result are continuously prevented from using urban space by a dedicated team of field rangers. Field rangers tend to focus efforts on adult males, as adult males have a large sway on group movement, were previously understood to be the main users of urban space and are larger and more assertive when in urban space. I investigated the group- and individual-level predictors of overall space-use and urban space-use in a troop of Cape chacma baboons, using high resolution tracking collars (recording 1Hz GPS) and field ranger survey data. I show that, whilst at a group level the troop spends most time in areas unchanged by humans, there is large variation in how individuals are using urban space. This variation is best predicted by low social integration in the troop proximity network and low dominance rank; i.e. low-ranking, socially-peripheral females use more of the urban space than other individuals. This result is likely driven by the fact that individuals that have high associations with the alpha male (i.e. high-ranking females and their offspring) are indirectly affected by management efforts focused on him. This focus allows low-ranking, socially-peripheral female baboons greater access to urban space. This is an important finding to incorporate in management decisions: focusing efforts on males will not unilaterally reduce all baboons using urban space. It highlights the importance of conducting behavioural studies alongside wildlife management, to ensure effective mitigation techniques.

INTRODUCTION

Wildlife that use urban space can have smaller home ranges (Davison et al., 2009; Klegarth et al., 2017; Poveda & Sánchez-Palomino, 2004; Šálek et al., 2015) with increased overlap with neighbours (Atwood & Weeks, 2003) and thus higher population densities (Šálek et al., 2015) than conspecifics that do not use urban space. Urban space-use tends to be driven by motivation to forage on high calorie, concentrated, human-derived food sources found in the urban space (Kaplan et al., 2011; Poveda & Sánchez-Palomino, 2004). Species that show strong preference for urban space therefore tend to be those that are behaviourally adaptable, with a high learning capacity and a wide and varied diet (Baruch-Mordo et al., 2014; Hoffman & O'Riain, 2012a), such as primates (Hoffman & O'Riain, 2012a).

Primate populations that use urban space show reduced day path lengths compared to populations that range only in natural habitats (Johnson et al., 2015; Klegarth et al., 2017; Poveda & Sánchez-Palomino, 2004) and adaptively alter their use of space (Fehlmann et al., 2017b; Hoffman & O'Riain, 2012a). For example, long-tailed macaques (*Macaca fascicularis*) in Bali preferentially select for sleeping sites in human-altered landscapes, near food sources (Brotcorne et al., 2014), and in Cape Town, South Africa, chacma baboons exploit human-derived food resources in urban spaces by adapting their use of refuges in accordance with risk (seen as uncertainty in the management approach) (Fehlmann et al., 2017b). These adaptive behavioural responses result in primates gaining access to high-quality human foods (Kaplan et al., 2011) which enhance growth (Beckmann & Berger, 2003a), longevity (Luniak, 2004), and reproductive output (Beckmann & Berger, 2003b; Strum, 2010). Primate species living in urban space can also show a variety of behavioural modifications associated with an altered use of space. Black-tufted marmosets (*Callithrix penicillata*) in Brazil avoid noisy areas within the urban space, even where food availability is high (Duarte et al., 2011), and individuals of both long-tailed macaques in Singapore and Barbary macaques in Gibraltar incorporate highways (roads) in their ranging spaces, even though these areas are strongly avoided by other primate species (Klegarth et al., 2017).

The mediation of risks and rewards in urban space can also vary among individual phenotypes within a group, resulting in an array of responses. Sex is an important determinant of urban space-use (Baker et al., 2007; Dowding et al., 2010; Maibeche et al., 2015; Marty et al., 2019; Merkle et al., 2013), for example male American black bears in Missoula, Montana use urban spaces more frequently than females and are 1.6 times more likely to be located next to a house (Merkle et al., 2013). Age differences account for different urban space-use patterns by red foxes in Bristol, UK; specifically, adults traverse more roads than juveniles due to differences in activity periods and home range sizes (Baker et al., 2007). Different age-sex classes can similarly drive variation in primate species' urban space-use. Adult male Barbary macaques inhabiting Gouraya National Park that borders the city of Bejaia in Algeria, eat more human foods than females or juveniles (Maibeche et al., 2015). Additionally, males and high-ranking individuals in nine urban groups in three macaque species (*Macaca fascicularis*, *Macaca mulatta* and *Macaca radiata*) across India and Malaysia, had higher access to anthropogenic foods (Marty et al., 2019).

In chacma baboons, previous research investigating urban space-use has focused on adult males (Fehlmann et al., 2017a), as they have priority access to, and obtain high yields of, human foods (Kaplan et al., 2011; Strum, 2010). Given the increased use of urban space by adult males in primate troops (Maibeche et al., 2015; Marty et al., 2019), and the resulting conflict and contact with humans (Fuentes & Gamerl, 2005; McLennan & Hockings, 2016; Strum, 2010), it has been suggested that management should consider focusing their efforts on this age-sex class (Baranga et al., 2012; Strum, 2010). Chacma baboons living at the urban edge in Cape Town, South Africa, appear a good candidate for the male-focused management model. Previous work has shown that adult males tend to use urban space more frequently (Fehlmann et al., 2017a) and have priority access in the troop to anthropogenic foods (Kaplan et al., 2011). Management efforts focusing on their space-use have tried a myriad of techniques: herding by baboon rangers, waste management, fencing, assisted dispersal and (in the last instance) euthanasia (Hoffman & O'Riain, 2012c). If management is successful, males should spend little time in urban space (Fehlmann, 2017). Such male-focused management can be doubly effective, as high-ranking males tend to have a strong influence on group-level movement decisions in this (Kaplan et al., 2011) and other populations (King et al., 2008; King & Sueur, 2011; Stueckle & Zinner, 2008; Sueur, 2011). For example, in Namibia, chacma baboon alpha males lead group foraging decisions to artificial food patches (King et al., 2008) and are consistently followed in departure movements from morning sleepsites (King et al., 2011b). Using this knowledge in Cape Town, when a baboon troop that used urban space was similarly presented with an artificial food patch, the top-ranked adult male led the whole troop to the food patch (Kaplan et al., 2011).

In this chapter, I explore how the Da Gama troop use the urban space at both a group and individual level. Given that previous research has shown that Cape baboons manage their space-use to mitigate risks and rewards in their environment (Fehlmann et al., 2017b), I predicted that the troop would avoid areas where field rangers act to strongly deter baboons (prediction 1) and/or where there is uncertainty in field ranger strategy (prediction 2) (Fehlmann et al., 2017b). All adults from the Da Gama troop, unlike other primate groups (Baranga et al., 2012; Fehlmann et al., 2017a), spend a considerable amount of time in urban space (Fig. III-3, Chapter 3), individuals or small groups temporarily fission from the main troop and make forays into urban space (Fig. III-4, Chapter 3) and there are differences between individuals in time spent in urban space (Fig. III-3, Chapter 3). Those individuals that spend increased time in urban space tend to be females without vulnerable offspring, who use urban space with other group-members (Chapter 3). It therefore seems these females are mediating the risks posed by urban space, and I therefore made the following predictions.

I expected that female rank and/or social cohesion would likely predict patterns of urban space-use (prediction 3) for a series of inter-connected reasons. In the case of dominance rank, lower-ranking females are more likely to engage in innovative and risky behaviours (Reader & Laland, 2001), are more likely to 'produce' information about foraging patches (King et al., 2009a), are of least concern from a management perspective (i.e. they are not individually identified in management reports: Richardson, 2018a, 2018b), and have low affiliation to the dominant male (who tends to be the focus of management: Fehlmann et al., 2017a). Low-ranked females also tend to have lower social cohesion in the troop; they are the last to join group movements (King et al., 2011b), they avoid joining others at foraging patches (King et al., 2009a), and spatially they tend to be peripheral to the core troop (Ron et al., 1996) - affording exploration of novel areas (Kurihara, 2016). Low-ranked females with low social cohesion may therefore be incentivised to leave the troop and access food rewards located across the urban space, rather than to remain with the dominant male (and his close affiliates), who tend to be the focus of management.

METHODS

Study site and subjects

I studied the Da Gama troop of baboons, which comprises 2 adult males, 19 adult females, 2 sub adult males, 3 sub adult females and approximately 25 juveniles of both sexes. The troop lives in the urban-rural matrix around the suburbs of Da Gama Park and Welcome Glen on the Cape Peninsula (S -34.161, E 18.403) (see Methods, Chapter 2 for more details), regularly using these areas throughout the day and night (one frequently-used sleep-site is on top of a block of flats: Fig. II-4c, Methods). I studied the troop between July and November, 2018, and here use data collected mainly during the austral winter (July, August) when the GPS collars were active and when the Peninsula baboons show greater use of urban spaces (van Doorn et al., 2010).

The Da Gama troop is continually herded through its range by a team of up to six rangers, who were managed at the time by the service provider “Human Wildlife Solutions”. The remit of field rangers is to keep the baboons out of urban space and away from human activity. They do this by using a variety of methods, from shouts, claps and whistles to the use of paintball marker guns (van Doorn & O'Riain, 2020).

To test the predictors of the troop’s space-use patterns, I first examined the whole home range of the baboons, testing the basic parameters that may influence where the troop spends time. I then looked at individuals’ urban space-use in more depth. To do this, I used information from 13 custom-built tracking collars, direct observations and field ranger surveys, all described in detail below.

Baboon collaring

To obtain information on the space-use patterns of the Da Gama troop, 16 adults were fitted with custom-built tracking collars containing GPS units (GiPSy 5 tags, TechnoSmArt, Italy) recording at 1 fix/second between 06:00 – 18:00 UTC (08:00 – 20:00 local time). I use “daytime” hours for the troop in analyses (08:00 – 18:00 local time). One collar was not found after release (Collar No. 3; Table III-1, Chapter 3) and two collars failed to record GPS data, providing GPS trajectories for n = 13 baboons (61% of all adults in the troop) for a mean average of 42.77 ± 9.92 days, range = 21 - 54 days (Table III-1, Chapter 3; Fig. II-6, Methods). Further details about collar ethics, trapping and GPS data processing can be found in methods chapter and data chapter 3.

Baboon space-use

I examined baboon space-use at a resolution of 150 m x 150 m, by adding grid cells over a raster image of the study area in QGIS, version 3.12 (QGIS.org, 2020). This grid cell size is consistent with previous studies (Fehlmann et al., 2017b), and was chosen as it is larger than the average spread of baboons in the Cape Peninsula (Hoffman & O'Riain, 2012b). I determined the intensity of grid cell-use using fixed kernel densities and an *ad hoc* method for choosing the smoothing parameter, with the function “getvolumeUD” from the package “adehabitat” in R (Calenge, 2006). This gave an intensity of cell-use score (between 0-100; with 0 indicating no use, to 100 indicating complete use) for each collared baboon across their 95% home range. To understand how individuals used this space I calculated hourly distances travelled, using the function “as.ltraj” in the “adehabitat” package in R (Calenge, 2006). These were mean averaged across individuals during the time period in which there was synchronous GPS data for all baboons (12 days), to create the troops’ mean ± SD distance travelled per hour.

Quantifying anthropogenic change

The troop’s home range was divided up into ‘habitat’ areas, defined by the degree of anthropogenic change in the area. Polygon and line shapefiles were created to delineate human built structures (buildings, roads and pathways) in the baboons’ range, and the polygon created in Chapter 3 was used to define the urban space. These were drawn using Google satellite imagery and OSM standard maps in QGIS. To account for the distance spanning out from manmade structures in which the baboons would still be ‘disturbed’, a 150m buffer was added to all shapefiles, using the ‘buffer’ tool in QGIS. Four habitat areas were then categorised from the degree of human change: total (urban space polygon and buffer), major (the main tarmacked road dissecting the home range, all buildings in the home range and the buffer around these), minor (all walking pathways and buffer) and none (all remaining areas) (Fig. IV-2b). All habitat areas (in both the home range and the urban space) were designated grid cells using the grid created in “Baboon space-use” (above), using the intersection tool between grid and polygon layers in QGIS.

I further examined areas used by individuals in the urban space polygon and buffer (area of total human change, n = 77 grid cells). Urban habitat areas were defined using polygon shapefiles in QGIS, constructed using Google satellite and OSM standard maps and researcher knowledge of the site (Fig. IV-1c). Each polygon was defined grid cells, into four habitat areas: “mountain” (natural habitat, n = 37 grid cells), “riparian” (riverbed and green areas within the urban space, n = 4 grid cells), “recreational” (a sports field, n = 7 grid cells) and “residential” (housing, n = 37 grid cells). I plotted mean average (Fig. IV-S3a) and standard deviation (Fig. IV-S3b) of troop use in each area.

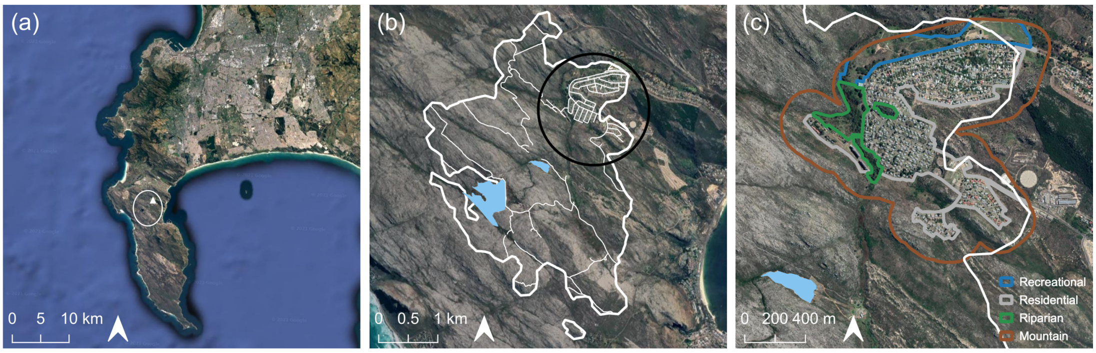

Figure IV-1. Study area and habitat. (a) the Cape Peninsula, with the urban space (Da Gama) indicated by a filled white triangle, and the home range indicated by a white circle; (b) the baboon troop home range (solid white line) estimated by a 95% kernel density, with roads and pathways indicated. The urban space is highlighted with a black circle; (c) the urban space divided by urban habitat. The polygon covers the area of total human change (the urban space and 150m buffer). The solid white line represents the home range, estimated by a 95% kernel density; all areas left of the line are included in the troops’ home range and therefore in analyses. Dams are represented as light blue areas in (b) and (c).

Management strategies and risk being herded

Herding intensity across the baboons’ home range was assessed through field ranger survey data. Each individual ranger was presented with a map of the baboons' home range, and was asked to colour in areas to show how they would herd the baboons, using a similar methodology to Fehlmann et al., (2017c): green = allowed in an area, orange = allowed some of the time, and red = never allowed. Interviews were anonymous and were conducted with the consent of field managers and rangers. A total of 12 maps was collected (e.g. Fig. II-9, Methods).

Pre-defined herding areas were created by drawing polygons around different sites in QGIS. Areas were pre-defined using local place names and landmarks (known to the rangers), by comparison of areas coloured by rangers across maps, and from researcher knowledge of the site. Each area was scored from 0 - 3: 0 = unsure (the area was either coloured with multiple colours, or was not coloured in), 1 = red (never allowed: high herding effort), 2 = orange (allowed some of the time: mid herding effort), 3 = green (allowed in an area: low herding effort). Pre-defined herding areas were similarly intersected with the grid (from "Baboon space-use", above). Scores for each grid cell were added together and divided by number of grid cells, to give an "average effort" for each cell. Agreement between rangers was calculated for each grid cell using the Simpson's diversity index (Fehlmann et al., 2017b).

Urban space-use

I examined urban space-use within the urban polygon (n = 55 grid cells). I calculated the response variable "difference in urban cell-use" for each grid cell; this was the difference in urban grid cell-use of each individual from the troop average. To do this, I averaged grid cell use across individuals, so that every grid cell had an average troop intensity use. From this, I subtracted each individual's grid cell use from the troop average.

Dominance rank

I expected that females with low dominance rank in the troop would make more use of the urban space. Calculation of dominance rank is explained in more detail in Chapter 3. In brief, dominance hierarchy was calculated for all adult female baboons from 634 interactions (median per adult: 96, range 11 – 129) (displacements, chases and aggressive displays) recorded *ad libitum* over 78 days of troop follows and determined using the packages “AniDom” and “Compete” in R (Sánchez-Tójar et al., 2018). Male dominance was calculated from 75 observations: M1 won 28 interactions (37%), M2 won 16 interactions (21%), with 31 interactions undecided (41%). M1 was ranked first. All adult males outrank adult females in chacma baboon troops (Engh et al., 2009; Kitchen et al., 2009). I standardized ranks between 0 and 1 (with 1 being the highest and 0 the lowest ranking individuals) using the function “rescale” from the “scales” package in R (Wickham, 2014).

Social cohesion

I also expected that females with low social cohesion in the troop would make more use of the urban space. To estimate baboon social cohesion, I calculated individual eigenvector centrality scores from proximity-based social networks for times all collared baboons were outside of the urban polygon, using the package “Spatsoc”, in R (Robitaille et al., 2019). Spatial networks were calculated by grouping GPS locations temporally (1-minute intervals) and then spatially (within 5 m: using the “chain rule”: Castles et al., 2014). The grouped data were then converted into a group by individual matrix (Farine, 2013) and the strength of associations between dyads of baboons (or network ‘edges’) were defined using the simple ratio index (SRI) (Farine & Whitehead, 2015). From this proximity-based network, I calculated individual eigenvector centrality scores. I created networks and calculated eigenvector centrality scores for periods over 40 days of synchronous GPS collar data when 10 or more collars were active (over 75% of the collared individuals, following a sensitivity analysis: Fig. III-S1, Chapter 3).

Statistical analyses

To explore if, and how, habitat attributes were associated with herding effort, I used partial mantel tests (function “vegdist”, package “vegan”, R: Oksanen et al., 2020, Spearman correlation, 999 permutations), to test for a correlation between human disturbance area and 1) average herding effort and 2) agreement scores between rangers, whilst controlling for spatial autocorrelation (variables considered were spatially autocorrelated to at least 3000 m; Fig. IV-S1). The distance matrices used were Euclidean distance between two grid cells of ‘difference’ in grid cell value.

To assess the overall predictors of baboon space-use, I used a spatial simultaneous autoregressive (SAR) lag model, which builds on the classic linear model by building a spatial weight matrix to account for spatial autocorrelation (packages “spatialreg”, R: Bivand & Piras, 2015 and “spdep”, R: Bivand et al., 2015). I built two models, the first testing the effect of habitat area (degree of human change) on troop space-use and the second testing the effect of management strategies on troop space-use, specifically: 1) average ranger herding effort and 2) agreement score between rangers. I used a square root transformation on the response variable (intensity of grid cell use: 0 - 100) to normalise model residuals in both models. Two models were used as habitat area was correlated with average ranger herding effort (Spearman’s rank correlation: rho = 0.40, Table IV-S1, Appendix).

To assess which individual attributes were predictive of difference from the troop in urban grid cell-use, I modelled the difference in urban cell-use as my response variable using a Gaussian generalized linear mixed model (GLMM) with a spatial autocorrelation (“fitme” function in the “spaMM” package in R: Rousset & Ferdy, (2014), with a Matérn covariance matrix and maximum likelihood method). Because dominance rank and eigenvector centrality were correlated (Spearman’s rank correlation: rho = 0.48, p = 0.09), I tested their effects in separate models (Suzuki et al., 2008), whilst controlling for sex (male, female) and fitting individual identity as a random effect, to allow for different intercepts (i.e. inter-individual differences) with respect to their difference in urban cell-use. I tested the significance of the random effect of individual ID using maximum likelihood ratio tests, as well as calculating the intraclass correlation coefficient (ICC) across individuals, using the function “ICCest” in the “ICC” package, R (Wolak et al., 2012). I identified the best performing model using Akaike Information Criteria (AIC), using the function “get_any_IC” in the “spaMM” package, R, and calculated AIC weights using the function “Weights” in the “MuMIn” package, R (Barton, 2009). Model fit was checked using graphical procedures (*Q*-*Q* plots and standardised residuals vs. predicted values) using the package “DHARMa” in R (Hartig, 2020). Full model results are presented in Table IV-S5, Appendix.

RESULTS

General patterns of space-use

Distance moved per hour for the Da Gama troop was 0.81 ± 0.49 km (mean ± SD, n = 13 baboons), and the 95% home range was 7.21 ± 0.47 km² (mean ± SD, n = 13 baboons (Fig. IV-1). The 95% home range was comprised: 18.34 % no human change, 43.73 % minor human change, 18.34 % major human change and 19.57 % total human change (Fig. IV-2b). Inter-individual differences in grid cell-use were highest in areas of total human change (urban space) (Fig. IV-S2).

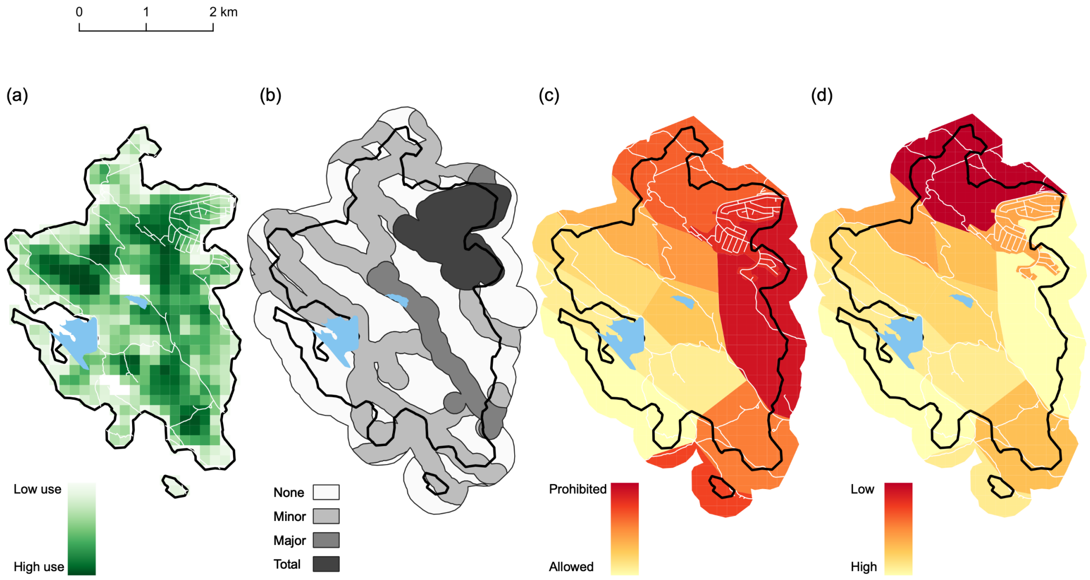

Figure IV-2. Factors affecting overall baboon space-use. 95% kernel home range of the baboon troop (black outline) showing (a) the intensity of grid cell use, (b) habitat areas, defined by degree of human change, (c) the average composite ranger effort, and (d) the agreement score between rangers for method of herding the baboons in different areas. In (a) dark green corresponds to areas of high use and light green to areas of low use, in (b) categorical habitat areas indicating areas of no human change (white), minor human change (light grey), major human change (grey) and total human change (dark grey), (c) red corresponds to high herding effort (baboons prohibited) and yellow to low herding effort (baboons allowed), and in (d) red corresponds to low agreement scores and yellow to high agreement scores between rangers. Black outline indicates 95% home range.

Average individual field ranger scores were high for areas of total human change (mean ± SD = 2.47 ± 0.38), lower for areas of major human change (mean ± SD = 1.81 ± 0.61) and similar for both areas of minor (mean ± SD = 1.57 ± 0.61) and no (mean ± SD = 1.62 ± 0.72) human change. This indicates that rangers expect to herd the baboons in more urbanised areas (Fig. IV-2b) and average ranger effort scores were strongly correlated to habitat type (partial mantel test: $R = 0.187$, $P < 0.001$; Fig. IV-2; Table IV-S2, Appendix). Ranger agreement scores ranged from 0.64 to 0.90, with the majority of cells having a high level of agreement (Fig. IV-2c). Ranger agreement scores were also highly correlated to habitat type (partial mantel test: R = 0.103, P < 0.001; Fig. IV-3; Table IV-S2).

Baboons' space-use was best explained by the level of urbanisation, with the troop using areas of no human change more than all other habitat categories, but significantly more than areas of minor human change (SAR: estimate: -0.32099; SE: 0.14215; Z = -2.2581, P < 0.05; Table IV-S3 & IV-S4, Appendix). Management effort and agreement did not predict patterns of troop space-use (effort: SAR: estimate: -0.08388; SE: 0.07707; Z = -1.0883, P = 0.27; agreement: SAR: estimate: -0.09359; SE: 0.63800; Z = 0.1467, P = 0.88).

The area of total human change (urban space plus buffer; dark grey area in Fig. IV-2b) comprised: 48.05% mountainous areas, 9.09% recreational areas, 37.66% residential areas and 5.19% riparian areas (Fig. IV-1c). The greatest variation across individuals in their urban cell use was in riparian and residential areas (Fig. IV-S3).

Urban space-use

The urban space (just the urban polygon) represented 13% of group's home range (Fig. IV-1b). Baboons spent mean 11% (range: 3% to 26%; Fig. IV-S4) of time in the urban space during the daytime (between 08:00 and 18:00 pm, local time).

Inter-individual variation in urban space-use

Some baboons used the urban space much more, and some much less, than the troop average (Fig. IV-3a) with baboon identity predicting variation in urban cell-use and indicating consistent inter-individual differences (GLMM: χ^2 LRT = 194.22, p < 0.001), confirmed with an Intraclass correlation coefficient (ICC) of 0.31, 95% CI 0.18 – 0.55. Baboon dominance rank and eigenvector centrality in the proximity network (Fig. IV-3b, IV-3c) predicted variation in urban cell-use, with lower-ranking, socially-peripheral baboons using a greater area of the urban space compared to other group-members. A model comparison showed eigenvector centrality and dominance rank to be comparable (network centrality AIC: 6061.93, AIC weight: 0.564; dominance rank AIC: 6062.45, AIC weight 0.436). Full model outputs are provided in Appendix (Table IV-S5).

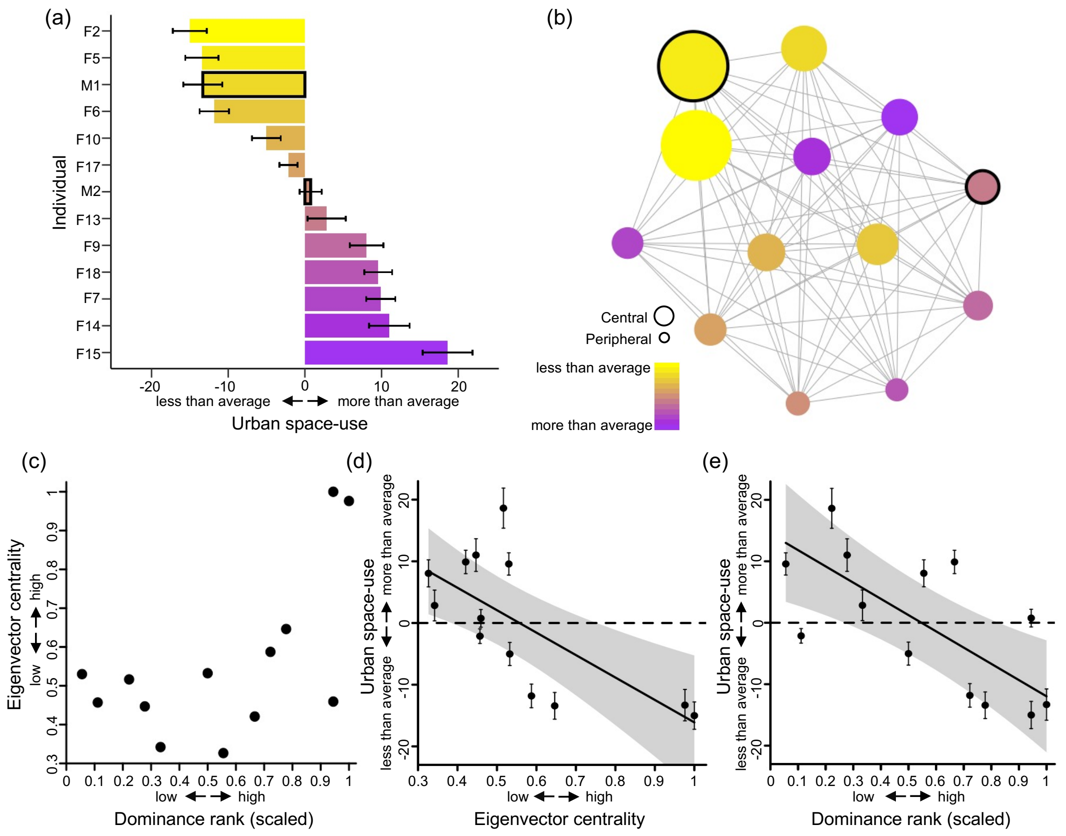

Figure IV-3. The influence of social factors on variation in urban space-use for the Da Gama troop, between July and September 2018. (a) Individual mean ± SE difference in urban cell-use; (b) baboon social network with increasing circle size indicating higher eigenvector centrality in the group proximity network, and yellow to purple colours representing higher (purple) or lower (yellow) than group mean of urban cell-use. M and F denote male or female individuals in (a), and two male baboons are represented with black outline in both (a) and (b); (c) correlation between dominance rank and eigenvector centrality in the group proximity network; (d) the influence of baboon eigenvector centrality in the group proximity network on mean ± SE individual difference from the group mean of urban cell-use; (e) the influence of baboon dominance rank on mean ± SE individual difference from the group mean of urban cell-use. For (d) and (e) the black line represents the predicted values, and the shaded area represents the confidence intervals using a spaMM model (Rousset & Ferdy, 2014), and the dashed line represents the group mean of urban cell-use, which is set to zero.

DISCUSSION

The results here add to the growing body of evidence that animals are adaptively altering their use of space in response to human-altered landscapes (Davison et al., 2009; Hamer & McDonnell, 2008; Roth et al., 2008; Šálek et al., 2015). At a group level the baboons use areas unchanged by humans, which also tend to be areas in which herding effort is low. However, individually there is large variation in individual urban space-use, with low-ranking, socially-peripheral female baboons showing greater use of the urban space. I discuss these results in turn.

At a troop level, baboons spend most time in areas unchanged by humans. Such areas also tend to be those where management agree not to herd the baboons, since habitat area is correlated with average herding effort and ranger agreement. In general, animals tend to avoid areas disturbed by humans (Markovchick-Nicholls et al., 2008), even within urban space (Duarte et al., 2011) and perhaps when the Da Gama baboons are not using urban space for food rewards (Fehlmann et al., 2021) they use spaces with lowest contact with humans. Indeed, this is reinforced by the fact the baboons also used areas of minor human change significantly less than other categories. This is possibly due to human food incentives; areas of minor human influence are not attractive enough to negate the human 'risk', as they do not include buildings (which present food rewards). I also found that the management team has a clear herding strategy: herding effort increases in areas of increasing human change, with correspondingly high agreement between rangers. Higher management effort in urban spaces was also found for a different baboon group within the same population (Fehlmann et al., 2017b), and since management strategy is to move baboons away from areas of high human presence (van Doorn & O'Riain, 2020), these results corroborate that management have a clear herding tactic. However, herding effort and/or agreement did not directly predict troop space-use. Instead, habitat type predicted baboon space-use, and herding effort differed according to habitat type. This may be due to the way in which space was classified in the study; ranger herding areas were delineated by eye. Perhaps had the maps been coloured in per grid cell, a clearer result may have been evident. Overall these results provide some evidence for the hypothesis that baboons are mediating risk with reward in their environment (Fehlmann et al., 2017b): on average, they seem either to use areas of low risk (low human change and low herding effort) or areas with high rewards (areas of high human change).

The greatest inter-individual differences were found in use of urban space (range: 3% - 26% of total time, n = 13 individuals, Fig. IV-3) than in the rest of the home range. Baboon management tend to focus on adult males, and the successful implementation of this approach has led to lower urban space-use of both males (especially the alpha). However, an unintended consequence of male-focused management is that it has afforded opportunities for low-ranking, socially-peripheral females to temporarily fission and use the urban space, where food rewards are plentiful (Fehlmann et al., 2021; van Doorn & O'Riain, 2020). Since low-ranked females tend to have weaker affiliation to dominant males (Archie et al., 2014b; Palombit et al., 2001), and occupy peripheral positions to the troop (Ron et al., 1996), they tend to fission under conflicts of interest (King et al., 2008), affording exploration of novel areas (Kurihara, 2016). Peripheral individuals also tend to gain less fitness benefits than socially-integrated baboons (Silk et al., 2003; Silk et al., 2010b). This likely results in higher incentives for them to access food rewards in the urban space rather than remain with the troop.

When in the urban space, the highest used grid cells were riparian and residential areas (Fig. IV-S3). These are generally riverbed areas with high vegetation cover, acting as ‘refuges’ in the urban matrix, inaccessible to the management team (*pers. obs.*). Previous research has highlighted the importance of riparian areas as a shelter resource for urban foxes (White et al., 2006) and bobcats (Young et al., 2019), and both refuges (trees) and urban space predict space-use in Cape baboons (Fehlmann et al., 2017b). Whilst green spaces are important for managing urban wildlife (Gallo et al., 2017), they can also exacerbate human-wildlife conflicts (Hosaka & Numata, 2016), as areas selected by wildlife are often near residential properties (Stillfried et al., 2017). For the Cape baboons, green spaces require careful consideration as they pose an obstacle for the management team when trying to restrict individuals' urban space-use. Since the greatest inter-individual differences in urban space-use were seen in riparian and residential areas (Fig. IV-S3), green areas close to human food rewards are likely to be an important refuge for urban space-users. Further investigation into the use of these areas may be informative for management.

This study will be important in management considerations for wild animal populations. Understanding the ways in which group structure influences urban foraging behaviour will help inform conservation strategies (Baranga et al., 2012). Adult male baboons tend to be more noticeable in urban spaces (as they are perceived to be more threatening to humans: Beamish, 2009), and therefore are particularly noted for urban space-use; however, the highest use of urban space in the current study was by low-ranking, socially-peripheral females. Large inter-individual differences in use of urban space demonstrates high fission-fusion dynamics in the Da Gama troop. These dynamics can lead to a permanent group fission (Sueur et al., 2011a) especially when social relationships are constrained at large group sizes (Lehmann et al., 2007). In other baboon populations, the exact group size at which fission occurs depends on several factors (Henzi et al., 1997), and on the Cape Peninsula such fissions have previously been observed for a range of group sizes (termed 'splinter groups': Forthman-Quick, 1986; Strum, 2010). There is not enough capacity to manage splinter groups' (i.e. in terms of budget and/or personnel), resulting in increased time in urban spaces compared to managed groups (Hoffman & O'Riain, 2012c). Constraining group sizes could potentially reduce conflict, as smaller groups are predicted to be more cohesive (Sueur et al., 2011a), less likely to fission (King et al., 2008), and therefore easier to manage. In the meantime, reducing human-baboon conflict through, for example, baboon-proofing fences, property and bins may help (see Fehlmann et al., 2021 Kaplan et al., 2011; Hoffman & O'Riain, 2012b for discussions). Integrating social sciences research to understand perceptions of individual baboons of different size and sex would further inform management of how and why these low-ranking females have greater access to urban spaces; for example, there may be differences in people's perception of the damage caused, and the threat posed, between male and female baboons (Mormile & Hill, 2017). Additionally, since local residents are integral to 'baboon-proofing' exercises, understanding residents' perceptions of both baboons and management will inform and promote their success.

In summary, at a whole group level, the management team successfully keeps the troop away from urban space and areas with increased human presence. However, certain individuals break from the troop to make trips alone or in small groups (Fig. III-4, Chapter 3) and this tends to be low-ranking, socially-peripheral female baboons. These results highlight the importance of examining responses of wildlife to human landscapes at an individual level: whilst overall the troop spent most time in areas unchanged by humans, the difference in individuals' urban space-use was considerable. Further investigation into individual movement trajectories may reveal more insights into urban space-use; for example, in identifying "keystone" urban foraging individuals (King et al., 2018), which may drive the urban foraging behaviour of other group members. Additionally, analysis of individual movement can uncover behavioural types (Merrick & Koprowski, 2017), and therefore plasticity (Hertel et al., 2020) in response to urban space, which could be key in identifying which individuals are more flexible to anthropogenic change.

APPENDIX

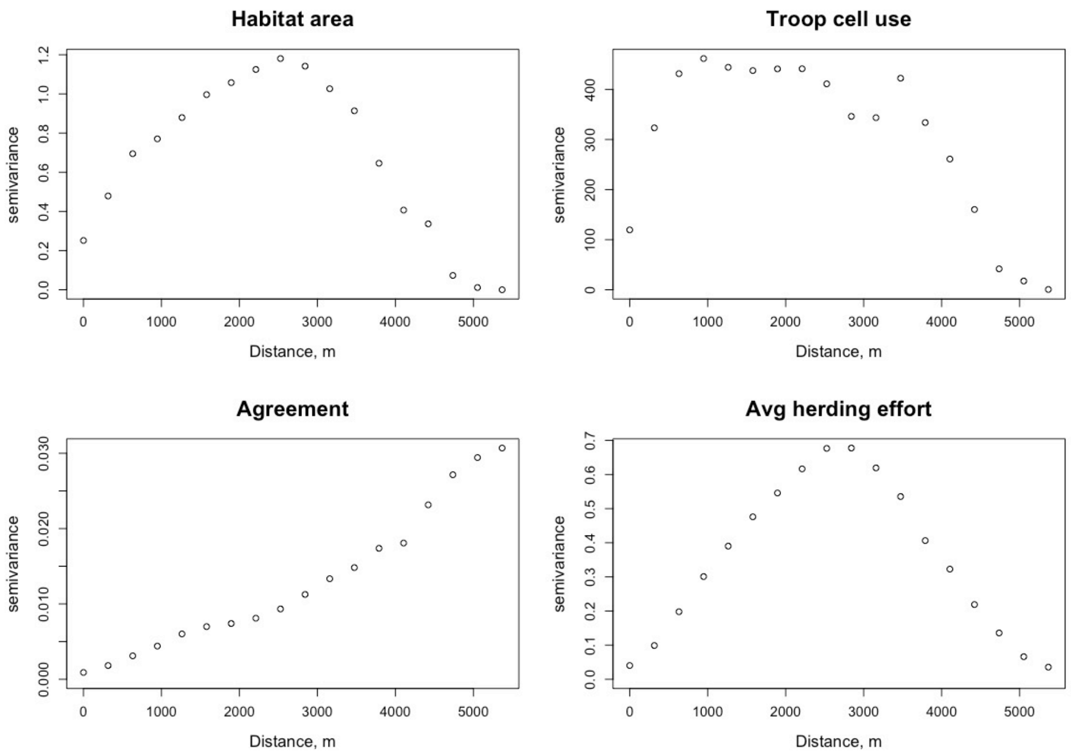

Figure IV-S1. Semivariogram for each factor studied. 1) Habitat area, 2) troop cell use, 3) agreement score between rangers, 4) average herding effort. All fixed effects are spatially autocorrelated to a distance of 3000m or greater.

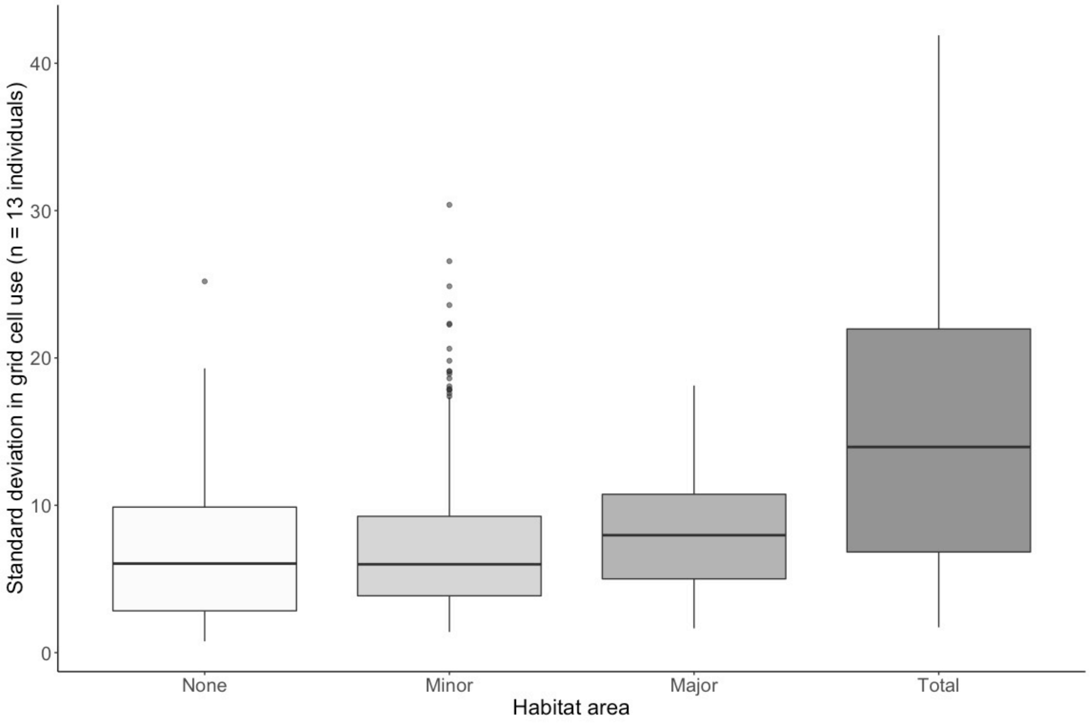

Figure IV-S2. Individual variation in grid cell-use. Standard deviation across individuals for different habitat areas (classified by the degree of human change).

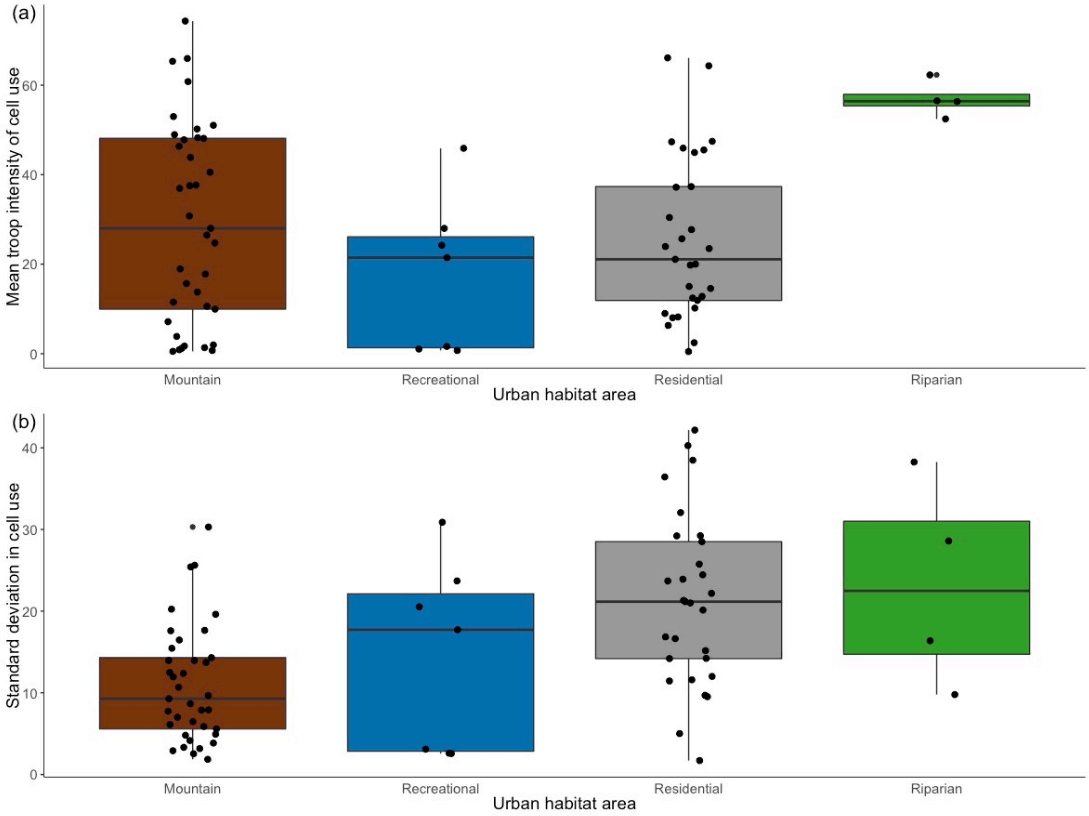

Figure IV-S3. Inter-individual use of urban habitat areas. (a) Average troop urban grid cell use: mean troop use **across grid cells** for different habitat areas. (b) Individual variation in urban grid cell use: standard deviation **across individuals** for different habitat areas.

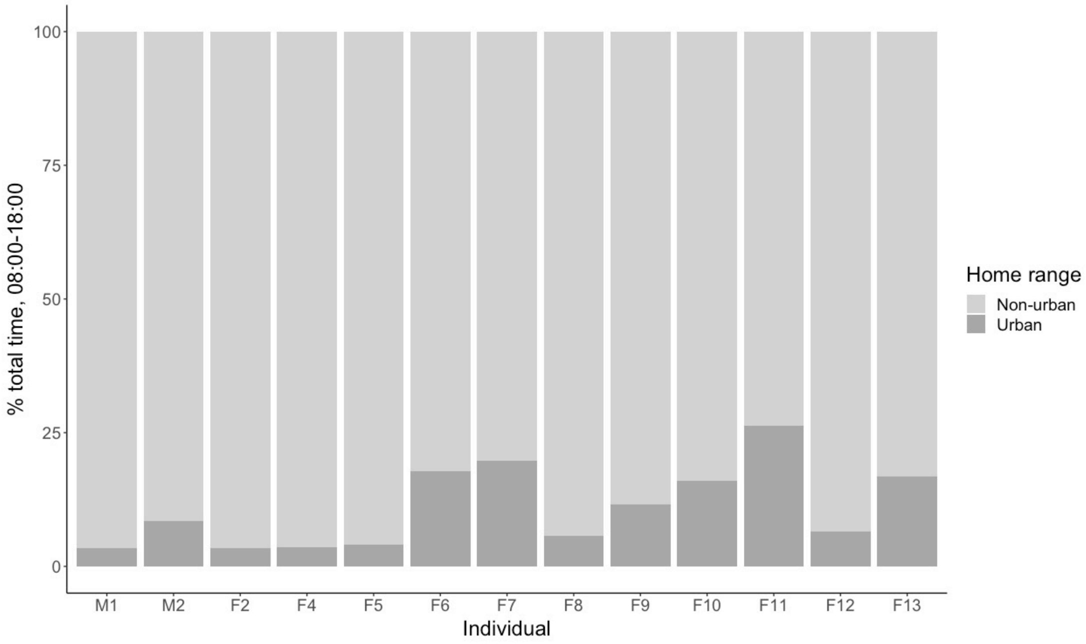

Figure IV-S4. Proportion of time (%) baboons spent in urban space for n = 13 individuals, using daytime data (08:00 – 18:00).

Table IV-S1. Correlation matrix (Spearman) of fixed effects considered to explain baboon space-use. Fixed effects correlated with a coefficient greater than 0.4 (highlighted in bold) were not added in the same model.

	Habitat area	Avg. score	Agreement
Habitat area			
Avg. score	0.40		
Agreement	-0.23	-0.12	

Table IV-S2. Results from Partial Mantel Tests (999 permutations) for the rangers' strategy according to the environmental fixed effect. Results show the Mantel statistic r and their significance.

	Average effort		Agreement	
	r	p	r	p
Degree of human change	0.1915	<0.01	0.1029	<0.01

Table IV-S3. Spatial Simultaneous Auto-Regressive lag models (SAR lag) predicting baboon space-use in 95% home range

Model	df	AIC	logLik	L.ratio	p
Habitat	6	1440.1	-714.05	454.2	<0.01
Management	5	1442.7	-716.35	469.25	<0.01

Table IV-S4. Factors explaining troop space-use. The best model explaining the intensity of cell use was estimated by a spatial Simultaneous Auto Regressive lag model (SAR lag) taking into account habitat area, with intensity of cell use significantly lower in areas of minor human change than areas with no human change (intercept). The spatial component rho was 0.9272, (LR test value: 469.25, p < 0.001) and spatial autocorrelation was found in the residuals (Moran I: 0.6244, p = < 0.01).

Model	Degree of human change	Estimate	SE	Z	p
Habitat	Intercept (None)	0.43661	0.13403	3.2575	<0.01
	Minor	-0.32099	0.14215	-2.2582	<0.05
	Major	-0.21300	0.17314	-1.2302	0.219
	Total	-0.10052	0.17150	-0.5861	0.558

Table IV-S5. Individual-level factors explaining baboons' urban space-use.

Model	Estimate	SE	t	χ^2 LRT	p LRT
m1: Centrality	-36.374	11.164	-3.258	7.761	0.005
m2: Rank	-26.440	8.493	-3.113	7.242	0.007

Chapter Five

Personality and plasticity in movement metrics for chacma baboons moving between urban and natural space

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Statement of contributions:

AB and AJK designed the study. AB and CC conducted and led the field work. AB compiled data and conducted analyses with advice from AJK. AB wrote the chapter which was critically reviewed by AJK.

This chapter has been prepared for submission to a scientific journal

ABSTRACT

Animal behaviour varies both among individuals (“personalities”) and within individuals (“plasticity”). Both personality and plasticity in behaviour can allow individuals to cope adaptively with changing environmental conditions and to anthropogenic change. Quantifying animal personality and plasticity for individuals in wild populations is difficult because it requires repeatable observations of behaviour over time and context. However, novel animal-attached tracking technologies now allow researchers access to high-resolution movement data on lots of individuals at once, affording repeatable estimates of movement-based behavioural metrics which are commonly used in studies of animal personality and plasticity. Here, I use high-resolution GPS data to investigate individual movement (step lengths, path tortuosity and residence times) for n = 13 adult baboons in a troop living on the urban edge in Cape Town, South Africa, testing for personality and/or plasticity in baboon movements between urban and natural spaces. I find that individual baboons: 1) consistently differ from one another in step length and path tortuosity (personality); 2) vary in the extent to which they alter all three movement metrics across environment (plasticity); moreover, 3) plasticity in step length and residency times are linked to differences in individual’s urban space-use (and indirectly their dominance rank and eigenvector centrality in the group spatial network) and 4) plasticity in path tortuosity is linked to individual personality. These findings reinforce emerging research linking individual movement ‘signatures’ to personality differences and highlights the relative importance of both phenotypic characteristics and intrinsic personality differences to individual responsiveness to environmental change.

INTRODUCTION

Animal behaviour varies both among individuals ("personalities") and within individuals ("plasticity") (Carter et al., 2012a; Dingemanse et al., 2010). This behavioural personality (Dingemanse et al., 2010) and plasticity (Carrete & Tella, 2011; Piersma & Drent, 2003; Sol et al., 2002) can predict how individuals cope adaptively with changing environmental conditions (Dingemanse & Wolf, 2013; Koolhaas et al., 1999; Réale et al., 2007) as particular phenotypes are typically more responsive to change (Quinn et al., 2012). With increasing human-induced changes to the environment, studies describing links between personality and individuals' use of human-altered landscapes are becoming more common (Honda et al., 2018; McDougall et al., 2006; Merrick & Koprowski, 2017; Sol et al., 2013). For example, bolder or more exploratory individuals can be more likely or more successful at invading urban environments (Atwell et al., 2012; Phillips & Suarez, 2015; Sol et al., 2013). However, studies of whether and how plasticity determines individuals' use of human-altered landscapes are less common, despite personality and plasticity co-varying in other contexts (e.g. to predation risk: Dingemanse et al., 2007; Fürtbauer et al., 2015; Quinn et al., 2012 or ambient temperature: Spiegel et al., 2015).

Studies of animal personality and plasticity have traditionally been conducted in controlled laboratory or open-field settings (Réale et al., 2007) and tend to take a "two-step approach"; firstly quantifying repeatable individual traits using an experimental set-up, and secondly linking these to natural behaviour in the wild (Niemelä & Dingemanse, 2014). Problems associated with this approach include the ambiguous interpretation of behaviours from experimental tests, as well as uncertainty around how applicable these behaviours are to those seen in the wild (Carter et al., 2013a; Carter et al., 2012c; Niemelä & Dingemanse, 2014). To investigate animal personality and plasticity in response to human-altered landscapes therefore ideally requires in-situ measurement of animal personality and plasticity with reference to the environmental gradient/change (Bombieri et al., 2021; Hertel et al., 2019; Wat et al., 2020).

The use of novel technologies enabling tracking of animal movements at high spatial and temporal resolution (Fehlmann & King, 2016) is now affording study of personality and plasticity in the wild (Hertel et al., 2019; Hertel et al., 2020; Spiegel et al., 2015). Indeed, because many personality traits have implicit movement-based definitions (Bailey et al., 2021; Hertel et al., 2019; Hertel et al., 2020; Spiegel et al., 2017) tracking data offers repeatable measures of personality (Hertel et al., 2020). For example, information on animal step lengths, distribution of turning angles and residency times correlate with more traditional behavioural metrics used in the animal personality literature (Bailey et al., 2021). Where many individuals can be tracked simultaneously (Hughey et al., 2018), studies of personality and plasticity in the wild becomes easier (Hertel et al., 2020) and has numerous applications for animal conservation (Hertel et al., 2019; Honda et al., 2018; Merrick & Koprowski, 2017). For example, consistent differences in individual movement can predict individual risk for hunting or poaching (Leclerc et al., 2019), locate “problem” individuals in a population (Honda et al., 2018; Merrick & Koprowski, 2017), and highlight individual differences in stress responses under anthropogenic change (Carere et al., 2010; Merrick & Koprowski, 2017).

Here, I use high-frequency GPS biologgers to study personality and plasticity (using individual movement trajectories) for chacma baboons that use both natural and urban spaces in Cape Town, South Africa. Baboons show extreme behavioural flexibility (Alberts & Altmann, 2006), allowing them to adapt to novel environments and situations (Fehlmann et al., 2017a; van Doorn et al., 2010). For example, studies of baboons in Cape Town have revealed that male baboons adapted to urban-foraging spend significantly less time foraging than naturally foraging baboons elsewhere (Fehlmann et al., 2017b), and research here on the current study group has shown that socially-peripheral, low-ranking female baboons show greater use of urban space because they have weaker social affiliations to higher-ranking, socially-connected baboons (i.e. the alpha male and high-ranking females) that tend to be deterred by field rangers (Chapter 4). There is also evidence of personalities in wild baboons (Seyfarth et al., 2012), with “bolder” individuals better at problem solving tasks (Carter et al., 2014) and foraging when information is unreliable (Carter et al., 2013b). Baboons therefore provide an ideal system to study the link between personality, plasticity, and anthropogenic change.

To test for personality (among individual differences) and plasticity (within individual differences) in movement trajectories, I explore common movement metrics (distances travelled, tortuosity of path, residency times) (Barraquand & Benhamou, 2008; Hertel et al., 2020) across individuals moving in natural and urban space. I predicted 1) consistent inter-individual differences in movement (personality) (Bailey et al., 2021; Hertel et al., 2020; Spiegel et al., 2015), 2) differences in the extent to which individuals change their movement across environments (plasticity) (Hertel et al., 2020; Stamps, 2016), and 3) covariation between personality and plasticity (Hertel et al., 2020; Spiegel et al., 2015). Because I have previously found that low-ranking, socially-peripheral females show greater use of urban space (Chapter 4), I also tested if and how individual personality and/or plasticity are linked to individual urban space-use, their dominance rank (Kohn et al., 2016; Seyfarth et al., 2014), and spatial network position (Moyers et al., 2018; Seyfarth et al., 2012).

METHODS

Study site and subjects

I studied a single baboon group (the Da Gama troop), who live on the Cape peninsula, South Africa. The troop comprised 2 adult males, 19 adult females, and approximately 30 subadults, juveniles and infants of both sexes. The troops range includes urban and natural space. The urban space is largely made up of housing, surfaced roads and local amenities, and dotted with small patches of alien vegetation (such as a riverbed and small stands of 5-6 trees).

The natural space is dominated by indigenous fynbos vegetation with smaller patches of exotic vegetation (Hoffman & O’Riain, 2011; van Doorn & O'Riain, 2020) and largely open. I studied the troop between July and November 2018 and here use data collected mainly during the austral winter (July, August) when the GPS collars were active and when the Peninsula baboons show greater use of urban space (van Doorn et al., 2010).

Collar data

To examine individual patterns of movement, n = 16 adults were fitted with SHOAL group in-house constructed collars (F2HKv3), which recorded GPS positional data at 1 fix/second between 08:00 – 20:00 local time (GiPSy 5 tags, TechnoSmArt, Italy). I use “daytime” hours for the troop in analyses (08:00 – 18:00 local time). Data from 15 collars were retrieved (one collar was not found after release) and two collars failed to record GPS, resulting in individual GPS data for n = 13 baboons (which represented 61% of all adults in the troop), over mean ± S.D. of 42.77 ± 9.92 days, range = 21 - 54 days (Table III-S1, Chapter 3). Further details about collar ethics, trapping and GPS data processing can be found in methods chapter and data chapter 3.

Designation of habitat

To examine individual trajectories in both natural and urban space, the groups 95% home range (calculated in Chapter 4) was divided into “urban space” (See Fig. III-2, Chapter 3), using QGIS (QGIS.org, 2020). I used the function “getRecursionsInPolygon” from the “Recurse” package, R (Bracis et al., 2018) to obtain seconds spent in the urban space. Using this I labelled all seconds spent by each baboon in urban space as “urban” and all other seconds as “natural”.

Movement metrics

Movement parameters can be calculated using GPS fixes summarised across different time intervals. Here, I sub-sample high-frequency GPS data and calculate parameters using GPS data at 1-minute intervals since this is expected to retain information about the movement path, whilst minimising any false movement that can occur at higher GPS resolutions due to positional error (McCann et al., 2021; McGavin et al., 2018; Noonan et al., 2019; Ranacher et al., 2016). Using different subsampling (10s, 30s, 60s, 120s) of the GPS data did not qualitatively affect the findings (Fig. V-S1 – V-S3). For analyses, I use daily mean and median values (mean presented in main text, median in Appendix) for each movement parameter, for each baboon, in both urban and natural space, on each day data were available; resulting in a mean of 60 values per baboon, range 33 – 74 (over a mean of 40 days per baboon, range 21 – 47).

I calculated movement parameters commonly used to analyse individual movement trajectories (Pasquaretta et al., 2021), that have been used for understanding responses of wildlife to anthropogenic landscapes (Troup et al., 2020) and in the identification of behavioural types (Hertel et al., 2020): step length, turning angles (calculated here as path “sinuosity”: Benhamou, 2004) and residence time (Fig. V-1).

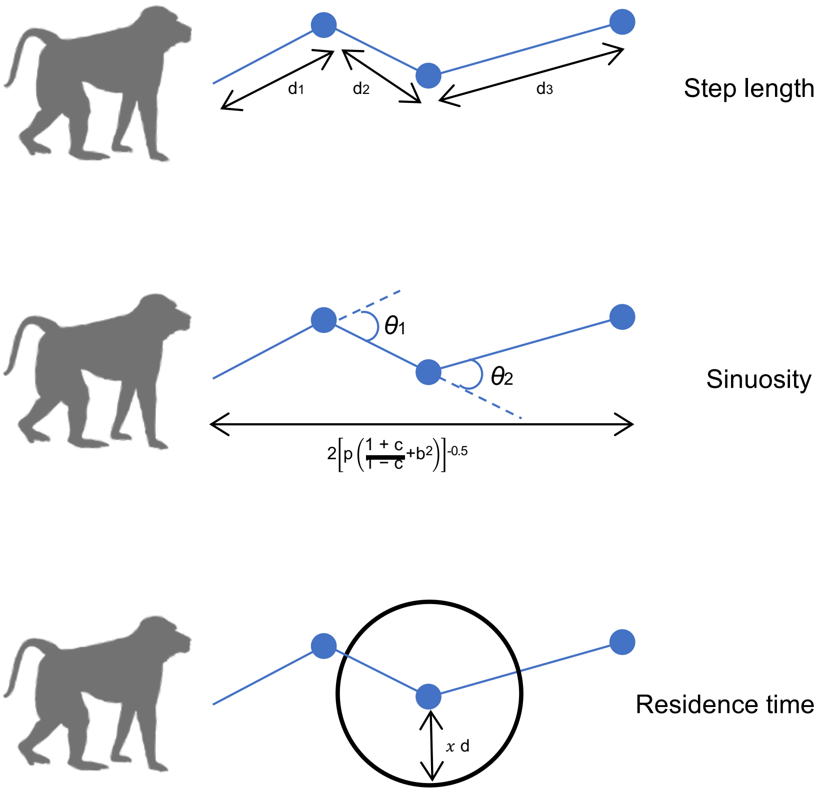

Figure V-1. Three movement metrics calculated for n = 13 baboon trajectories from high-resolution GPS tracking data.

Because step length is a “stepwise” path characteristic (Edelhoff et al., 2016) mean daily averages were calculated based upon values for each minute (i.e. distance between steps: Calenge et al., 2009). Sinuosity is a measure of the tortuosity of a path and is calculated as a function of the mean cosine of turning angles (Fig. V-1; Benhamou, 2004), where high values indicate a more tortuous path. Sinuosity is a “path” metric, and requires multiple relocations (a “path-segment”) (Edelhoff et al., 2016), and was therefore calculated for periods of time in natural or urban space of over 5 minutes in duration; time periods less than this (e.g. baboons moving quickly into or out of each habitat) were considered not appropriate, and were not included in calculating sinuosity. Residence time is commonly calculated as the length of time an individual spends inside a circle of the radius of its mean step length centred on its GPS fix location, without leaving the patch for more than a specified cut-off time (Fig. V-1; Calenge, 2006). Residence time is also a “stepwise” path metric (Edelhoff et al., 2016), however since it requires a “cut off” time (within which the individual remains in a specified radius centred on each GPS fix), I calculated residence time for trajectories with a minimum of five consecutive GPS fixes whilst setting the cut-off time at five minutes. This increases the likelihood residence time was calculated only for times individuals were in either urban or natural space. If there were multiple path-segments in urban or natural space in a day, a mean average was taken to give a daily measure in urban and natural space.

Individuals’ urban space-use

Calculation of individual urban space-use has previously been described in Chapter 4. Briefly, I determined urban space-use by overlaying the urban polygon with 150 m x 150 m grid cells (larger than the average spread of a group on the Cape Peninsula: Hoffman & O'Riain, 2012b) in QGIS, and then calculating the intensity of cell-use using fixed kernel densities and an ad-hoc method for choosing the smoothing parameter, with the function “getvolumeUD” from the package “adehabitat” in R (Calenge, 2006). This resulted in n = 55 intensity of cell-use values for each individual (as there were 55 urban grid cells), between 0 - 100; with 0 indicating no use, to 100 indicating complete use. I examined variation in individual baboons’ urban space-use by subtracting an individual’s urban grid cell-use from the group average, the result indicating whether an individual used a given cell more or less than the group average. I obtained a single urban space-use score for each individual by taking the mean average of these 55 values.

Dominance rank

Calculation of dominance rank has been outlined previously (Chapter 3), but in brief was determined from direct *ad libitum* observations over 78 days, of aggressive interactions (displacements, chases and aggressive displays) between pairs of baboons, and following the clear submission of one individual. Female dominance rank was calculated from 634 interactions (median = 96, range 11 – 129) using the IS&I method and the packages "AniDom" and "Compete" in R (Sánchez-Tójar et al., 2018). Male dominance rank was calculated from 75 interactions: M1 won 28 interactions (37%) and M2 won 16 interactions (21%), with 31 interactions undecided (41%), and therefore M1 was ranked first. Adult males outrank adult females in baboon groups (Engh et al., 2009; Kitchen et al., 2009). Ranks were standardised between 0 and 1 (with 0 being the lowest and 1 being the highest ranking individuals), using the function "rescale" from the "scales" package, R (Wickham, 2014).

Social cohesion

Calculation of individual social cohesion has been described previously (Chapter 3), but in brief, I extracted eigenvector centrality from proximity-based social networks, based on occasions that 10 or more individuals were outside the urban space (following a sensitivity analysis: Fig. III-S1, Chapter 3). Association networks were constructed using the "Spatsoc" package in R (Robitaille et al., 2019). Baboon GPS fixes were grouped spatiotemporally, where individuals within 5 metres and 1 minute of one another were assumed to be in association using the "chain rule" (Castles et al., 2014) and a gambit-of-the-group approach (Franks et al., 2010). Network edges (the strength of associations between baboon dyads) were weighted using the simple ratio index (Farine & Whitehead, 2015).

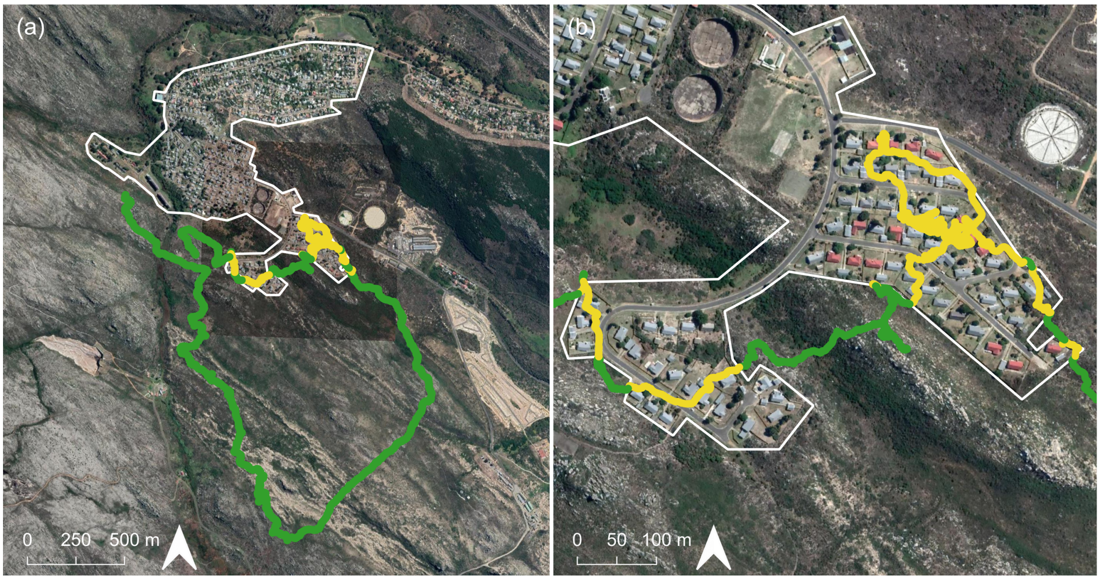

Figure V-2. Trajectory for a single baboon, on 26-08-2018, moving in both natural (green line) and urban (yellow line) space. (a) is the whole days trajectory, (b) is zoomed in to urban space.

Statistical analyses

I used a linear mixed model approach following the R tutorial published in Hertel et al., (2020). First, I fit linear mixed models with each movement parameter as the response variable using the lme4 package in R (Bates et al., 2015), and fitted individual ID and date as random factors, and area (natural, urban) and sex (male, females) as fixed categorical effects. Additionally, I added eigenvector centrality in the spatial network, dominance rank, or mean urban space-use as a continuous fixed effect in separate models, as they correlate with one another (Table V-S1). Where fixed effects were non-significant, I removed them from the model. To test for consistent among individual variation (personality) in traits, I use the "rpt" function in the "rptR" package, R (Stoffel et al., 2017). To obtain confidence intervals around the repeatability estimates, I bootstrapped all models over 1000 iterations. To test if personality and plasticity co-vary (I x E effects), I then fit the same model whilst also including space (natural, urban) with the random effect of ID and compared model fits using Akaike Information Criteria (AIC). I log transformed all response variables (step length, sinuosity and residence time) to meet normality criteria, which was assessed using graphical procedures (histograms and Q-Q plots). Correlation of intercept (m1) and slope (m2) with phenotype (dominance rank, eigenvector centrality and mean urban space-use) was assessed using a Spearman’s rank correlation analysis.

RESULTS

Movement metrics

Step length was negatively correlated with sinuosity (Spearman’s rho: -0.703, n = 13, p = 0.009; Fig. V-S4b), indicating that individuals which travel further take straighter paths. Residence time was not correlated with step length (Spearman’s rho: -0.429, n = 13, p = 0.146; Fig. V-S4a) or with sinuosity (Spearman’s rho: 0.297, n = 13, p = 0.325; Fig. V-S4c). Median values are presented in Table V-S2, Appendix.

Personality and Plasticity

Repeatable individual differences (personality) were found for step length and sinuosity (intercept; Table V-1; Figure V-3a-c). All metrics (step length, sinuosity and residence time) changed across natural and urban space, indicating plastic responses to the environment (slope) (Table V-1; Figure V-3a-c).

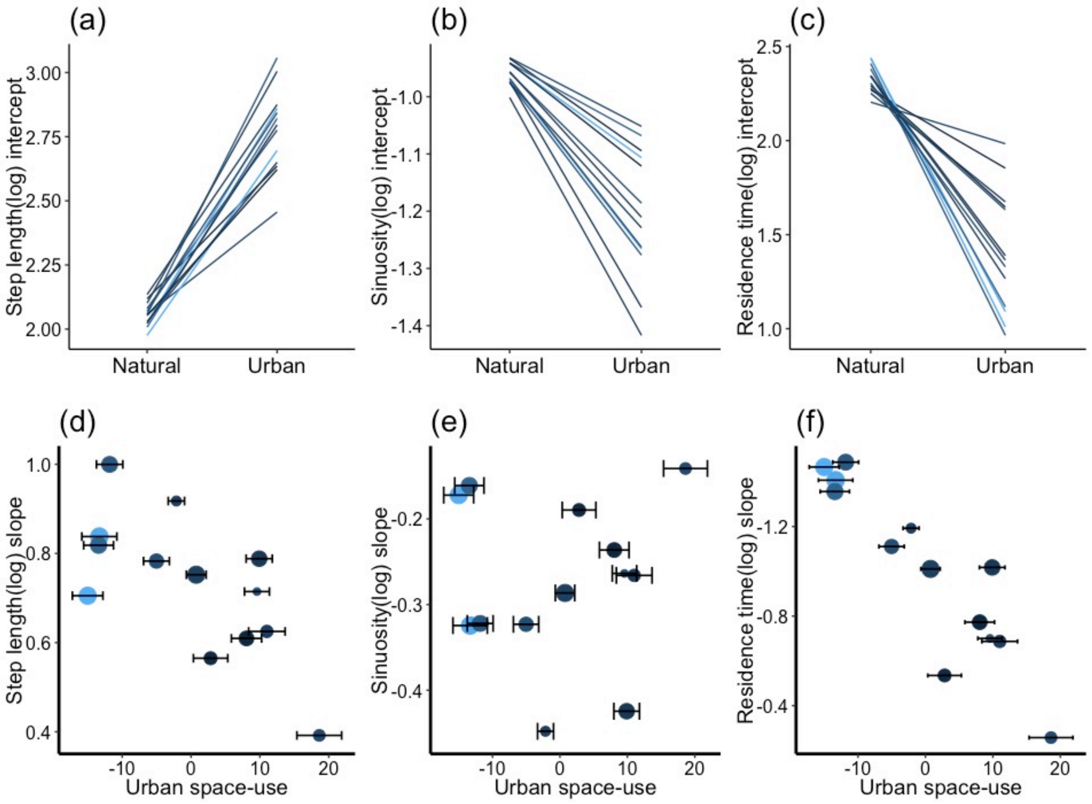

Figure V-3. Personality and plasticity in movement metrics. Individual intercept and slope for (a) step length, (b) sinuosity and (c) residence time calculated from n = 13 baboon trajectories when ranging over natural and urban space. Each line represents data for an individual and is coloured according to its eigenvector centrality in the spatial network. (d) Negative correlation between the slope of mean step length (log) and mean urban space-use. (e) No correlation between the slope of mean sinuosity (log) and mean urban space-use. (f) Positive correlation between the slope of mean residence time (log) and mean urban space-use. Residence time y-axis in (f) is inverted to aid interpretation of results since lower urban space-use values are associated with a steeper slope. In (d-f) error bars represent standard error around individual mean urban space-use values (across 55 urban grid cells). Individuals which exhibit greater use of urban space tend to have low eigenvector centrality (indicated with darker blue colours (lines in a-c, points in d-f), and tend to be of low dominance rank (indicated with smaller point size in (d)-(f); Chapter 4).

Personality was not correlated urban space-use, dominance rank, or social network position (Table V-S3, Appendix). In contrast, plasticity in step length was correlated with urban space-use, where individuals that used less of the urban space showed greater plasticity (increasing their step lengths to a higher degree in urban space than individuals which used more urban space: Fig. V-3a). Plasticity for residence time was predicted by dominance rank, social network position and mean urban space-use (which are all correlated: Table V-S1), whereby high-ranked, socially-connected baboons that use less urban space showed more plastic behaviour (i.e. they decreased their residency times to a higher degree in urban space than low-ranked, socially-peripheral baboons) (Table V-1; Fig. V-3c). Plasticity for sinuosity was not predicted by urban space-use, dominance rank, or social network position (Table V-1; Fig. V-3b).

Covariation in personality and plasticity (I x E)

Personality (intercept) was positively correlated with individual plasticity (slope) for sinuosity, indicating individuals that travelled straighter paths on average travelled even straighter paths in urban space (Table V-1; Fig. V-3b) and showed greater plasticity in response to being in urban space. Personality (intercept) was also negatively correlated with individual plasticity (slope) for residency time indicating that individuals with high residency times on average decreased their residency times in urban space to a greater extent than individuals with low residency times on average (Table V-1; Fig. V-3c).

Table V-1. Personality and plasticity in movement parameters for baboons in natural versus urban space in Cape Town, South Africa. Mean daily values for movement metrics are presented. Personality repeatability estimates (R), with 95% confidence intervals (CI) and corresponding p-values are presented using the “rptR” package, R (Stoffel et al., 2017). Plasticity to environment is determined by a lower AIC value for the model allowing individual ID to vary across environment (m2) (Hertel et al., 2020). Correlation between intercept (personality) and slope (plasticity) is determined from m2 (Hertel et al., 2020), and correlations between social factors and mean urban space-use with slope (plasticity) are calculated with a Spearman’s Rank Correlation analysis.

Metrics (mean)	Personality (intercept)	Plasticity (slope)	Correlation			
		AIC	I x E	Rank x E	Centrality x E	Mean urban space-use x E
Step length	**_R_ = 0.034** **CI = [0.005, 0.075]** **_p_ < 0.001**	m1: 733.712 **m2: 711.088**	-0.18	rho: 0.336 *p* = 0.262	rho: 0.434 *p* = 0.140	**rho: -0.566** **_p_ = 0.047**
Sinuosity	**_R_ = 0.027** **CI = [0.002, 0.065]** **_p_ < 0.001**	m1: 503.376 **m2: 492.679**	**0.59**	rho: -0.041 *p* = 0.894	rho: 0.104 *p* = 0.737	rho: 0.060 *p* = 0.849
Residence time	*R* = 0.009 CI = [0, 0.03] *p* = 0.073	m1: 1537.673 **m2: 1483.881**	**-0.85**	**rho: -0.638** **_p_ = 0.019**	**rho: -0.687** **_p_ = 0.012**	**rho: 0.863** **_p_ < 0.001**

DISCUSSION

I provide evidence for repeatable individual differences in movement in a troop of baboons and examine how these are flexible to environmental change. Specifically, I demonstrate that individual baboons: 1) consistently differ from one another in certain movement metrics, showing evidence of personality; 2) vary in the extent to which they alter certain movement metrics across environment, showing evidence of individual plasticity; 3) find that variation over environment in some movement metrics is linked to how much the baboons use urban space (which is determined by individual phenotype, i.e. dominance rank and eigenvector centrality in the group spatial network) and 4) show that plasticity in other movement metrics over environment is linked to individual personality. I discuss these findings in turn.

Individual baboons showed repeatable differences in their step length and sinuosity, and these two measures are negatively correlated, indicating that directed paths (low sinuosity) is related to higher activity (greater travel distances), and these traits consistently differ among individuals. This negative correlation may be a result of variation in individual energetics or locomotor capacity (e.g. due to age, sex, body size, reproductive state: Ceccarelli et al., 2020; Harel et al., 2021). Previous work on olive baboons in Kenya has indicated that smaller-bodied individuals spend more time moving in an effort to keep up with the group during collective movements (Harel et al., 2021). It may be the case that smaller-bodied adults in the Da Gama troop travel further and pause less to forage when moving, therefore taking more directed paths. These inter-individual differences in step length and sinuosity did not correlate with an individual’s sex, dominance rank, social network position, or amount of urban space-use, therefore suggesting intrinsic differences in movement indicative of a personality trait. Indeed, individuals that travel further are more active; a trait correlated with being bolder or more exploratory (Kurvers et al., 2009; Patrick et al., 2017) and directedness of travel has been linked to exploration tendency (Tsalyuk et al., 2019), where some individuals explore novel areas more quickly and superficially and others more slowly and methodically (Bailey et al., 2021; Dingemanse et al., 2002).

Individuals did not consistently differ from one another in residence time. Residence time of an individual in a given area is indicative of spatial heterogeneity of the environment: areas where individuals spend more time are likely more profitable (Barraquand & Benhamou, 2008). If spatial heterogeneity is controlled for, than individual differences in residence time can be interpreted as differences in exploration behaviour (Hertel et al., 2020). I did not find inter-individual differences in residence time however, which may be due to the cohesive structure of baboon troops (Lehmann et al., 2007), as well as their movement being influenced by field ranger practices (Fehlmann et al., 2017a; Fehlmann et al., 2017b), both of which may result in no individual spending more time in one area than another.

Baboons increased their step length in urban space. Greater travel distances in urban space is likely due to the heterogeneous distribution of food resources, along with higher environmental risks and rewards (Fehlmann et al., 2021). Indeed, adult male Cape baboons have previously been shown to adopt a “sit-and-wait strategy”: spending much time on the urban edge and then making high-activity forays to the urban space (Fehlmann et al., 2017b), which likely translates into greater step lengths in urban space. The magnitude of increase did vary across individuals, with individuals with lower urban space-use increasing their step lengths even more so in urban space compared to individuals with higher urban space-use, but this was not linked to their intercept (personality). Because individuals with higher urban space-use tend to be lower ranked and spatially peripheral (Chapter 4), plasticity in step length was also correlated with dominance rank and eigenvector centrality. I therefore interpret plasticity in step length across natural and urban spaces as a management effect. Management of the Da Gama troop disproportionately focuses on adult males and high-ranking, socially-connected females (Chapter 4), which means that (i) these baboons spend less time in urban space, and

(ii) when they are in urban space, they tend to be herded by rangers resulting in greater travel speeds (and therefore greater step lengths).

Mean sinuosity also showed plastic individual differences across environment – individuals decreased their sinuosity in urban space. Increased directedness of paths in urban space is likely because of goal-oriented movements between food resources (Benhamou, 2004) that are more predictable in space and time (i.e. waste bins, fruiting trees, compost heaps), and the effect of field rangers herding them out of urban space (van Doorn & O'Riain, 2020). Unlike plasticity in step length, plasticity for sinuosity was positively correlated with personality, where individuals which repeatedly travelled more directed paths (low "sinuosity") travelled in an even more directed manner in urban space than individuals which tend to travel more tortuous paths overall. It therefore seems the case that higher exploration tendency of individual baboons, measured by path directedness, is related to increased plasticity of response to urban space. Evidence from other species also indicates the importance of individual exploration behaviour in urban space-use: in the brushtail possum (*Trichosurus vulpecula*) more exploratory individuals ranged further within an urban habitat (Wat et al., 2020).

Residence time was also plastic across environment – with individual baboons decreasing residency time within an area when in urban space. Urban spaces have a patchy distribution of high quality food resources combined with greater environmental risks (Fehlmann et al., 2021), which likely leads to baboons spending less time in a given area then when in natural space. Individuals that changed their residency times to a greater extent between environments tended to be those higher ranked, socially-connected baboons that use the urban space less. Additionally, intercept and slope were negatively correlated, suggesting individuals with high residency times on average spent less time in one area when in urban space than individuals with low residency times overall. These findings therefore again suggest that plasticity in behaviour in urban space is driven by environmental changes associated with the effects of management.

Overall, whilst I find that individuals that tended to travel more directed paths overall (personality) showed a greater plasticity of response to urban space than other individuals (I x E effect), this was not true of the other movement metrics. Instead, those individuals that changed their movement less used urban space more. Flexibility in behaviour is often touted as key to coping with anthropogenic change (Sol et al., 2013; Sol et al., 2002; Wright et al., 2010) and so this is an initially puzzling result. But, context matters, and here, those baboons showing the most flexible behaviour are those that are disproportionately affected by field ranger management practices in the urban space. Baboons that show less flexible movement do so because they are not required to – they are less at risk of being herded. These findings therefore contribute to the growing body of literature linking personality to movement (Bailey et al., 2021; Hertel et al., 2020) providing some of the first direct evidence of how intrinsic individual movement patterns are changed in human-altered landscapes.

APPENDIX

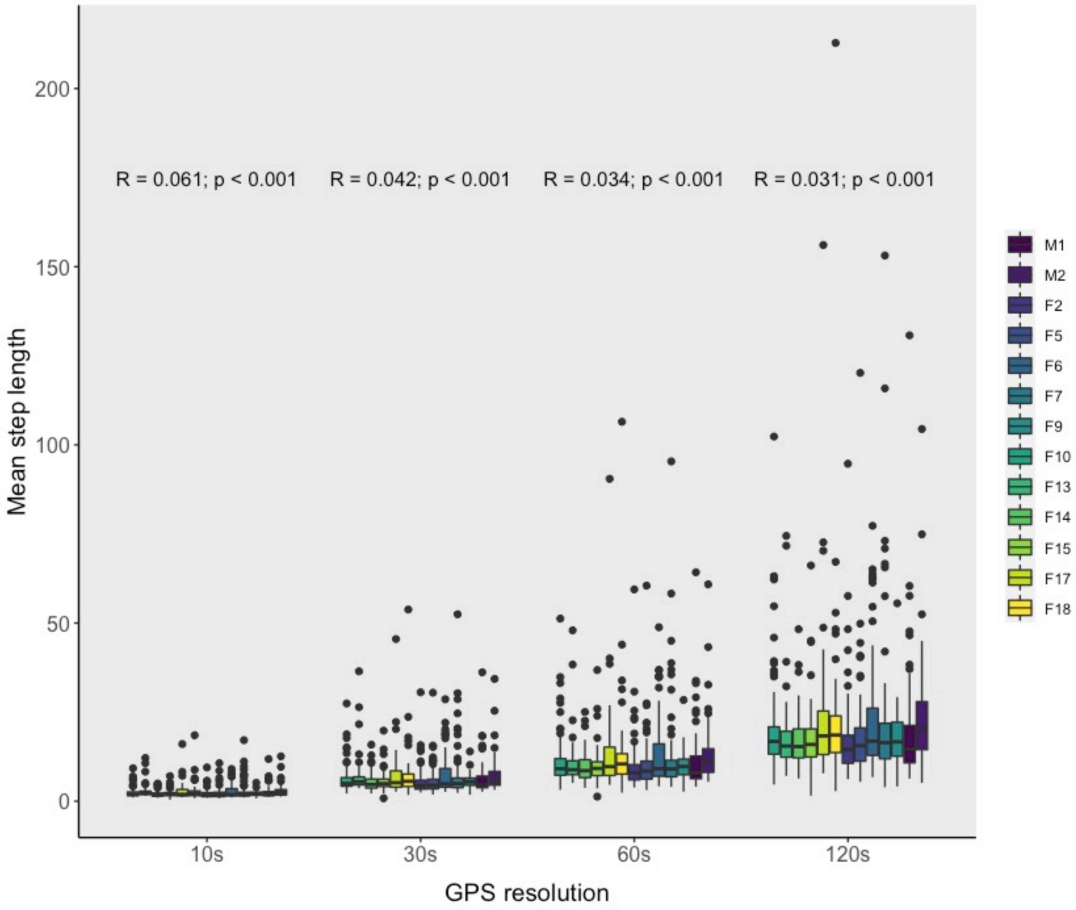

Figure V-S1. Repeatability estimates for mean step length (log) for different GPS resolutions (10s, 30s, 60s, 120s), calculated using the “rptR” package, R (Stoffel et al., 2017).

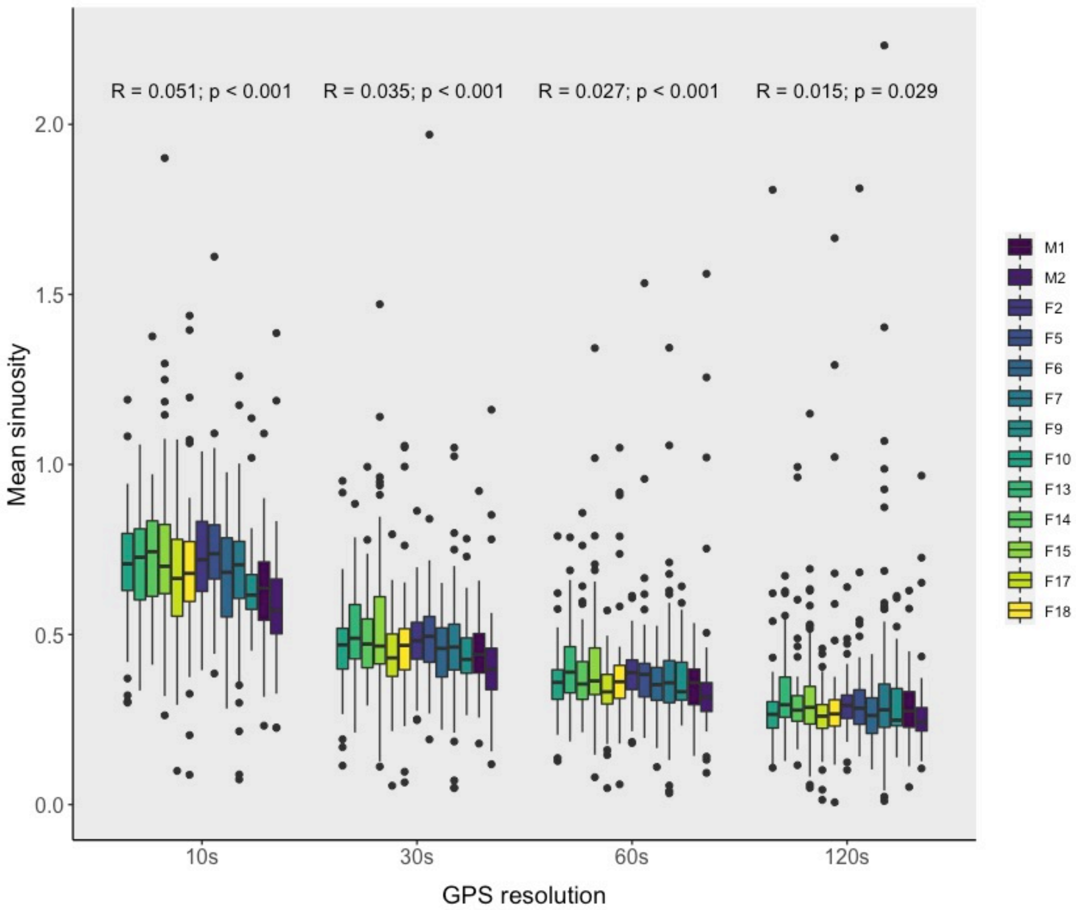

Figure V-S2. Repeatability estimates for mean sinuosity (log) for different GPS resolutions (10s, 30s, 60s, 120s), calculated using the "rptR" package, R (Stoffel et al., 2017).

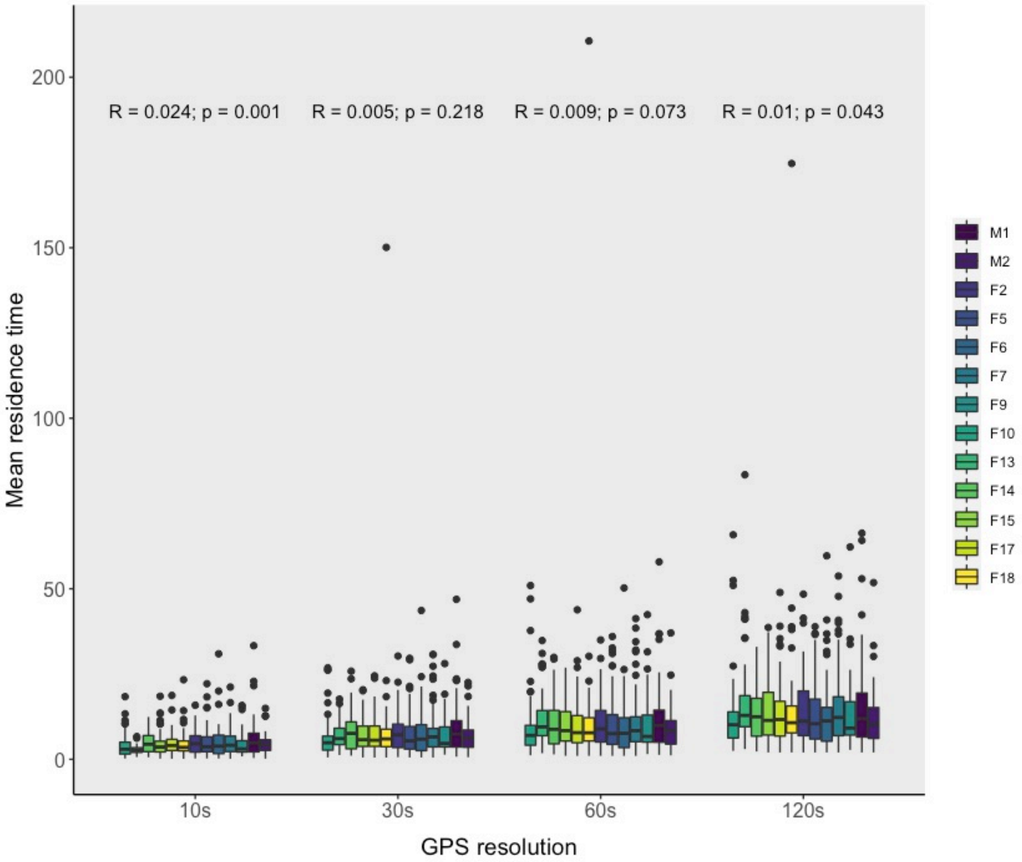

Figure V-S3. Repeatability estimates for mean residence time for different GPS resolutions (10s, 30s, 60s, 120s), calculated using "rptR" package, R (Stoffel et al., 2017).

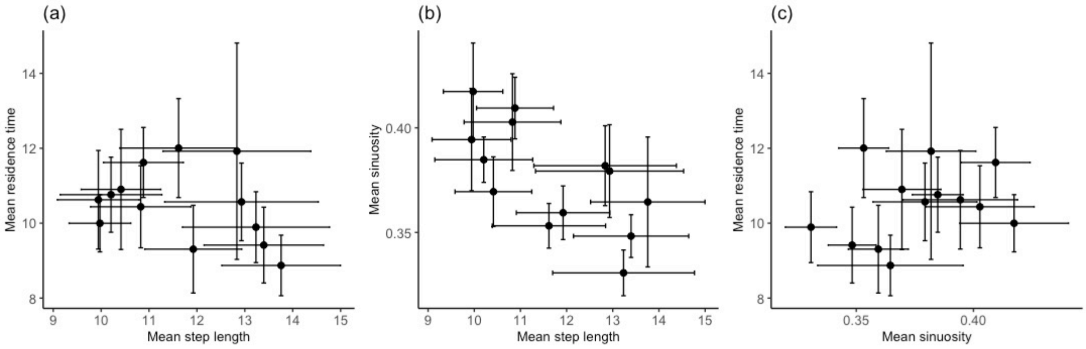

Figure V-S4. Correlation plots of metrics, for n = 13 individuals. (a) No correlation between mean step length and mean residence time; (b) negative correlation between mean step length and mean sinuosity; (c) no correlation between mean sinuosity and mean residence time. Error bars indicate standard error.

Table V-S1. Correlation matrix (Spearman) of individual fixed effects (n = 13 individuals), tested in separate models.

	Rank	Centrality	Mean urban space-use
Rank			
Centrality	0.48		
Mean urban space-use	-0.66	-0.73	

Table V-S2. Correlation matrix (Spearman) of median value (across days and area) for each movement parameter, for n = 13 individuals.

	Step length	Sinuosity	Residence time
Step length			
Sinuosity	0.06		
Residence time	0.13	-0.09	

Table V-S3. Results of linear mixed models examining the importance of phenotype on personality for n = 13 individuals in a group of baboons living on the urban edge in Cape Town, South Africa. Estimates, t-values, p-values for each model are presented. Fixed effects were correlated and therefore tested in separate models with the fixed effect of area (natural, urban), whilst controlling for individual ID and date.

	Model	Estimate	Std. Error	*t*-value	*p*-value
Mean step length (log)	Centrality	-0.139	0.122	-1.143	0.278
	Rank	-0.014	0.083	-0.166	0.871
	Urban space-use	-0.001	0.002	-0.623	0.546
Mean sinuosity (log)	Centrality	0.010	0.101	0.108	0.916
	Rank	-0.036	0.064	-0.565	0.583
	Urban space-use	0.002	0.002	0.83	0.424
Mean residence time (log)	Centrality	-0.083	0.147	-0.572	0.578
	Rank	-0.089	0.090	-0.995	0.341
	Urban space-use	0.005	0.002	1.961	0.076

Table V-S4. Personality and plasticity in movement parameters for baboons in natural versus urban space in Cape Town, South Africa. Median daily values for movement metrics are presented. Personality repeatability estimates (R), with 95% confidence intervals (CI) and corresponding p-values are presented using the “rptR” package, R (Stoffel et al., 2017). Plasticity to environment is determined by a lower AIC value for the model allowing individual ID to vary across environment (m2) (Hertel et al., 2020). Correlation between intercept (personality) and slope (plasticity) is determined from m2 (Hertel et al., 2020), and correlations between social factors and mean urban space-use with slope (plasticity) are calculated with a Spearman’s Rank Correlation analysis.

Metrics (median)	Personality (intercept)	Plasticity (slope)	Correlation			
		AIC	I x E	Rank x E	Centrality x E	Mean urban space-use x E
Step length	***R* = 0.044** **CI = [0.007, 0.093]** ***p* < 0.001**	m1: 1631.538 **m2: 1604.576**	**-0.75**	**rho: 0.657** ***p* = 0.015**	**rho: 0.560** ***p* = 0.049**	**rho: -0.670** ***p* = 0.015**
Sinuosity	***R* = 0.033** **CI = [0.004, 0.078]** ***p* < 0.001**	m1: 417.326 **m2: 406.892**	**0.49**	rho: 0.0578 *p* = 0.851	rho: 0.054 *p* = 0.086	rho: 0.0714 *p* = 0.821
Residence time	***R* = 0.027** **CI = [0.002, 0.63]** ***p* < 0.001**	m1: 1530.877 **m2: 1509.235**	-0.24	**rho: -0.629** ***p* = 0.021**	**rho: -0.593** ***p* = 0.036**	**rho: 0.786** ***p* = 0.002**

Chapter Six

Human-managed chacma baboons reduce their social cohesion and coordination, but maintain leader-follower roles, when using urban space

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Statement of contributions:

AB and AJK designed the study. AB and CC conducted and led the field work. AB compiled data and conducted analyses with advice from AJK and IF. AB wrote the chapter with advice from AJK and all contributors.

This work was part of the following publication:

Bracken, A. M., Christensen, C., O'Riain, M. J., Fürtbauer, I., & King, A. J. (2022). Flexible group cohesion and coordination, but robust leader–follower roles, in a wild social primate using urban space. *Proceedings of the Royal Society B: Biological Sciences, 289*, 20212141.

A reprint of the publication is available at the end of the thesis

ABSTRACT

Social wildlife species are particularly well equipped to exploit opportunities presented by human-altered landscapes. However, little is known of how the collective behaviour of groups changes when in these landscapes, though collective behaviour has a critical influence on social structure and organisation, individual fitness and social evolution. Here, I study the cohesion, coordination and leadership of a managed troop of chacma baboons that use both natural and urban spaces in Cape Town, South Africa, using 1 fix/second GPS data for the majority of adults in the group, over 36 ± 7 days (mean ± SD per individual). I demonstrate baboon-typical patterns of collective behaviour in natural space: strong spatial associations and coordinated movement when travelling, with spatial associations and leader-follower dynamics structured by social dominance. In contrast, when in urban space (where there are increased risks, but increased potential for high-quality food rewards), baboons show extreme flexibility in collective behaviour, where the group shows weak spatial association, modular spatial networks, higher and more variable travel speeds and poorer group coordination. However, leader-follower roles are retained in urban space, where adult males have a disproportionate influence on the movement of group members. This supports the management tactic employed by field rangers of curbing the movements of adult males, which indirectly deters the majority of the group from urban space. These findings highlight both flexibility and robustness in collective behaviour when groups are presented with novel resources and heightened risks.

INTRODUCTION

As human populations rise, wildlife must adapt to human-altered landscapes or risk going extinct (Lowry et al., 2013). The associated sharing of space can result in negative consequences for both humans and wildlife (Dickman, 2010). Animals tend to use urban space for shelter and in order to acquire high-quality human foods (Lowry et al., 2013) which provide benefits such as increased time for resting and socializing (Saj et al., 1999; Strum, 1994, 2010), increased growth (Strum, 1994) and reduced inter-birth intervals (Strum, 2010). Urban species tend to be social (Kark et al., 2007), as group-living buffers against predators and enhances food searching (Sueur et al., 2011a) particularly in a patchy environment (Sueur et al., 2011b). However, urban space-use itself can cause disruption of social structure (Marty et al., 2019, Morrow et al., 2019), which directly influences collective behaviour and decision-making (Fischhoff et al., 2007; Jolles et al., 2019; King et al., 2008; Sueur et al., 2011b).

Urban space can have multiple effects on group-level processes. The physical composition of urban space (being more fragmented and noisy: Alberti et al., 2003; Duarte et al., 2011; Slabbekoorn & Peet, 2003) can result in group members becoming visually and acoustically isolated, increasing inter-neighbour distances (Braune et al., 2005; He et al., 2019). Additionally, direct interactions with humans can lead to reduced time spent maintaining social bonds, as individuals invest time in monitoring human activity (Marty et al., 2019). Varying phenotypes (e.g. age, sex, state, personality) within a social group may also differ in their motivation to perform particular activities, social responsiveness, or energetic requirements (Conradt et al., 2009; Jolles et al., 2019; Ling et al., 2019), resulting in differences in attraction and use of urban space (Lowry et al., 2013; Riley et al., 2003), which can exaggerate differences in motivation or hunger among individuals (Fehlmann et al., 2021; Jolles et al., 2019). Lastly, urban space can have reduced predation pressure (predators often avoid these environments: Bateman & Fleming, 2012) and provide access to high-quality food rewards (Fehlmann et al., 2021), which can lead to within-group competition (Altmann & Muruthi, 1988; de Souza Lins & Ferreira, 2019), where individuals are motivated by extraneous ecological factors rather than social factors. As a result, certain individuals may adjust their behavioural parameters and have a disproportionate effect on group movement, which can lead to group fragmentation (Conradt et al., 2009; Fehlmann et al., 2021; Ioannou et al., 2019). Urban space can thus give rise to inter-individual conflicts of interest (Conradt et al., 2009; Sueur et al., 2011b), and greater consensus costs for certain individuals when a collective decision is reached (Kaplan et al., 2011; King & Cowlishaw, 2009b; King et al., 2008), and when these costs are too great, this can lead to group fission (Fehlmann et al., 2021 ; Jolles et al., 2019; Sueur et al., 2011b). It is therefore imperative to examine the collective behaviours of animal groups when using urban space in order to better understand the underlying individual and group patterns of behaviour (Fehlmann et al., 2021).

Studies investigating the collective behaviour of animal groups tend to adopt a self-organising perspective (Camazine et al., 2020; Sumpter, 2006) and model simple “rules of interaction” between individuals (Aoki, 1982; Couzin & Krause, 2003; Couzin et al., 2002; Reynolds, 1987) that can result in complex patterns of group-level behaviours (Parrish et al., 2002; Pettit et al., 2013). Specifically, by exploring inter-individual speed, turning behaviour, and social attraction/repulsion (Couzin et al., 2002; Giardina, 2008; Herbert-Read, 2016), research has shown how group-level properties (such as cohesion, coordination, structure, shape and leadership) emerge in animal groups (Hemelrijk & Hildenbrandt, 2012; Jolles et al., 2020; Strandburg-Peshkin et al., 2017), resulting in collective behaviours such as flocking in birds (Pettit et al., 2013; Sankey et al., 2019) and schooling in fish (Herbert-Read et al., 2011; Katz et al., 2011). Understanding whether interaction rules are flexible (i.e. change depending on context) or robust (i.e. are fixed irrespective of context) will allow us a better understanding of how species respond to novel human-altered landscapes, especially for social systems characterised by large inter-individual heterogeneity (i.e. in social roles) (King et al., 2018). Previous research has been conflicting about group responses to human-altered landscapes: chimpanzee (*Pan troglodytes verus*) groups in Bossou, Guinea, increase party cohesiveness when engaging in risky crop raids (Hockings et al., 2012), but in a group of moor macaques (*Macaca maura*) that use a provisioned road in South Sulawesi, Indonesia, inter-individual differences in the macaques tendency to be along the road resulted in social networks becoming less cohesive when the macaques were nearby to humans (Morrow et al., 2019).

The most significant advances in collective behaviour have come from laboratory studies where individuals and groups can be monitored and tracked in near real-time (Deneubourg & Goss, 1989). However, recent advances in the size and weight of wildlife biologging devices (Fehlmann & King, 2016) has allowed for the monitoring of animal position, movement and behaviour in the wild (Hughey et al., 2018) providing “whole-system” information about social groups in the ecological contexts in which they have evolved and live (King et al., 2018). This new perspective offers researchers insights into how individuals achieve coordinated behaviour over space and time in a range of species (Cook et al., 2017; Merkle et al., 2015; O'Bryan et al., 2019; Peignier et al., 2019; Strandburg-Peshkin et al., 2015). For example, fine-scale tracking of inter-individual baboon movement in Kenya has revealed how both local interaction rules as well as habitat type can influence emergent group properties (Strandburg-Peshkin et al., 2015; Strandburg-Peshkin et al., 2017). As the world becomes increasingly urbanised (Alberti et al., 2003), these new technologies will be invaluable in quantifying the response of animal collectives to anthropogenic change (King et al., 2018).

The collective behaviour of primate groups and their use of urban spaces provide an excellent case study for investigations of collective behaviour in response to changing environments. Indeed, much work has investigated the collective dynamics of primate groups (King et al., 2011b; Sueur et al., 2011b; Willems & van Schaik, 2015) when determining how groups with high heterogeneity in phenotype maintain group coordination (Jolles et al., 2019). Primates tend to form complex social associations between group members which can influence group size (Lehmann et al., 2007), collective movement (King & Sueur, 2011; Strandburg-Peshkin et al., 2015) and cohesion and stability (Lehmann et al., 2007). Baboon species in particular provide a suitable study system when investigating collective behaviour (Cowlishaw, 1999; Johnson et al., 2015; King & Cowlishaw, 2009b; King et al., 2008; King et al., 2011b; Strandburg-Peshkin et al., 2015; Strandburg-Peshkin et al., 2017), as they typically form cohesive, mixed-sex social groups (Cheney & Seyfarth, 2008), with strong and differentiated associations (Cheney et al., 2016; Silk et al., 2010b). Baboon groups also show high synchrony in activities (King & Cowlishaw, 2009a) and high-ranking socially-connected individuals (in particular adult males) have a large influence on group movement decisions (Kaplan et al., 2011; King et al., 2008; King & Sueur, 2011; Stueckle & Zinner, 2008; Sueur, 2011). Though there is a wealth of information on baboon collective processes (King & Cowlishaw, 2009b; King et al., 2008; Strandburg-Peshkin et al., 2015; Strandburg-Peshkin et al., 2017), it is yet to be understood as to how these are affected by human influence.

In this chapter, I use high-frequency GPS biologgers to investigate the collective behaviour of a baboon troop living at the urban edge in Cape Town, South Africa. Contact between humans and baboons on the Cape Peninsula is common (Hoffman & O'Riain, 2012c), and therefore troops are managed daily by a team of rangers whose remit is to keep the baboons out of urban space (Fehlmann et al., 2017b). Earlier analyses revealed that baboons in the study troop do not use urban space equally (Chapters 3 & 4), with socially-peripheral, low-ranking females making more use of the urban space than their socially-connected, higher-ranking counterparts (Chapter 4). These inter-individual differences in urban space-use are as a consequence of both baboon socioecology and management practices: management tend to focus efforts on adult males which allows low-ranking, socially-peripheral females greater access to the urban space, and, with weaker ties to the dominant male, means they are more likely to split from the core of the troop. This results in fission and fusion of the troop (Chapters 3 & 4). However, there are occasions where the whole troop is in urban space, which offers the opportunity to directly compare troop coordination and collective behaviour between natural and urban spaces.

To examine patterns of collective behaviour for the study troop in natural and urban space, I investigated several parameters commonly used to characterise group behaviour and collective motion. In the case of group behaviour, I examined the group spread (Michelena et al., 2008; Strandburg-Peshkin et al., 2017; Shelton et al., 2015), group shape (stretch and sphericity: Strandburg-Peshkin et al., 2017) and group cohesion (MacGregor et al., 2020; Sibbald et al., 2009); the clustering of individuals (Morrow et al., 2019) and the resulting spatial networks (average among-individual spatial associations: Morrow et al., 2019). In the case of collective motion, I examined the speed of the troop centroid, both the mean and variation in speed, variation in turning angle, the alignment of individuals in space and the relationship between speed and travel direction (Ginnaw et al., 2020; Strandburg-Peshkin et al., 2017; Ward et al., 2018). Additionally, I investigated which individuals had most influence on collective movement in natural and urban space, using functions as developed in Strandburg-Peshkin et al., (2015) (and detailed in Methods). Because my earlier analyses suggest variation in how individuals use the urban space, and therefore a break-down in collective behaviour (Chapters 3 & 4) I expected that when the troop is in urban space they would show greater inter-baboon distances (prediction 1), resulting in groups spread over a larger area and with more variable shape (prediction 2), a more patchy distribution of individuals (prediction 3), and therefore sparser spatial associations (prediction 4) compared to when the troop is in natural space. In addition to changes in group properties due to conflicting individual preferences, baboons are more active in urban space to avoid conflict with people and to access human-derived foods (Fehlmann, 2017). I therefore expected to see an absence of collective motion and coordinated behaviour in urban space compared to natural space, with higher speeds (prediction 5), greater variation in turning angles (prediction 6), and weaker alignment of individuals (prediction 7). Additionally, as previous work on chacma baboons in this and other populations have highlighted the importance of adult males in influencing the movement patterns of group-members (Kaplan et al., 2011; King et al., 2008; Stueckle & Zinner, 2008; Sueur, 2011) and because spatial associations are correlated with dominance rank in the Da Gama troop in natural space (Chapter 4), I expected to see a relationship between leadership roles and dominance rank in natural space (prediction 8). However, as I predicted greater inter-individual distances and patchy spatial networks, I also expected the relationship between leadership centrality and dominance rank would be reduced in urban space (prediction 9), because of a limited opportunity to influence neighbour behaviour.

METHODS

Study site and subjects

I studied the 'Da Gama troop', in the City of Cape Town, South Africa. The troop comprised of 2 adult males, 19 adult females, and approximately 30 subadults, juveniles and infants of both sexes. The troop's home range includes both urban and natural space (Fig. VI-1). Urban space encompasses two residential suburbs and natural space is mostly within Table Mountain National Park and dominated by indigenous fynbos vegetation with smaller patches of exotic vegetation (Hoffman, 2011; van Doorn & O'Riain, 2020). I studied the troop from July to November 2018, and here I use data collected mainly during the austral winter (July, August) when the collars were active and when the Peninsula baboons show greater use of urban spaces (van Doorn et al., 2010).

Collar data

To examine differences in collective behaviour between natural and urban space, n = 16 adults were fitted with SHOAL group in-house constructed collars (F2HKv3), recording GPS positions at 1 fix/second between 08:00 – 20:00 local time (GiPSy 5 tags, TechnoSmArt, Italy). Data from 15 collars were retrieved (one collar was not found after release). Two collars failed to record GPS data, resulting in data for n = 13 baboons (representing 61% of all adults in the troop), for a mean ± S.D. of 42.77 ± 9.92 days, range = 21 - 54 days (Table III-1, Chapter 3). I use “daytime” hours for the troop in analyses (08:00 – 18:00 local time; Fig. II-7, Methods). Further details about collaring and GPS processing can be found in Methods chapter and Chapter 3.

Designation of habitat

I divided the baboon’s 95% home range (calculated using fixed kernel densities: Chapter 4) into ‘urban’ and ‘natural’ space (Fig. VI-1a). Urban space was defined using the polygon in Chapter 3. All areas outside of this urban space were defined as natural space (Fig VI-1a). Baboons’ urban space represented 0.77 km^2 and 13 % of the troop home range, whilst natural space represented 9.67 km^2 and 87 % of the troops’ home range. To obtain seconds spent in the urban space I used the function “getRecursionsInPolygon” from the “Recurse” package, R (Bracis et al., 2018). Using this, I was able to label each recorded position for each baboon as either “urban” or “natural” (i.e. whether they were inside or outside the urban polygon).

I used times when 10 or more collars were recording since I wanted to directly compare “whole group” behaviour patterns, and because key features of the baboons’ spatial association networks remain stable where ten or more collars are analysed in natural space (Fig. III-S1, Chapter 3). This gave a median average of 39 days of data across individuals (range: 17 – 39 days). These criteria meant that I had an abundance of data for natural space – where the baboons are often seen as a whole group – but much less data for urban space, where baboons are more frequently alone or in small groups (i.e. there is a fission of the troop: Fig. VI-1b). For natural space, a mean ± SD of 384 ± 209 mins per day met the above criteria (Fig. VI-1c) and these occasions were approximately uniformly distributed throughout daytime hours (Fig. VI-1d). For urban space, a mean ± SD of 25 ± 27 mins per day met these criteria, occurring on 11 days (Fig. VI-1c) and at times that tended to be focused in early morning and afternoon (Fig. VI-1d).

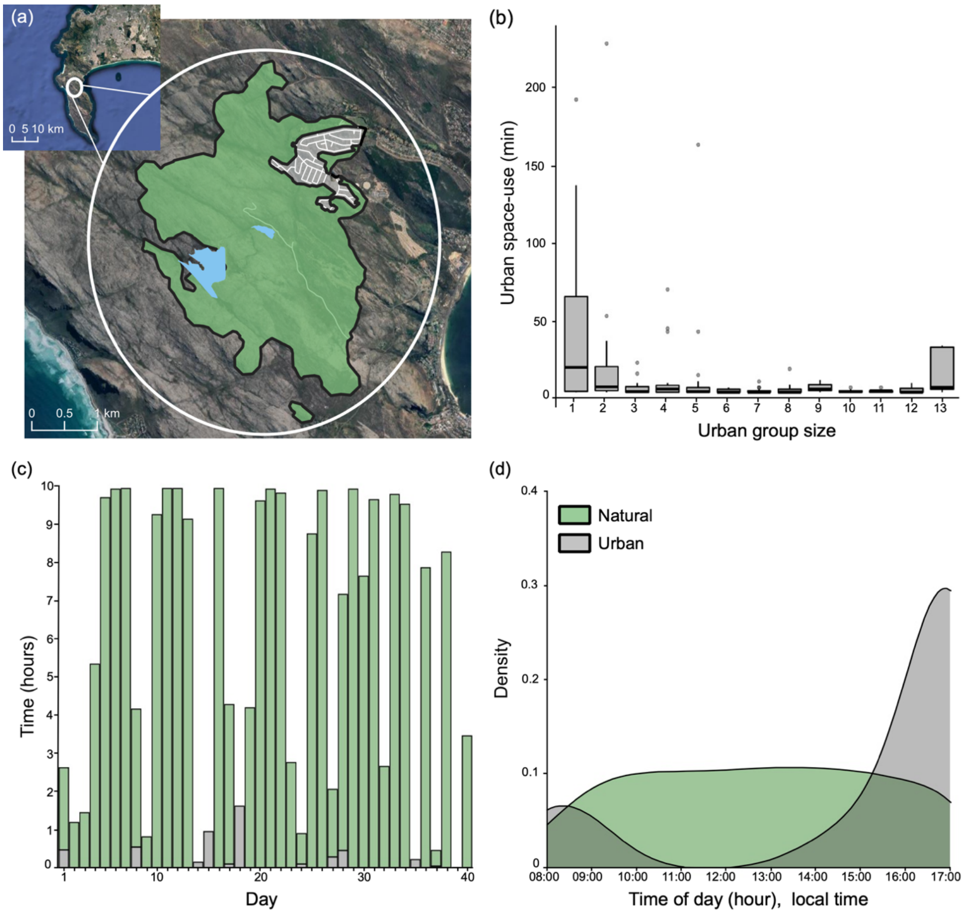

Figure VI-1. Baboon space-use. (a, inset) Position of the baboon home range on the Cape Peninsula; (a, main) Da Gama troop 95% home range (estimated by fixed kernel densities, see Chapter 4) with natural space represented in green and urban space in grey; (b) time spent (minutes) in urban space according to the number of baboons inside the urban space, i.e., “urban group size”; (c) total time (hours) where 10+ baboon collars were recorded in urban and natural spaces grouped by observation day (1-40). These represent occasions where all 10 individuals were together in either natural or urban spaces, and therefore days with little or no data are a result of the group being split across areas for most or all of the day; (d) density of time spent by baboons in urban and natural spaces as a whole group (10+ active collars) across hours of the day. In (a, main), (c) and (d) natural spaces are in green and urban spaces in grey. In (a, main) dams are represented by blue areas and roads by white lines. In (b) boxplots indicate median, upper and lower quartiles, whiskers indicate inter-quartile ranges, and filled grey circles indicate outliers.

Collective parameters

To identify when the baboons were commonly within the vicinity of one another (or in discrete groups) I created spatiotemporal groupings in either setting of within 1 minute and 150 m (Fig. VI-3), using the "Spatsoc" package in R (Robitaille et al., 2019). A spatial threshold of 150 m was chosen as it is larger than common troop spread on the Cape Peninsula (Hoffman & O'Riain, 2012b). Additionally, I used the "swaRm" package in R (Garnier, 2016), version 0.5.0, to extract several group-level spatial and movement metrics for each minute in both spaces, namely: 1) convex hull area and perimeter; 2) mean nearest neighbour distance; 3) mean distance to the troop centroid; 4) troop shape (stretch and sphericity); 5) speed of the troop centroid; 6) mean linear speed; 7) standard error in linear speed; 8) standard error in heading angle and 9) polarization of the troop (alignment of individuals in direction of travel) in either setting, going from 0 (not aligned) to 1 (aligned) (Table VI-1). Convex hull area may be particularly sensitive to missing individuals (Worton, 1995). I also calculated polarization of identified subgroups (< 150m; Fig. VI-S2) in urban space.

Table VI-1. Metrics for comparison of urban and natural collective behaviour.

	Metric	Definition and usage
Spatial	Convex hull	Area of the smallest convex polygon containing a given set of locations (Calvão & Brigatti, 2019) at a given time point. Used to assess group spread and cohesion (Sibbald et al., 2009).
	Mean nearest neighbour distance	Distance to an individuals nearest neighbour, averaged across individuals at a given time point (Biro et al., 2006; Viscido et al., 2004, 2005). Used to assess group spread (Strandburg-Peshkin et al., 2017; Michelena et al., 2008; Shelton et al., 2015).
	Mean distance to the troop centroid	Average distance across individuals to the centre point of the group, at a given time point (MacGregor et al., 2020). Used to assess group spread and aggregation (Szorkovszky et al., 2018).
	Troop shape	The sphericity and stretch of the troop, estimated by fitting a confidence ellipse on all individuals' locations (Garnier, 2016). Used to assess group spatial structure and coordination (Couzin et al., 2005; Gueron et al., 1996).
Movement	Troop speed	The speed of consecutive centroid locations of the troop (distance between locations divided by time taken to travel that distance) (Couzin et al., 2005; MacGregor et al., 2020; Strandburg-Peshkin et al., 2017; Viscido et al., 2004). Used to assess group travel speed (Viscido et al., 2004, 2005).
	Mean speed	Average speed across individuals from between consecutive time points. Used to assess group travel speed.
	SE speed	Error in speed across individuals at a given time point. Used to assess how aligned individuals are in travel speed.
	SE heading	Error in heading (travel direction) across individuals at a given time point. Used to assess how aligned individuals are in travel direction.
	Polarization	The collective order of an animal grouping (MacGregor et al., 2020; Szorkovszky et al., 2018; Viscido et al., 2004), from 0 (all individuals pointed in different directions) to 1 (all individuals pointing in same direction). Used to assess alignment in travel direction (Strandburg-Peshkin et al., 2017).
Social networks	Strength	Sum of all edge weights for each individual in a network (Farine & Whitehead, 2015; Peignier et al., 2019). Used to assess the "importance" of an individual based on their ties to other individuals (Morrow et al., 2019).
	Eigenvector centrality	Sum of centralities of an individuals' neighbours (Farine & Whitehead, 2015). Used to assess the "importance" of an individual in a network based on their own and their neighbours centralities (Morrow et al., 2019).

Association networks

Association networks were constructed for urban and natural space using the package "Spatsoc" in R (Robitaille et al., 2019) (Fig. VI-4ac). Networks were constructed using 40 days of synchronous GPS collar data (median: 39; range: 17 – 39 days across individuals), for times when all active collars were present in either urban space or natural space. Locations were grouped spatiotemporally where individuals within 5 meters and 1 minute of one another were assumed to be in association using the "chain rule" (Castles et al., 2014) and a gambit-of-the-group approach (Franks et al., 2010). Network edges were weighted using the simple ratio index. I obtained two metrics: eigenvector centrality and strength (Table VI-1), two commonly used metrics in social network studies (Farine & Whitehead, 2015; Morrow et al., 2019). I also used the walktrap community algorithm ("cluster_walktrap", "igraph" package, R: Csardi & Nepusz, 2006) to identify clusters of densely connected individuals in the networks using random walks, where individuals within a cluster have stronger ties than between clusters (Morrow et al., 2019). A modularity score, *Q*, is given for each cluster.

Leader-follower networks

In order to calculate leader-follower networks from the data, I first identified "pulls" between baboon dyads, using functions as developed in Strandburg-Peshkin et al., (2015) and made available at: http://crofoot.ucdavis.edu. These functions identify sequences in which one individual (the "leader") initiates movement away from another individual (the potential "follower"), who then either joins the first individual (this would be a successful "pull") or remains where they are and the leader returns (an unsuccessful "anchor"), within a predetermined distance threshold (here 5 m; Fig. VI-4i). The "disparity" and "strength" thresholds were set at 0.1, as used in Strandburg-Peshkin et al., (2015). I extracted pulls and anchors for all seconds for when 10+ collars were active in either natural (median: 828781, range: 333797 – 832063 secs) or urban space (median: 17118, range: 7012 – 17156 secs). In my main results, I present analyses using 5 m thresholds, as used in Strandburg-Peshkin et al., (2015), but also tested different thresholds; these results are presented in the Appendix. I created two N x N matrices (using successful ‘pulls’ in natural and urban space) where “leaders” are rows and “followers” are columns, with the frequency of dyadic pulls in a cell. I then created directed leader-follower networks using the package “igraph” in R (Csardi & Nepusz, 2006) and extracted eigenvector centrality in the network as a measure of the relative importance of individuals in leading the troop; a measure used previously in studies investigating leader-follower dynamics (King et al., 2011b; Sueur & Petit, 2008).

Dominance rank

Dominance ranks were calculated from direct observations of aggressive interactions (displacements, chases and aggressive displays), following the clear submission of one individual, collected *ad libitum* over 78 days of group follows. Female dominance rank was calculated from 634 interactions (median = 96, range 11 – 129) using the packages “AniDom” and “Compete” in R (Sánchez-Tójar et al., 2018). Male dominance rank was calculated from 75 interactions: M1 won 28 interactions (37%) and M2 won 16 interactions (21%), with 31 interactions undecided (41%), and therefore M1 was ranked first. Adult males outrank adult females in baboon groups (Engh et al., 2009; Kitchen et al., 2009). Ranks were standardised between 0 and 1 (with 0 being the lowest and 1 being the highest ranking individuals), using the function “rescale” from the “scales” package, R (Wickham, 2014). Calculation of individual dominance rank is described further in Chapter 3.

Statistical analyses

To examine differences in collective properties between urban and natural space, I fit linear models using generalised least squares (“gls” function in “nlme” package, R) to test for the effect of area on each parameter, whilst fitting a temporal autocorrelation structure to account for each minute of data.

Additionally, I tested the interacting effects of mean speed and area, and standard error in speed and area, on troop polarization. Given large differences in sample sizes between area (48x more minutes for the whole troop in natural space), I bootstrapped all models with 48 repetitions, where I randomly sampled from the natural space dataset for the number of minutes in the urban dataset, to verify differences in metrics between spaces were repeatedly observable and not due to large differences in sample size. I extracted model coefficients at each iteration, averaged each coefficient (across iterations) and calculated 95% confidence intervals for the bootstrapped data. In my models, I log-transformed (using the natural log) the following variables to meet normality criteria: convex hull area, convex hull perimeter, mean nearest neighbour distance, mean distance to the troop centroid, speed of the troop centroid and mean linear speed, which was assessed using graphical procedures (Q-Q plots and standardised residuals vs. predicted values).

To examine differences between urban and natural space in association and leader-follower networks, I used generalized linear mixed models (GLMMs) (“lmer” function in “lme4” package, R: Bates et al., 2015) and fitted network strength (association networks) and eigenvector centrality (both association and leader-follower networks) as response variables. I fitted individual ID as a random effect, and standardised dominance rank as a fixed effect to control respectively for repeated values of individual and the effect of dominance rank (which is strongly correlated with association network metrics in natural space: Chapter 4 and leader-follower networks in both settings: Fig. VI-4h). Best performing models were selected by Akaike Information Criteria (AIC). Model fit was checked using graphical procedures (Q-Q plot and standardised residuals vs. predicted values). I tested for correlations between variables using Spearman’s rank correlation, and tested for correlations among dyadic associations or interactions in natural and urban space using matrix correlations (Spearman’s rank).

RESULTS

Group spread

In urban space, troop members achieved greater inter-baboon distances (nearest neighbour distance: urban: 30.47 ± 1.21 m, natural: 11.96 ± 0.21 m (hereafter median ± SE); $p < 0.001$; Table VI-2; Fig. VI-2a) resulting in greater average baboon distance to the troop centroid (urban: 129.15 ± 3.63 m, natural: 36.11 ± 1.47 m; $p < 0.001$; Table VI-2; Fig. VI-2b), and therefore increased troop spread when in urban space (convex hull area: urban: 38379.36 ± 2511.88 m², natural: 3733.90 ± 233.68 m², $p < 0.001$; Table VI-2; Fig. VI-2c; convex hull perimeter: urban: 947.26 ± 23.57 m, natural: 282.95 ± 7.74 m, $p < 0.001$; Table VI-2; Fig. VI-2d).

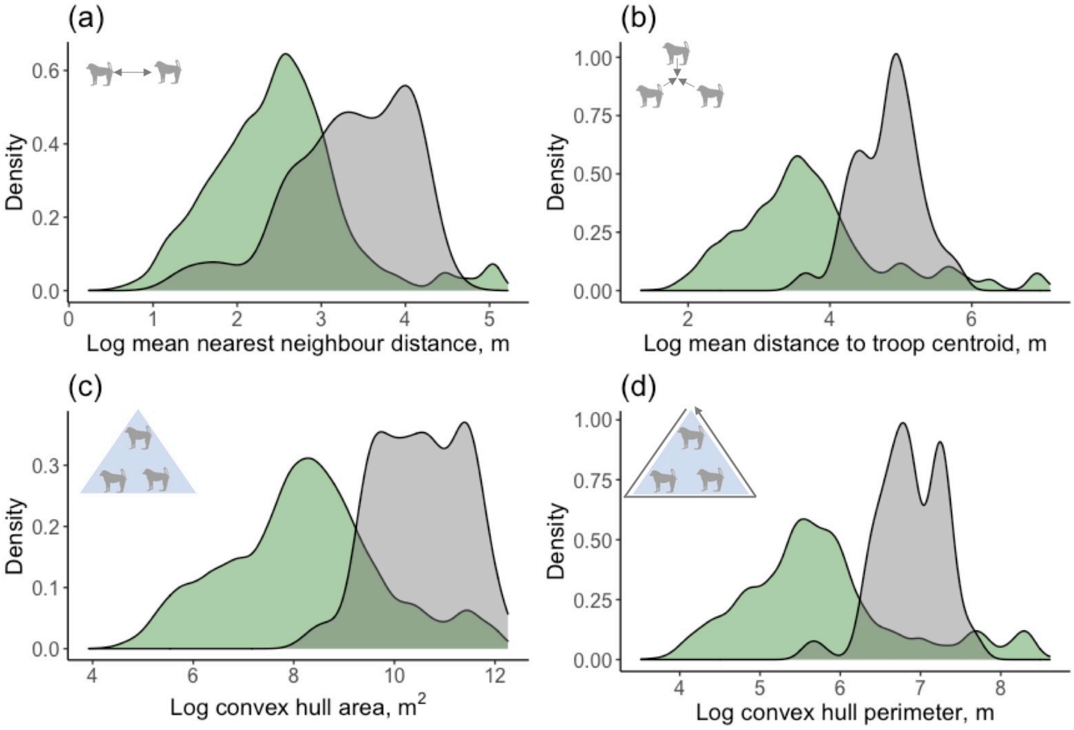

Figure VI-2. Density plots of group structure metrics in natural (green) and urban (grey) space. (a) mean nearest neighbour distance; (b) mean distance to troop centroid; (c) convex hull area; (d) convex hull perimeter. 'Log' indicates the natural log scale.

Table VI-2. Results of a nonparametric bootstrap (48 iterations) of a generalised least-squares model for the effect of space (urban, natural) on each of eleven collective parameters for the Da Gama baboon troop. Estimates, *t*-values, and *p*-values are the mean average taken across bootstrap iterations. 95% confidence intervals indicate the 95% distribution of the estimates, and standard errors represent the error around the estimates. 'Log' indicates the natural log scale. With the exception of 'stretch', positive estimates indicate a parameter increase in urban space and negative estimates indicate a parameter decrease in urban space. 'Stretch' decreases in urban space despite a positive estimate. Significant terms are given in bold (*p*-values below 0.05).

Model	Estimate	SE	t	p	95% CI	
Social cohesion parameters						
Convex hull area (log)	2.295	0.015	17.262	**< 0.001**	2.108	2.481
Convex hull perimeter (log)	1.085	0.008	15.042	**< 0.001**	0.986	1.191
Mean nearest neighbour distance (log)	0.846	0.007	8.481	**< 0.001**	0.773	0.937
Mean distance to group centroid (log)	1.083	0.007	14.132	**< 0.001**	0.972	1.192
Sphericity	0.046	0.001	1.886	0.098	0.019	0.070
Stretch	0.036	0.006	0.316	0.698	-0.039	0.118
Group coordination parameters						
Speed of group centroid (log)	0.426	0.132	3.636	**0.005**	0.252	0.588
Mean speed (log)	0.655	0.007	7.712	**< 0.001**	0.567	0.746
Standard error in speed (log)	0.796	0.007	9.195	**< 0.001**	0.720	0.913
Standard error in heading	0.035	0.001	3.152	**0.009**	0.020	0.049
Polarization	-0.124	0.001	-6.353	**< 0.001**	-0.146	-0.108

Group shape

Troop shape did not differ between urban and natural space, with the troop having similar "sphericity" (i.e. closer to circle shape) (urban: 0.449 ± 0.010, natural: 0.382 ± 0.001 (hereafter median ± SE), p = 0.08, Table VI-2), and "stretch" (urban: -0.344 ± 0.049, natural: -0.308 ± 0.007, p = 0.698, Table VI-2) in both spaces.

Group cohesion

To better understand the consequences of greater and more variable baboon inter-individual distances in urban space (Fig. VI-2ab) I calculated the number of individuals found within 150 m of each other for data in urban space and natural space (Fig. VI-3). In urban space baboons were rarely all found within 150m of each other (Fig. VI-3c), and often seen in dispersed subgroups (Fig. VI-3a). In contrast, in natural space baboons were often all found within 150m of each other and rarely in dispersed subgroups (Fig. VI-3b). Where small subgroups or single individuals were identified within 150m in natural space, this was likely due to baboons travelling alone or in small groups in and out of urban space (Fig. VI-S1).

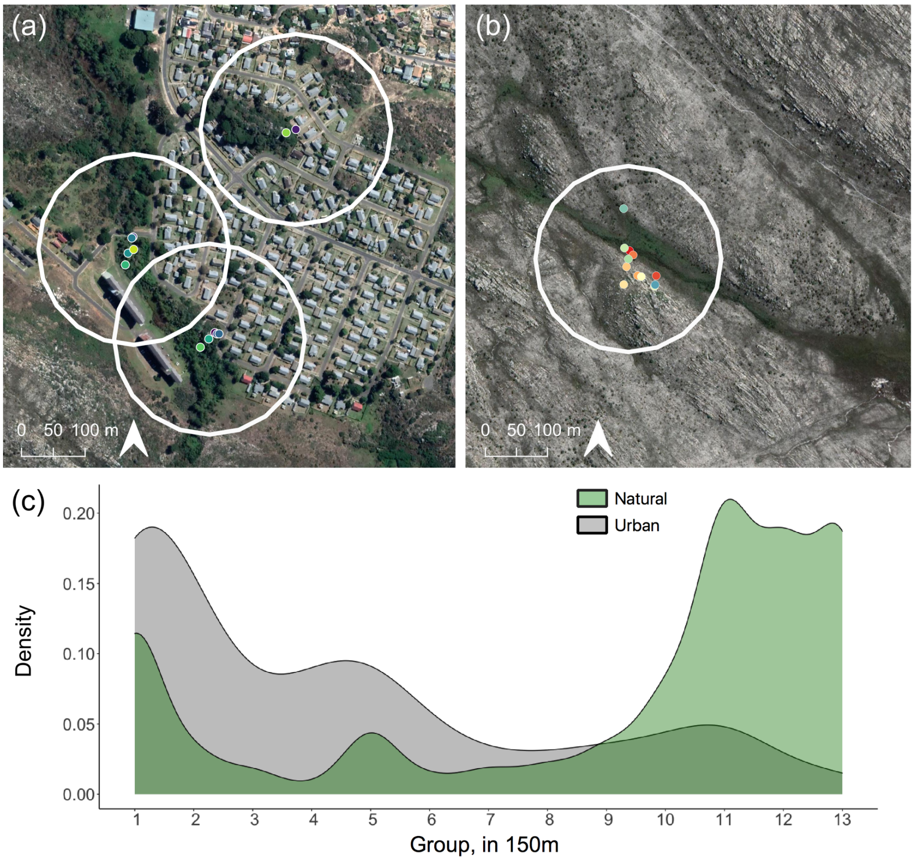

Figure VI-3. Reduced group cohesion in urban compared with natural space. Examples of troop cohesion (mean convex hull area) in (a) urban and (b) natural space. Baboons (n = 12) are identified by coloured dots. White circles of 150m diameter are used to illustrate differences in group cohesion in natural and urban space. (c) Frequency density plot showing the number of baboons observed within 150m of each other (chain rule, see methods) in urban and natural space.

Association networks

Association networks differed between urban and natural space (Fig. VI-4ac) with the network in urban displaying lower density and higher modularity (density = 0.718; Q = 0.429) compared to the network in natural (density = 1; Q = 0.118), reflecting lower cohesion in the urban space, where baboons are further apart (Fig. VI-2ab) and more frequently in subgroups (Fig. VI-3a). These network differences result in different individual-level network statistics.

Individuals' association strength was significantly lower in urban space (median: 0.108, range: 0.048 – 0.245) in comparison to natural space (median: 0.339, range: 0.228 – 0.545) (GLMM: estimate ± SE = -0.214 ± 0.023, $p < 0.001$) and whilst individual eigenvector centrality scores were similar in both the urban and natural space (GLMM: estimate ± SE = -0.055 ± 0.080, $p = 0.504$), the positive correlation between eigenvector centrality and dominance rank (common in baboon troops: King et al., 2011a; King et al., 2011b) was absent in urban space (Spearman's rank correlation: natural: rho = 0.481, $p = 0.096$; urban: rho = 0.160, $p = 0.603$, Fig. VI-4g). Additionally, dyadic relationships present in natural space were retained in urban space (Spearman's rank correlation: rho = 0.445, $p < 0.001$).

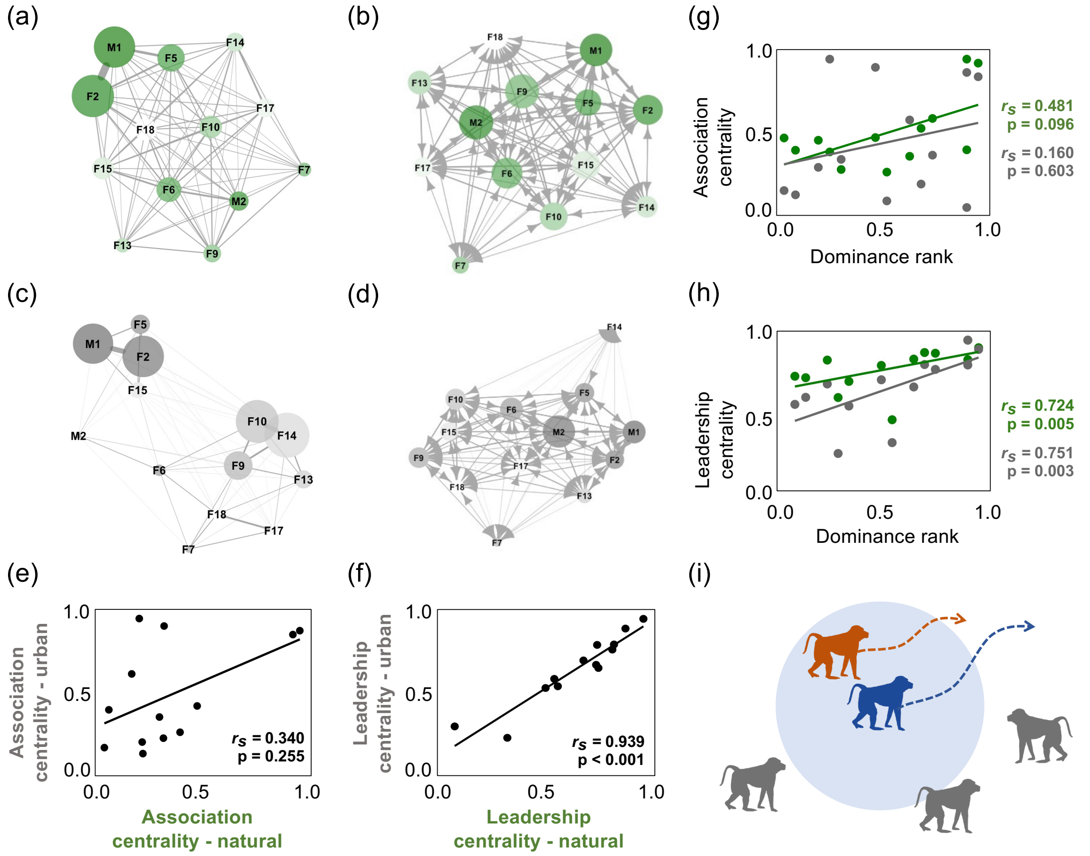

Figure VI-4. Interrupted networks in urban space, but retention of leader-follower roles. (a) Baboon association network (undirected) and (b) leader-follower network (directed) in natural space; (c) Baboon association network (undirected) and (d) leadership network (directed) in urban space; In (a)-(d) high to low eigenvector centrality is represented by large to small circle sizes, and high to low dominance rank from dark to light colours. (e) Relationship (not statistically significant) between association network eigenvector centrality (undirected) for baboons when in natural and urban space; (f) Relationship (statistically significant) between leadership network eigenvector centrality (directed) for baboons when in natural and urban space; (g) Trend for higher dominance-ranked baboons being more central in the association network (undirected) in natural space, but not in urban space; (h) Higher-ranked baboons are more central in the leadership network (directed) in both urban and natural space; (i) Five baboons: the orange baboon is the blue baboon's closest spatial neighbour, within a 5m radius (shown by the light blue circle). If two baboons are often observed within 5m of each other they will have a strong link in (a) and (c). If the blue baboon (initiator) moves >5m away from a group member who then follows by >5m (orange baboon, follower), then this is considered a local leadership event, where one baboon influences the movement of another. Baboons with greatest influence on others' movements will have high eigenvector centrality in (b) and (d).

Collective motion

The speed of the troop centroid was higher in urban space compared to natural space (median ± SE urban: 0.08 ± 0.01 m/s, natural: 0.05 ± 0.00 m/s (hereafter median ± SE), $p = 0.005$, Table VI-2, Fig. VI-5a). The troop mean speed was higher in urban space compared to natural space (urban: 0.16 ± 0.01 m/s, natural: 0.09 ± 0.00 m/s, $p < 0.001$, Fig. VI-5b), and was more variable (urban: 0.07 ± 0.00, natural: 0.03 ± 0.00, $p < 0.001$, Table VI-2, Fig. VI-5c). Variation in baboons' heading was also greater in urban space compared to natural space (urban: 0.533 ± 0.006, natural: 0.505 ± 0.001, $p < 0.009$, Table VI-2, Fig. VI-5d) resulting in reduced polarization in urban space (urban: 0.290 ± 0.010, natural: 0.401 ± 0.002, $p < 0.001$, Table VI-2, Fig. VI-5e). The positive relationship between polarization and speed – where polarization increases as the troop travel quickly towards a shared destination – was present in urban and natural space (Fig. VI-6ab) but this relationship was weaker in urban space (mean speed*urban space: estimate ± SE = -0.837 ± 0.108, $t = -7.751$, $p < 0.001$). Similarly, polarization increased with increasing error in speed (Fig. VI-6cd), but this relationship was weaker in urban space (standard error in speed*urban area: estimate ± SE = -2.631 ± 0.502, $t = -5.204$, $p < 0.001$; Fig. VI-6c). Finally, increasing number of subgroups in urban space had no effect on whole group polarization (estimate ± SE = -0.002 ± 0.013, $t = -0.168$, $p = 0.867$), though polarization within subgroups was greater than whole group polarization (Fig. VI-S2). This was attributed to greater coordination between dyads (Fig. VI-S3 & Fig. VI-S4), rather than an artefact of calculating polarization over fewer individuals.

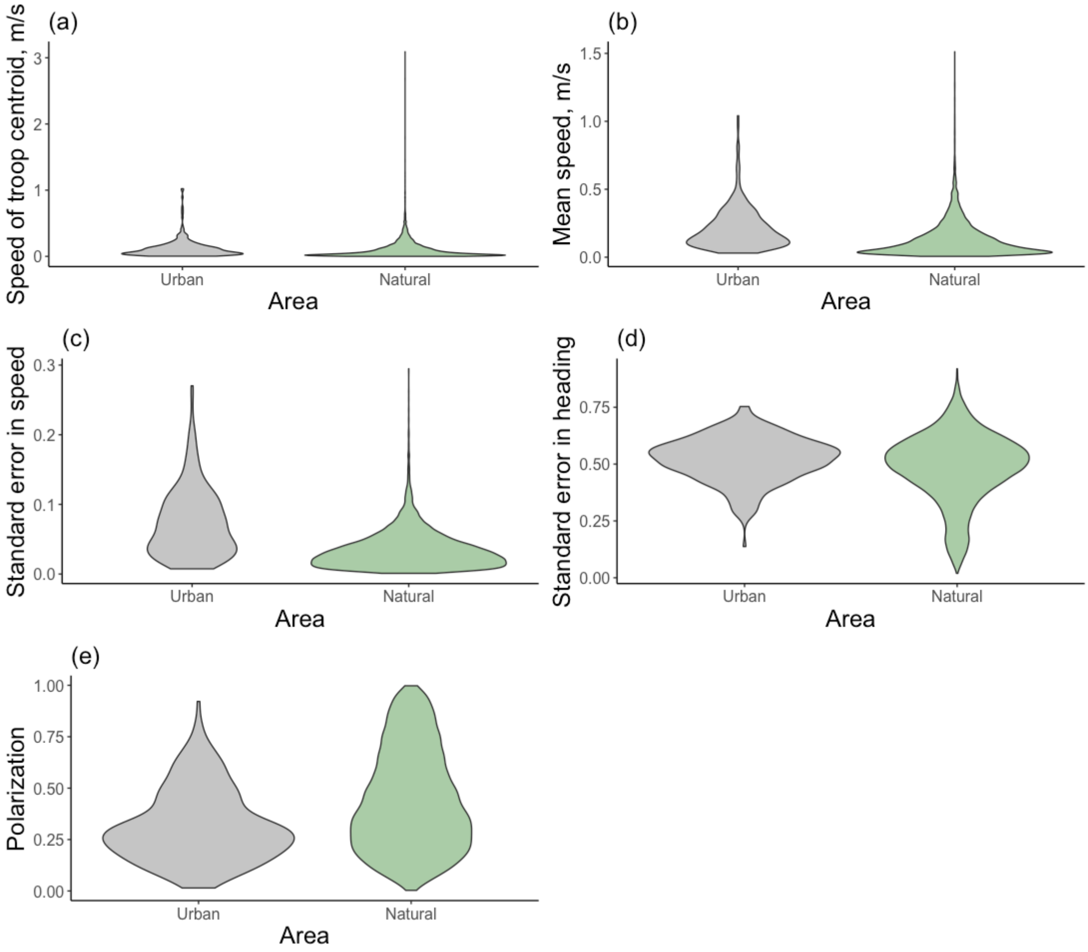

Figure VI-5. Violin plots of collective movement metrics in urban (grey) areas natural (green) space. (a) Speed of the troop centroid; (b) mean speed; (c) standard error in speed; (d) standard error in heading; (e) polarization.

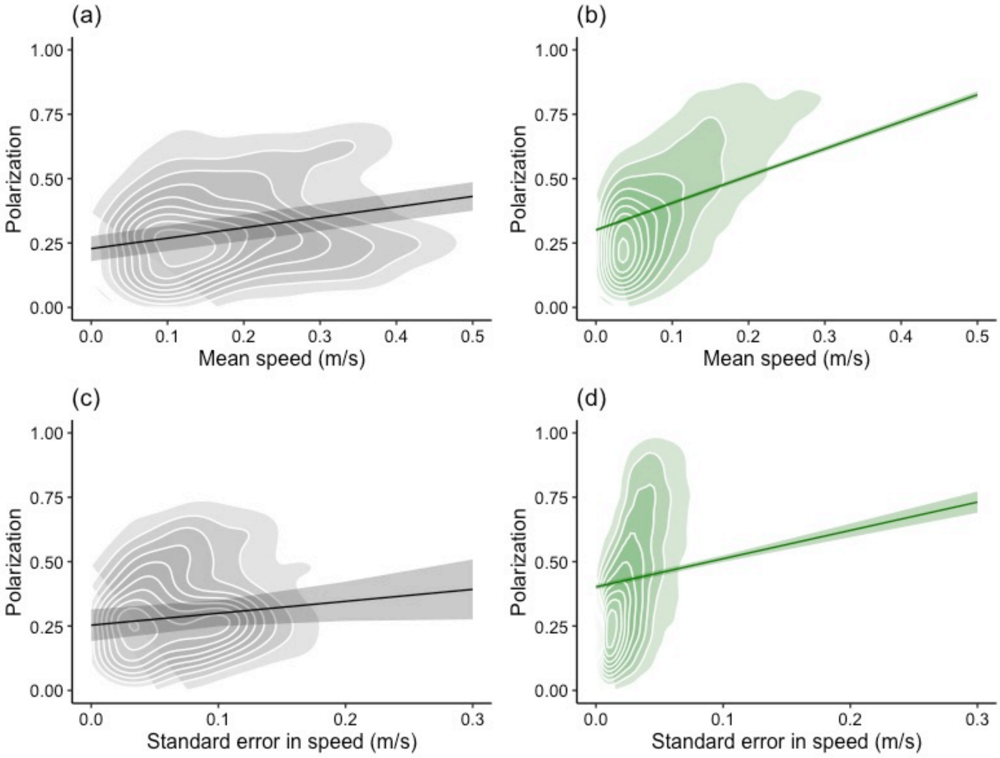

Figure VI-6. Reduced group coordination and synchrony in collective motion in urban space. Two-dimensional density plots of group polarization and mean group speed in (a) urban and (b) natural space; and group polarization and standard error in group speed in (c) urban and (d) natural space.

Leader-follower networks

Leader-follower networks differed between urban and natural space (Fig. VI-4bd) with the network in urban displaying a lower density (density = 0.942) than the network in natural (density = 1). Leadership eigenvector centrality was significantly correlated with dominance rank in natural space (Spearman's rank correlation: rho = 0.724, p = 0.005, n = 13; Fig. VI-4h), and this relationship was maintained in urban space (Spearman's rank correlation: rho = 0.751, p = 0.003, n = 13; Fig. VI-4h). Leadership eigenvector centrality scores were significantly lower in urban space (median: 0.677, range: 0.163 – 1.000) compared to natural space (median: 0.853, range: 0.412 – 1.000) (GLMM:

estimate ± SE = -0.143 ± 0.029, p < 0.001). Dyads with many leader-follower events in natural space (Fig. VI-4b) also had more frequent leader-follower events in urban space (Fig. VI-4d) (Spearman's rank correlation: rho = 0.788, p < 0.001), and leader-follower networks (Fig. VI-4bd) were correlated with spatial association networks (Fig. VI-4ac) (Spearman's rank correlation: natural: rho = 0.436, p < 0.001; urban: rho = 0.191, p = 0.010). However, individual eigenvector centrality values in association and leadership networks were not correlated (Spearman's rank correlation: natural: rho = 0.538, p = 0.061; urban: rho = 0.032, p = 0.921).

DISCUSSION

I provide evidence that chacma baboon troop cohesion and collective behaviour breaks down in urban space. Although the Da Gama troop spend only 2% of their time as a whole group in the urban space, the troop's social behaviour is significantly altered in comparison to their behaviour in natural space. In particular, when in urban space the troop was more spread out and less cohesive, with a higher clustering into subgroups. The troop also obtained higher speeds, had a greater error in heading, and were less polarized in urban space. However, leader-follower networks, though interrupted in urban space, retained dominance-related roles. I discuss these results in turn.

Baboon social cohesion and association networks were significantly reduced in urban space. This is in line with research examining the influence of human proximity on social and spatial relationships in moor macaques (Morrow et al., 2019), where groups are less cohesive, and individual social relationships constrained, when near to humans. Urban environments are heterogenous and unpredictable (Grimm et al., 2008), with patchy food sources and high levels of contact with humans (for our troop this includes both residents and rangers). Previous research indicates that when there is high spatial variability in the environment (for example in food patches or predation risks) there is a greater scope for inter-individual conflicts of interest, and groups are predicted to fission into subgroups of individuals with similar requirements (Sueur et al., 2011b). It is likely that this is what is being seen in the Da Gama troop; conflicts in motivation between individuals when in the urban space causes a splitting of the group into subgroups and, with a lack of natural predators, this is preferential to social cohesion (Fehlmann et al., 2021). Indeed, I found greater inter-baboon distances, greater individual distances to the group centre and a larger group spread in the urban space, as well as a retention of spatial associations and leader-follower interactions at the dyadic level. Moreover, the spread of the group in urban space had an uneven distribution. Individuals were often seen in dispersed subgroups, which translated into sparser urban spatial networks (network “strength” was significantly reduced in urban space) with a higher cluster modularity score than natural spatial networks. This is further evidenced by the multi-modal distribution of urban inter-individual distances, which has recently been used to determine “units” in multi-level societies (Maeda et al., 2021), and here represents a greater clustering of individuals in urban space.

I found no differences in group shape (stretch and sphericity) between natural and urban space. Group shape arises from multiple local interactions and indicates the degree of coordination between individuals (Gueron et al., 1996) and their collective response to external stimuli. For example, elongated formations can indicate rapid, directed movement in schooling fish (Couzin & Krause, 2003). Additionally, elongated formations can arise when a small proportion of individuals have pertinent information and therefore occupy frontal positions in the group; this is particularly the case in large groups (Couzin et al., 2005). When considering measures of stretch and sphericity in the current study with other measures of group spread and cohesion, it appears that the fragmented structure of the Da Gama troop in the urban space meant that the shape of the troop in the urban space was not very informative. Indeed, sphericity was greater in the urban space (though not significantly so). This may be more indicative of a reduction of the elongated cohesive travel of the troop that is seen in natural space; this is unlikely to occur in urban space as the troop is so dispersed.

Baboon group coordination was disrupted because of fragmentation of the collective structure in urban space. The group was observed travelling at higher speeds and group members were more variable in their speed and heading, resulting in a less polarized group in urban as opposed to natural space. Since the group is spread out and clustered into subgroups in the urban space, it follows that travel direction and speed are highly variable across individuals. Previous research on the Cape baboons has found that, when using urban space, adult males adopt a “sit-and-wait strategy”, spending a lot of time close to the urban edge and then making high-activity forays into urban space (Fehlmann, 2017; Fehlmann et al., 2017a). High speed in urban space is presumably indicative of high risk, and is likely to be the result of individuals quickly monopolising patchy high caloric food sources and subsequently being exposed to risks from residents, dogs, rangers, etc. Indeed, the relationship between speed and polarization (as group speed increases, so does group polarization: Parrish et al., 2002), was significantly reduced in comparison to natural space (Fig. VI-6ab). This indicates that individuals are less polarized in travel direction whilst travelling at high speeds in urban space compared to natural space. This is likely to be due to group fragmentation in the urban space; here, within-subgroup polarization was greater than whole group polarization (Fig. VI-S2), indicating that, while subgroups align in collective motion, whole group alignment is reduced. Interestingly, I also found polarization to increase with increasing error in speed in natural space (Fig. VI-6d) and this relationship was reduced in urban space (Fig. VI-6c); higher values of standard error in speed were associated with lower values of polarization more commonly than in natural space. Together these results may be indicative of subgroups aligning in travel direction when moving off independently of one another – resulting in low whole group coordination in movement.

The final finding revealed that, though leadership networks were interrupted and leadership eigenvector centrality was significantly reduced in urban space, roles as predicted by dominance rank remained stable. This finding therefore offers partial support for the final prediction. The retention of dominance-related leadership in urban space – where the group tended to be fragmented and poorly coordinated – is surprising but highlights the importance of high-ranked, socially-connected individuals upon the movement patterns of group members, which is seen throughout the species range. Indeed, in other populations, dominant individuals (namely, high-ranking adult males) have a strong influence on group movement and therefore collective movement decisions (Bonnell et al., 2017; Kaplan et al., 2011; King et al., 2008; King & Sueur, 2011; Stueckle & Zinner, 2008; Sueur, 2011). However, because the study troop has just two adult males, they may be afforded more opportunity to elicit followers.

High-ranking individuals are more successful than other group members at making movement initiations across both natural and urban space. Movement initiations are extracted regardless of inter-individual distance within a dyad (see Methods), which means that, even if the group is fragmented and poorly coordinated, fine-scale movement is still captured. In this way, we see that leadership is robust to other social changes seen in urban space; or, put another way, leader-follower dynamics are density independent (Conradt et al., 2009; King et al., 2009b; Sueur et al., 2011b). However, using different spatial criteria for identifying leadership “pulls” did reveal that in urban space, the greater influence on group movements by dominant individuals is present for movement initiations at up to 20m, whereas in natural space they occur for movements of up to 5m (Table VI-S2). This shows that group members tend to follow high-ranking individuals in urban space at a more global scale. In both cases group members are responding to initiations, but in urban space other individuals tend to be further away (mean nearest-neighbour distances are more than doubled in urban space, and baboons tend to only have a few neighbours even at distances of 20m: Fig. VI-S6).

The finding that this chacma baboon group exhibits leader-follower dynamics structured by dominance rank differs to the findings in olive baboons (*Papio* *anubis*), where dominant individuals do not strongly influence group movement decisions (Strandburg-Peshkin et al., 2015). However, it is important to note that I use the leader-follower data in a different way to the Strandburg-Peshkin et al., (2015) study. There, the authors took the leader-follower information and used this to explore collective movement decisions when baboons were faced with different options regarding where to travel. Here, I examined an individual's influence on other baboons' behaviour by creating leader-follower networks based upon "pulls" across the whole dataset. It would therefore be informative to compare both datasets at different scales (i.e., different threshold distances with shorter or longer lag times between movement) and for different types of movement events, to examine how collective movement is shaped by differences in context or species.

Together, these results demonstrate how chacma baboons in the Cape Peninsula have adapted to exploit urban space, adopting lower group cohesion and smaller group sizes. This, I expect, reduces competition for high-quality, patchy food resources (Lowry et al., 2013) and increases their chance of evading rangers who attempt to deter them from urban space (*pers. obs.*). The current work therefore provides further evidence of how social flexibility allows animals to cope with accelerated human-induced changes to their environment (Lowry et al., 2013; Morrow et al., 2019), and provides a basis for understanding these responses in other species. Future work could further examine leader-follower dynamics in wildlife groups inhabiting urban space, identifying when key decisions are made, and how and when groups split and reform (King & Cowlishaw, 2009b).

APPENDIX

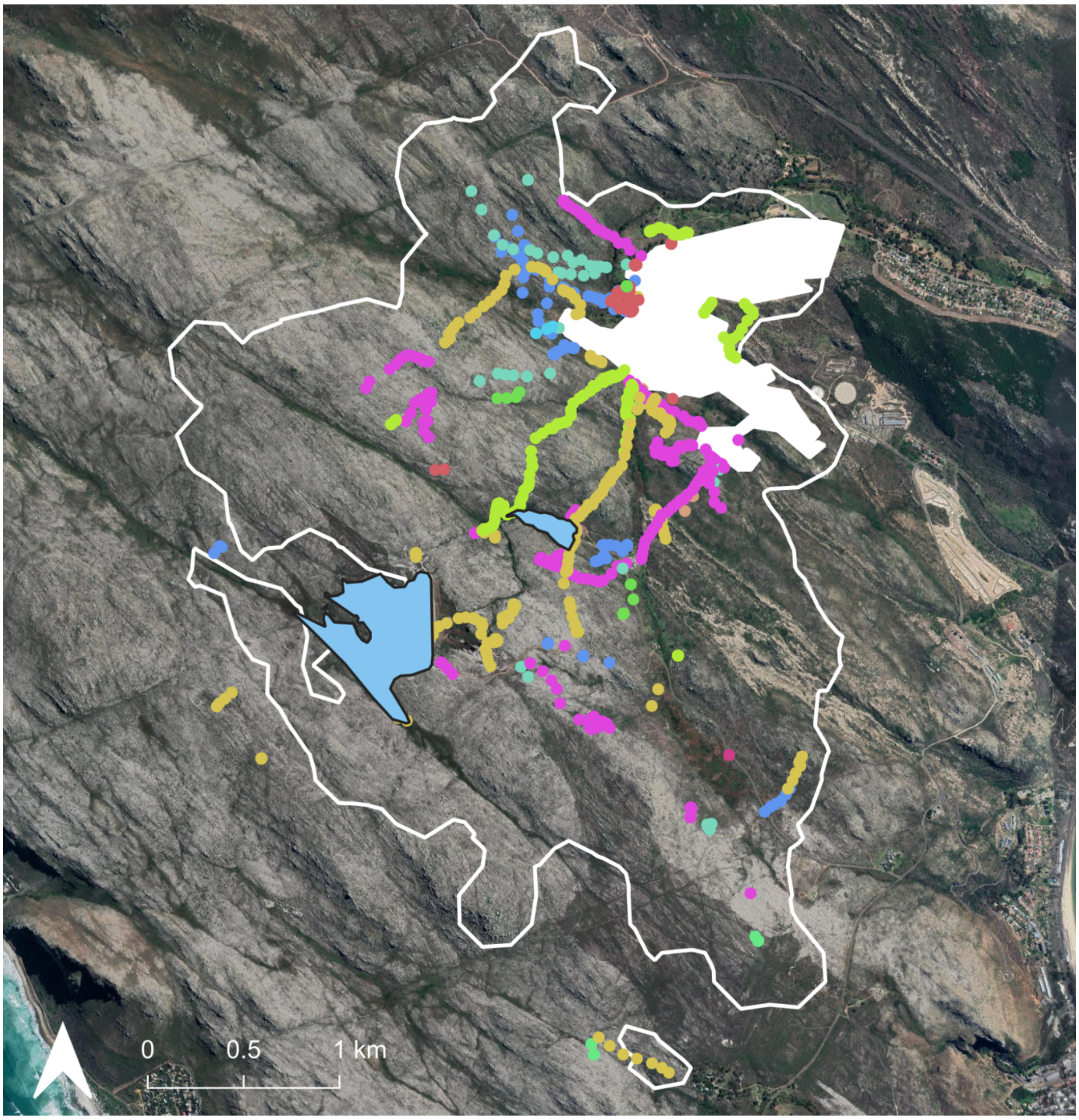

Figure VI-S1. Instances of single baboons identified alone in 150m in natural space is largely due to individuals travelling to/returning from urban space. Individuals are represented by coloured dots. Baboon group home range is represented as a white outline, and the urban space as a solid white polygon. Dams are represented as light blue areas with a solid black outline.

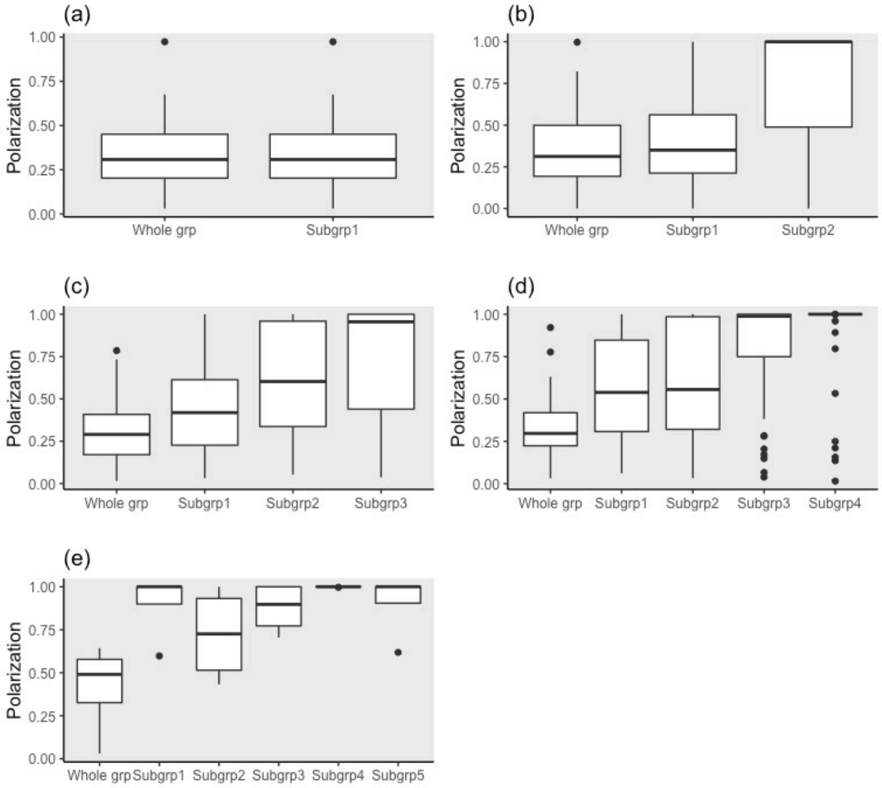

Figure VI-S2. As the number of subgroups in the urban space increases, whole group polarization remains low, but polarization within subgroups increases. (a) Comparison of polarization between whole group and when one subgroup is present (i.e. when all individuals are in 150m of one another); n = 60 mins, group size mean ± SD: 11 ± 1; (b) Polarization between all individuals ("whole group") when split into two subgroups, and the polarization within those subgroups; n = 59 mins, group size mean ± SD: 5 ± 4; (c) Polarization between all individuals ("whole group") when split into three subgroups, and the polarization within those subgroups; n = 101 mins, group size mean ± SD: 4 ± 2; (d) Polarization between all individuals ("whole group") when split into four subgroups, and the polarization within those subgroups; n = 57 mins, group size mean ± SD: 3 ± 2; (e) Polarization between all individuals ("whole group") when split into five subgroups, and the polarization within those subgroups; n = 4 mins, group size mean ± SD: 2 ± 1. Where one individual is present in a subgroup, polarization = 1. Boxplots indicate median, upper and lower quartiles, whiskers indicate inter-quartile ranges, and filled grey circles indicate outliers.

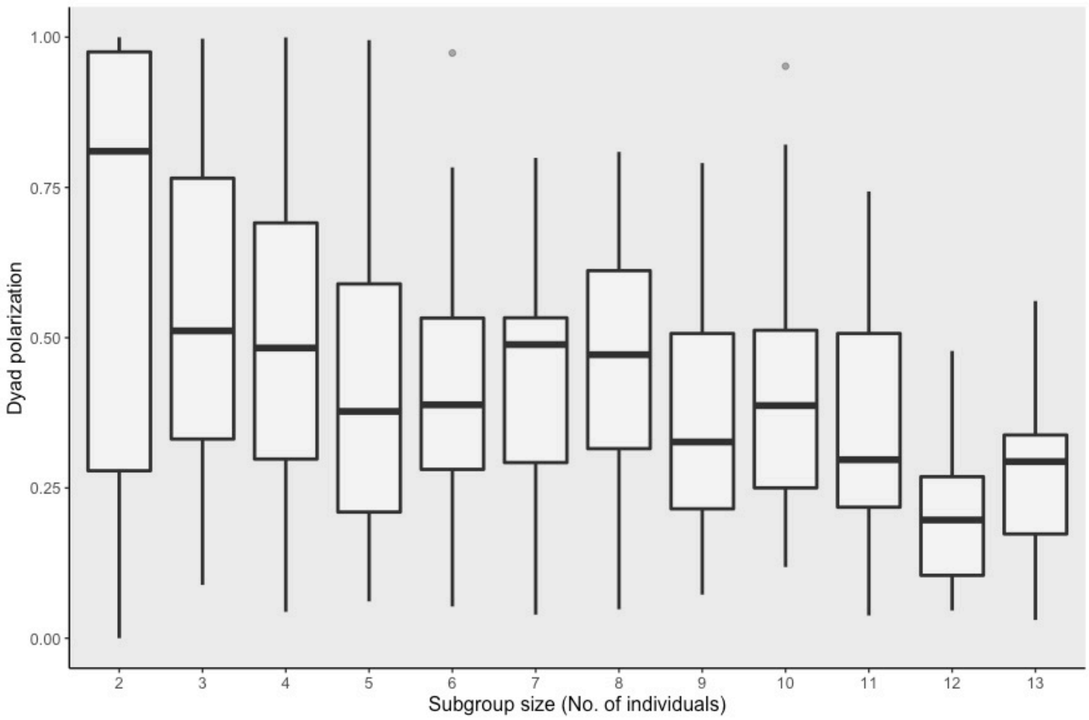

Figure VI-S3. Polarization between baboon dyads, sampled from different subgroup sizes in urban space, using all data.

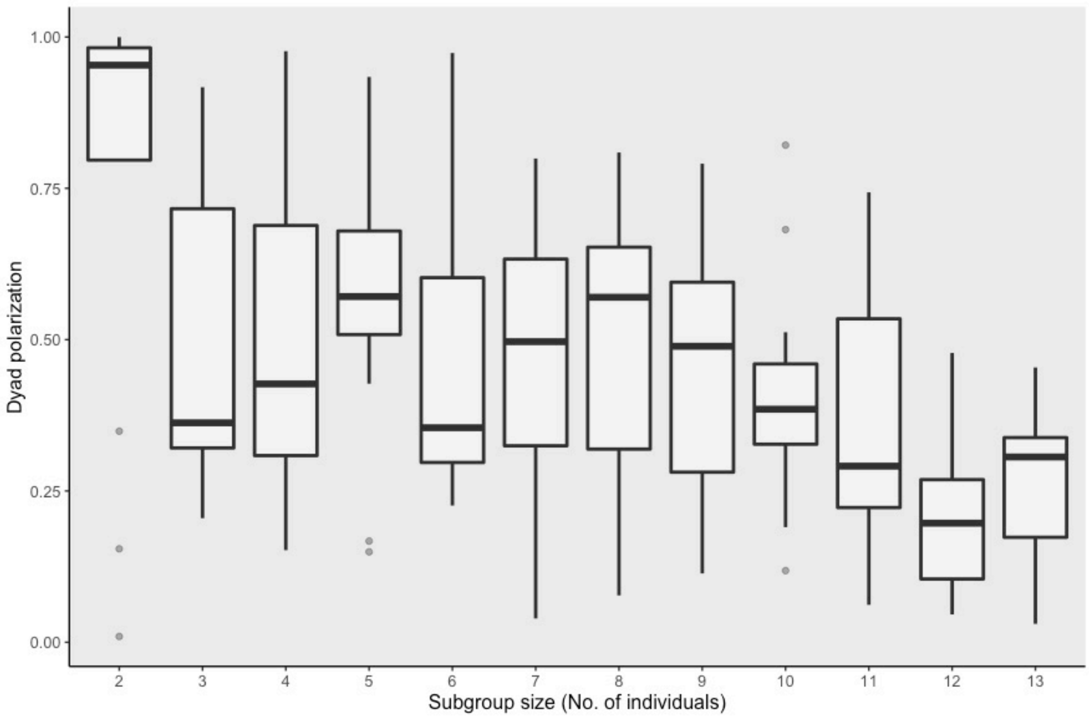

Figure VI-S4. Polarization between baboon dyads, sampled from different subgroup sizes in urban space, using all data.

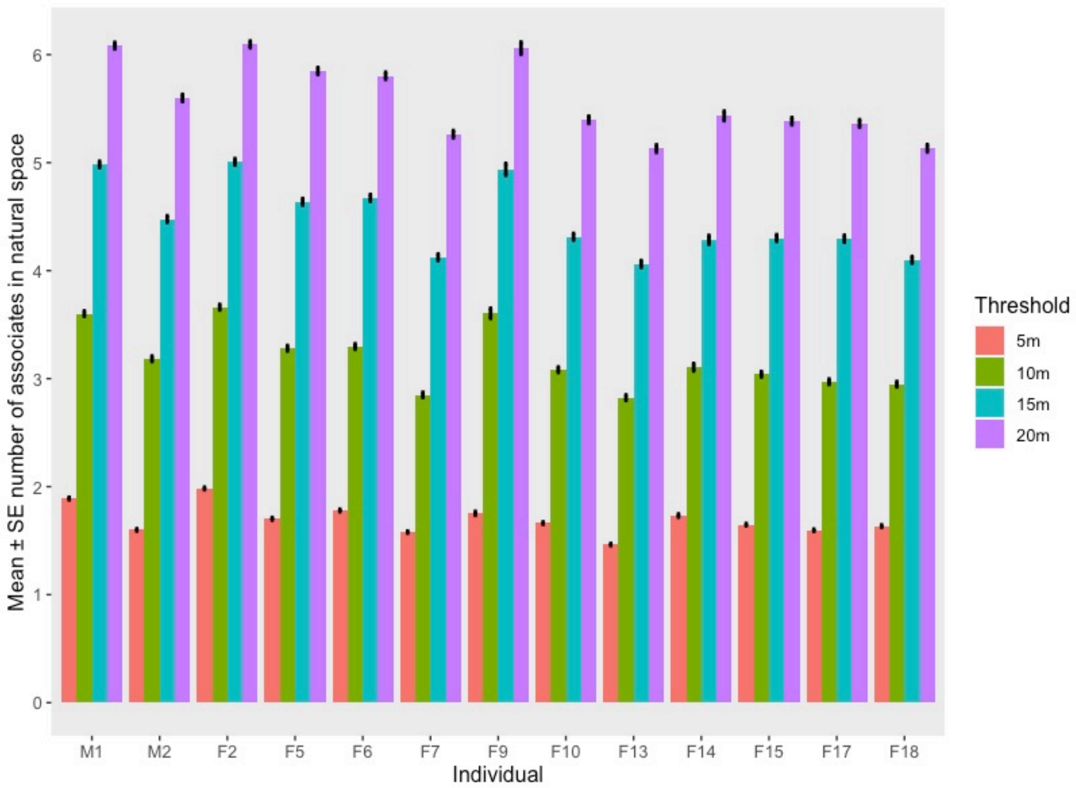

Figure VI-S5. Average (mean) number of associates of each baboon (on x-axis: ordered high – low dominance rank from left – right) in natural space, within 4 distance thresholds (5, 10, 15 and 20 m). Standard error is represented by error bars.

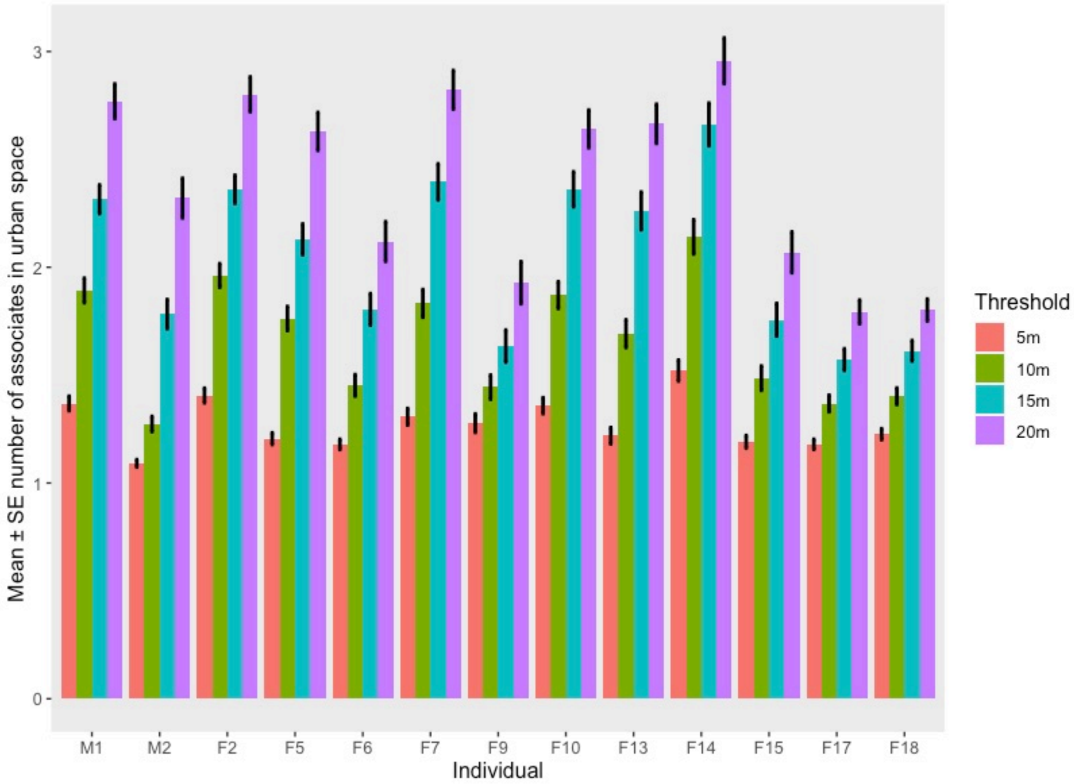

Figure VI-S6. Average (mean) number of associates of each baboon (on x-axis: ordered high – low dominance rank from left – right) in urban space, within 4 distance thresholds (5, 10, 15 and 20 m). Standard error is represented by error bars.

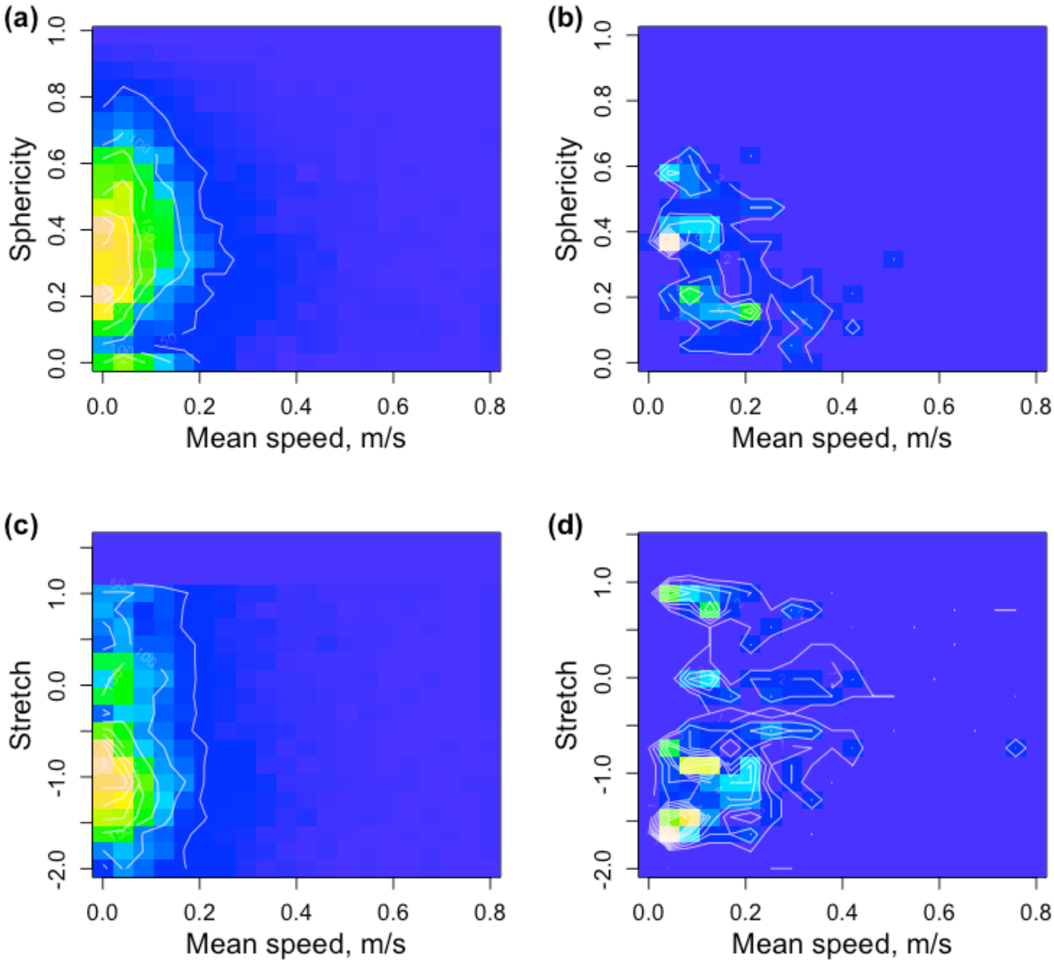

Figure VI-S7. Two-dimensional histograms of troop shape (sphericity and stretch) and troop speed in (a, c) natural and (b, d) urban space.

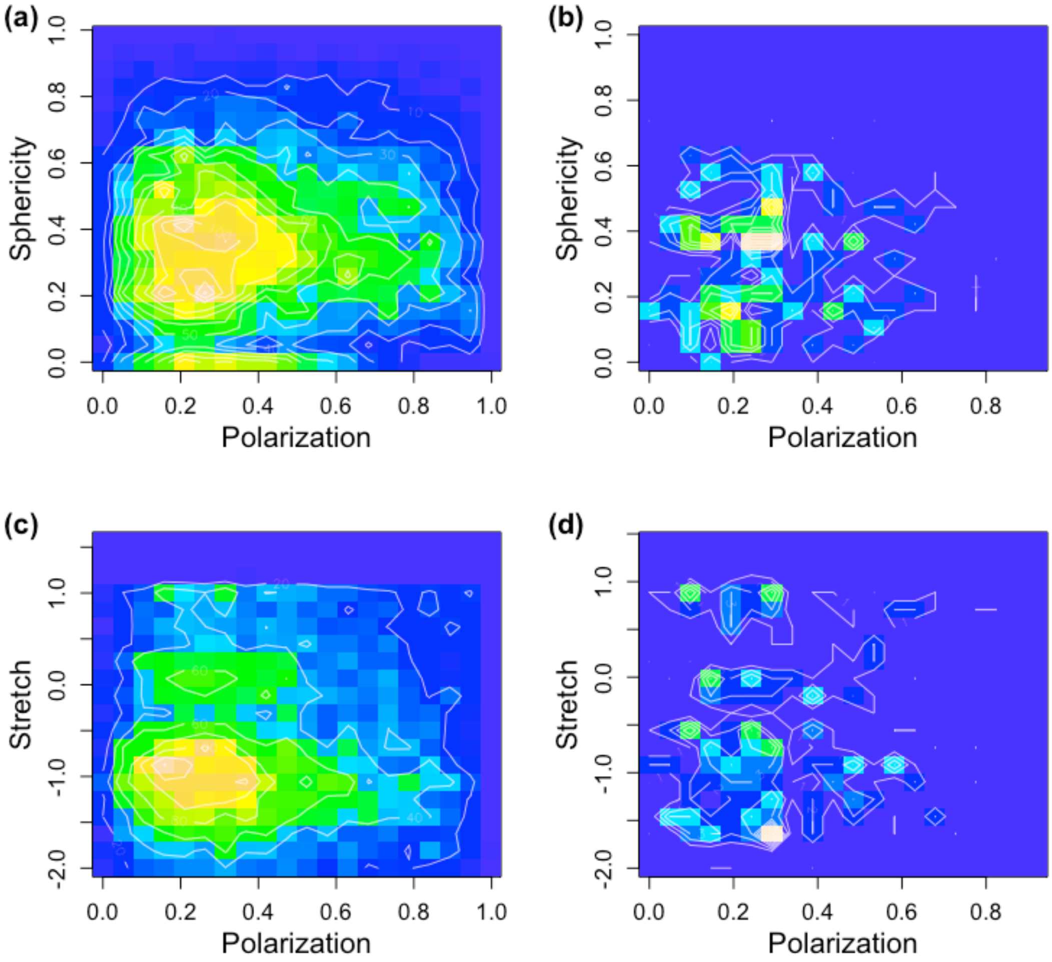

Figure VI-S8. Two-dimensional histograms of troop shape (sphericity and stretch) and troop polarization in (a, c) natural and (b, d) urban space.

Table VI-S1. Results of a linear mixed effects model for the effect of area (urban, natural) on baboon eigenvector centrality in a leadership network, using different spatial thresholds. Significant values are in bold.

Spatial threshold	Estimate	SE	t	p
5 m	-0.167	0.031	-5.322	**<0.001**
10 m	-0.173	0.335	-5.169	**<0.001**
15 m	-0.115	0.037	-3.129	**0.009**
20 m	-0.081	0.035	-2.278	**0.042**
25 m	-0.077	0.036	-2.16	0.052
30 m	-0.082	0.040	-2.029	0.065
150 m	-0.229	0.091	-2.510	**0.027**

Table VI-S2. Spearman's correlation coefficient and associated p-value for the relationship between baboon eigenvector centrality in a leadership network and baboon dominance rank, using different spatial thresholds, in both urban and natural areas. Significant values are in bold.

Spatial threshold	Urban	Natural
5 m	rho: 0.792 **p = 0.001**	rho: 0.666 **p = 0.013**
10 m	rho: 0.801 **p = 0.001**	rho: 0.429 p = 0.143
15 m	rho: 0.759 **p = 0.003**	rho: 0.151 p = 0.623
20 m	rho: 0.597 **p = 0.031**	rho: -0.008 p = 0.979
25 m	rho: 0.512 p = 0.074	rho: -0.008 p = 0.979
30 m	rho: 0.391 p = 0.187	rho: -0.085 p = 0.782
150 m	rho: 0.025 p = 0.936	rho: 0.069 p = 0.823

Chapter Seven

Discussion

THESIS OVERVIEW

Across the African continent baboons have colonised almost all natural habitats (Barrett & Henzi, 2008), which is largely attributed to their high behavioural flexibility (Bergman & Kitchen, 2009; Fehlmann et al., 2017a; Schino & Aureli, 2008). Baboons have also learned to exploit anthropogenic resources in natural and urban spaces throughout their distribution (Hill, 2000; Warren, 2009 Findlay & Hill, 2021a; Hoffman & O'Riain, 2012a; Strum, 2010), consistently adjusting their behaviour to secure high caloric foods, and to reduce the risks of such behaviour (Kaplan et al., 2011; Fehlmann et al., 2017a).

In this thesis I have attempted to provide a comprehensive understanding of the individual drivers, and both individual and group-level consequences, of urban space-use by a troop of managed baboons living at the urban edge in Cape Town (Fig. VII-1). To investigate this, I have primarily used spatial analyses from high-resolution GPS data, collected using bespoke tracking collars. I led the construction and deployment of these collars in collaboration with another PhD student. The results will be interrogated by the Urban Baboon Program, NCC, in Cape Town, to improve current strategies that aim to prevent the baboons from using urban spaces and to reduce the negative consequences to both communities and baboons in the process. In this respect the PhD has direct application to local conservation and management authorities in the Cape Peninsula, with broader lessons for wildlife management in peri-urban spaces globally.

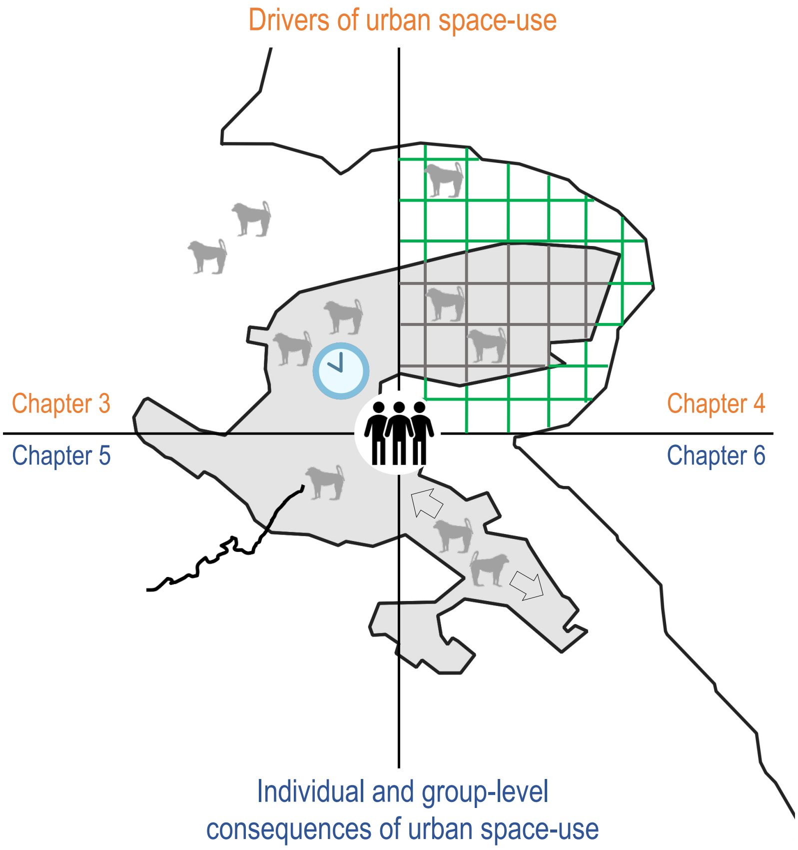

Figure VII-1. Schematic of thesis data chapters (as shown in thesis introduction). Chapter 3 (top left) explores the individual drivers (sex, social factors, presence of an infant, physiology) of time spent in urban space; Chapter 4 (top right) investigates both the drivers of whole troop space-use (degree of anthropogenic change, management risk) and individual urban space-use (social factors); Chapter 5 (bottom left) assesses the consequences of urban space-use on individual movement (personality and plasticity); Chapter 6 (bottom right) looks at the consequences of urban space-use on whole group movement (group cohesion, coordination and leadership). Baboon management represents a constant environmental factor for the baboons and is represented as human icons in the centre of the schematic.

Previous research of social animals in urban environments has largely been restricted to investigating group responses (Kark et al., 2007). This is because of the difficulties in obtaining information on multiple individuals simultaneously (Hughey et al., 2018), especially in highly fragmented habitats (Tigas et al., 2002). In this study I was able to track most of the adults in a baboon group using high-resolution spatial data for each individual, allowing the investigation of both individual and group-level differences in urban space-use (Balasubramaniam et al., 2020; Merrick & Koprowski, 2017). My results reveal large differences in how individuals respond and adapt to urban spaces, and how this impacts group cohesion and movement decisions.

Fine-scale spatial analyses revealed that females of low rank and low social cohesion exhibit the greatest use of urban space (Chapter 4). Females with young infants also spend less time in urban space than other individuals, and baboons spend more time in urban space when other baboons are present (Chapter 3). The finding that low-ranking, socially-peripheral females display the greatest use of urban space was unexpected, as previous research has indicated that male baboons are more habitual urban space-users, being more risk prone (Fehlmann, 2017). I argue that management's focus on preventing adult males, who have a greater leadership role in the troop (Chapter 6), from entering urban space inadvertently grants these more peripheral females greater opportunities to access urban space (Chapter 4). Since the sample size for males was low (n = 2), the relative proportion of time that females use urban space is arguably inflated. However, the sample size of males is typical for troops on the Cape, where there is a large sex bias towards females (Beamish, 2009), and therefore representative of the population. In other baboon populations, females of low rank and social cohesion tend to occupy peripheral positions in the troop, which can lead to higher predation risk (Ron et al., 1996), lower access to food resources (Alberts, 2019) and lower reproductive success (Silk et al., 2003; Silk et al., 2009). In the absence of natural predators (Skead, 1980), baboon females in the Cape have fewer costs associated with leaving the troop, and experience less competition from higher-ranking females by exploiting food resources in urban space.

Individuals in this study tend to use urban space with close associates (Fig. III-5, Chapter 3), which has also been shown for male African elephants

(*Loxodonta africana*), where individuals that crop-foraged were shown to have close associates that also crop-foraged (Chiyo et al., 2012). Additionally, crop-foraging female baboons tend to have strong social ties to crop-foraging males (Strum, 2010). In other parts of the species range baboons tend to preferentially use low-risk habitats (Cowlishaw, 1997), but perhaps social use of urban space acts as a buffer against increased risk of persecution. It may also be indicative that urban space-use behaviour is socially learned (Chiyo et al., 2012; Donaldson et al., 2012; Hoppitt & Laland, 2008).

Individual baboons show plasticity in their movement when using urban space (Chapter 5). Low-ranking, socially-peripheral females use a greater area of the urban space and change their movement (increasing step length and decreasing residence time) much less than their more socially-connected, higher-ranking counterparts (Chapter 5). This may in part be because the movement of low-ranking, socially-peripheral females is less constrained by management, which focuses on adult males (Fehlmann et al., 2017a) and the social core of the group, which typically comprises higher-ranking individuals with more leadership pull (Chapter 6). Urban space-use also has implications for collective dynamics (Chapter 6), with individuals splitting up into subgroups which are asynchronous in travel speed and direction (Fig. VI-3, Fig. VI-5 & Fig. VI-6, Chapter 6). It is difficult to disentangle the contributing environmental effects modulating individual and group response to urban space. It is likely that this is due to a combination of environmental parameters; the urban space presents physical barriers to movement, disrupting inter-individual communication (Braune et al., 2005; He et al., 2019; Rondinini & Doncaster, 2002). It also has a very different resource and risk distribution compared to natural areas (Fehlmann et al., 2021; Lowry et al., 2013; McKinney, 2002; Prange et al., 2004; Shochat et al., 2006), with patchy, high caloric food sources (Fehlmann et al., 2021) and heightened environmental risk (Fehlmann et al., 2017b; van Doorn & O'Riain, 2020). Cape baboons have the additional pressure from management, who use aversive conditioning to herd the baboons consistently away from urban spaces (Hoffman & O'Riain, 2012c; van

Doorn & O'Riain, 2020). This leads to reduced group cohesion and coordination in urban space (Chapter 6).

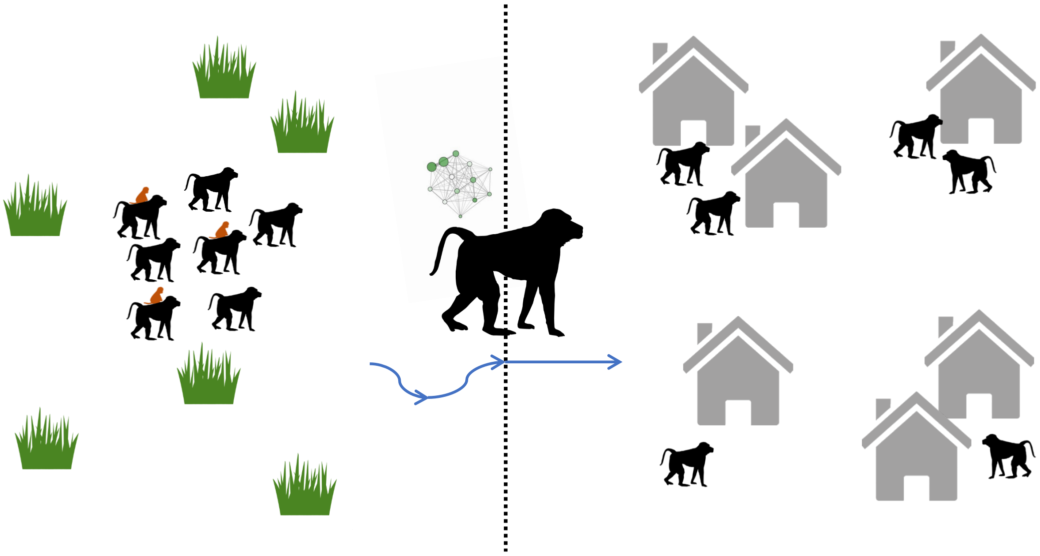

Figure VII-2: Schematic of main thesis results. Baboons with infants (orange icon riding on back of females) use urban space less. Individuals that use urban space more often (represented by baboon, centre) tend to be low-ranking and socially peripheral. All individuals change their movement in urban space (represented by baboon trajectory, centre); low-ranking, socially-peripheral individuals do this to a lesser degree than other high-ranking, socially-connected group members. Group cohesion and coordination is reduced in urban space (represented by individual baboons in natural (left) and urban (right) space).

HOW THE FINDINGS IN THIS THESIS LINK WITH CURRENT MANAGEMENT STRATEGIES

I have shown the great influence that management has on individual response to urban space. The management tactic of targeting adult males (and therefore core high-ranking individuals of the troop) is useful, since individuals of high rank have most sway in troop movement (Chapter 6). It has therefore been proposed that management of wild groups should focus on those individuals that tend to steer group activities (King et al., 2018). However, this focus has allowed low-ranking socially-peripheral females greater access to the urban space (Chapter 4), which has consequences for individual-level movement (where individuals of high rank and social cohesion show greater plasticity in urban space) (Chapter 5). Additionally, focusing on males is likely to heighten inter-individual conflicts of interest in travel direction, which, along with patchy food rewards and the physical make-up of urban space, exacerbates the breakdown in group collective dynamics (cohesion and coordination: Chapter 6).

The herding of the troop away from urban space is largely successful in keeping individuals out of town for most of the time (Fehlmann et al., 2017a; van Doorn & O'Riain, 2020, Chapter 3). It is clear, however, that other strategies are also required to prevent solitary or small groups of low-ranking, socially-peripheral females from using the urban space. One of the management options is to remove individuals that frequent urban space (i.e., capture and humanely kill). This is despite efforts to deter them using field rangers, educating the public in reducing attractants on their properties (e.g., bird feeders, vegetable gardens) and improving the management of waste in urban space (refer to guidelines on NCC Environmental Services, 2021). Adult females that habitually forage in urban space and enter occupied houses to obtain food have been euthanised in the Cape. This is because such behaviour is recognised as leading to poor welfare outcomes for the individual baboon (Beamish, 2009). It also encourages other baboons to enter urban space (two females were euthanised following BTTG3 guidelines - Baboon Technical Team, 2019, page 5 - as they were making solitary trips to urban space and then calling back to attract the troop) and causes damage to property (van Doorn & O'Riain, 2020), while posing health risks to residents (Drewe et al., 2012). Public opposition to such interventions (Kaplan & O'Riain, 2015; O’Riain, 2015) means that lethal management is typically restricted to baboons that threaten people and/or break into occupied houses to obtain human-derived foods. When the perceived threat posed by baboons is high, residents are more likely to harbour negative attitudes towards baboons (Mormile & Hill, 2017), and both to harm them (Beamish & O'Riain, In press) and demand their removal by local authorities. Most of the baboons that are perceived to pose a threat are adult males (Beamish, 2009), typically older, deposed alpha males or younger, dispersing males (Justin O'Riain, personal communication). Identifying and removing "problem" individuals within a group, who may be more assertive and experience increased contact with humans, could aid wild animal management (Found & Clair, 2016; Merrick & Koprowski, 2017). This might be achieved by research into animal "personalities" (Chapter 5) and could potentially be used to target specific individuals (Found & Clair, 2016). For example, it has been proposed that removing bolder individuals, in order to deliberately select for shyer individuals, will reduce human-wildlife conflict (Honda et al., 2018). While there is therefore incentive to remove bolder or more exploratory individuals from a management perspective, the repercussions for group social dynamics still needs to be tested; though, from these results, removal of low-ranking socially-peripheral females would appear to have the least impact on group movement and cohesion.

The Cape baboon population is consistently growing (Beamish & O'Riain, In press), with numbers increasing from 248 individuals in 2006 to 445 in 2020 (TimesLIVE, 2020). Consequently, as has been highlighted previously, contraception has been proposed as a potential non-lethal mechanism to restrict numbers within troops on the Cape, and thus to ensure an optimal ratio of field rangers to baboons, and with that, more effective management. Contraception has been successfully used for primates in captive settings (Plowman et al., 2005), but it is unclear as to how this would translate to use in wild animals. As females with vulnerable offspring tend not to use the urban space due to the associated risk of leaving the troop (Chapter 3), if low-ranking, socially-peripheral females are prevented from reproducing they may use urban space more frequently as the risks would be lessened. Additionally, since reproduction is fundamental for female baboons' life histories (signalling female quality: Domb & Pagel, 2001 and driving social relationships between males: Seyfarth, 1978 and other females: Seyfarth, 1976), removal of the reproductive cycle may have a number of unintended social consequences. If this mitigation method is pursued it would be important to include wildlife biologists in order to evaluate the approach (Warren, 1995) by conducting a ‘before and after’ comparative study.

Cape baboon management also consistently advocate for better waste disposal (Richardson, 2018a, 2018b), with the use of baboon-proofing for properties and bins (van Doorn & O'Riain, 2020). Despite this having been achieved in a small town called Rooiels in the Western Cape (Mormile, In prep; Institute for Communities and Wildlife in Africa (iCWild), 2021), baboons in Rooiels continue to enter the urban space on a daily basis, revealing their clear preference for low-lying land, which is typically encroached upon by humans for urban and rural development (Hoffman & O'Riain, 2012b). Thus, while education of residents on improved waste management can restrict baboon intake of human-derived foods, it does little to restrict spatial overlap between humans and baboons in an urban setting (Mormile, In prep). By contrast, the Da Gama troop has regular access to human-derived foods (e.g. bins, compost heaps and fruiting trees), which are typically more calorie dense than natural food sources. Multiple, high-return patchy food sources in urban space are likely to play a significant role in driving reduced cohesion and coordination of the troop in these settings (Chapter 6), as individuals are drawn in different directions. Moreover, once they find food they are not likely to want to share it, particularly if they are low ranking (low ranking baboons typically “produce” foraging information: King et al., 2009a). This poses huge logistical issues for management, who find it exceptionally difficult to dislodge baboons from urban space and hence focus on preventing them from gaining access in the first place. Better waste management, including earlier and more regular removal of household waste by municipal services, and education of residents on baboon-proofing would remove the most accessible attractants in urban space and would therefore likely reduce urban incentives and increase group cohesiveness. Together, the above challenges speak to the need for a change in human behaviour (Baruch-Mordo et al., 2009), perhaps by incorporating local communities and human attitudes in field studies (Bezanson & McNamara, 2019; Mormile & Hill, 2017; Riley & Bezanson, 2018), whilst simultaneously keeping baboons out of urban space using field rangers and aversive conditioning.

CAN THIS THESIS BE APPLIED MORE GENERALLY TO DIFFERENT SPECIES/CONTEXTS?

This study provides one of the first examples of the variability of individuals within a group in their response to anthropogenic change. It will be important to investigate this across species and populations (Lowry et al., 2013). The development of biologging techniques is opening possibilities in understanding individual-level differences in response to various levels of human impact. For example, current baboon research using high-resolution tracking collars is examining individual responses to crop fields in Limpopo, South Africa (led by PhD student Ben Walton) and individual differences in bark-stripping behaviour in a pine plantation in Mpumalanga, South Africa (led by PhD student Michelle Pretorius). Crop-foraging baboons are deterred from fields by guards employed by farmers (Findlay & Hill, 2021a) and by field rangers in the City of Cape Town (van Doorn & O'Riain, 2020), with the main difference being that baboons in peri-urban areas are typically very habituated and less easily deterred than their counterparts in rural areas, where lethal deterrents are commonplace (Findlay, 2016; Kifle, 2021; Warren, 2009). Understanding how risk and reward in other baboon study systems shapes inter-individual differences in problem behaviours (i.e., crop-foraging and bark-stripping) will be interesting to compare with my results.

I have predominantly found social factors to be key for individuals using urban space (Chapter 3, Chapter 4). In other species and contexts, sociality is similarly important for individuals using human-altered landscapes (Balasubramaniam et al., 2020; Baranga et al., 2012; Chiyo et al., 2012; Srinivasaiah et al., 2019). For example, in a comparative study on 10 peri-urban macaque groups in three species, spatially-peripheral individuals were more likely to interact with humans (Balasubramaniam et al., 2020), and male African and Asian elephants tend to use human-altered landscapes with other males (Chiyo et al., 2012; Srinivasaiah et al., 2019). Additionally, I identified how personality and management can influence plasticity in individual movement to urban space (Chapter 5). Previous studies into animal personalities have highlighted how bolder temperaments may more easily move through human-altered landscapes (Lowry et al., 2013; Sol et al., 2013), and that selective management often inadvertently focuses on bolder or more detectable personality types (Biro & Post, 2008; Ciuti et al., 2012; Leclerc et al., 2017b). I demonstrate how this focus affects individual movement. Finally, I show that collective dynamics break down in urban space (Chapter 6), which has been shown in moor macaques; group structure along a human-provisioned road caused reduced group cohesion (Morrow et al., 2019). Together, this research highlights how both social and ecological factors can influence individual use of human-altered landscapes.

Other studies examining the response of animals to anthropogenic habitats tend either to compare individuals in their proximity to human landscapes (Bombieri et al., 2021; Hertel et al., 2019), identifying individuals in a group that perform “problem” behaviours (i.e. crop- or urban- foraging, or interaction with humans) and comparing them to “no-problem" group members (Balasubramaniam et al., 2020; Chiyo et al., 2012), or to compare urban individuals and groups with their rural counterparts (Evans et al., 2010; Kark et al., 2007; Møller, 2010; Stillfried et al., 2017; Troup et al., 2020). In this study, I was able to use the comparative approach (i.e. comparing movement between natural and urban spaces), and to explore the same individuals as they moved from natural to urban space within very short time frames. This allowed for an improved understanding of how an individual adjusts its behaviour while controlling for other variables (e.g., weather, levels of satiation, reproductive status) and hence provides a measure of an individual’s overall behavioural flexibility. Additionally, having positional data at such a fine temporal resolution has allowed me to identify solitary or small-group trips made by low-ranking socially-peripheral females (which tend to be short in duration). These frequent trips in and out of the urban space are most problematic from a management perspective as they lead to the public perception that the troop is constantly in the urban space and, hence, that management is failing in their goal of keeping them in natural space. Retrieving these individuals and herding them back to the troop is exceptionally difficult, given the barriers to human movement in urban space (e.g., roads, buildings, fences) and the baboons' superior agility (Hill, 2005; Hoffman & O'Riain, 2012c). Consequently, management prioritises the core of the troop (comprised predominantly of high-ranking individuals) allowing low-ranking, socially-peripheral females greater access to urban space and reinforcing their behaviour of foraging on human-derived foods. Intriguingly, these females always rejoined the troop if they gave birth, which is likely to be due to the risks involved with using urban space (Beamish, 2009) and the benefits of being with the core of the troop (i.e., protection from males: Palombit et al., 2001 and more individuals: Sueur et al., 2011a).

FUTURE DIRECTIONS; LIMITATIONS OF THE STUDY

An important piece of information that was missing from the current study was on management itself; i.e. I can only infer that management pressure influences movement. Being able to record ranger movements (by GPS tracking of groups of rangers who were staying with the main troop or following baboons to town) would have allowed for an assessment of their differential response to individual baboons, and how baboons in turn respond to these differences. It would also have shown the movements of females of different rank and social cohesion in relation to ranger movements (for example, identifying the way in which certain individuals are able to evade management; on several occasions baboons were observed to hide behind rocks and in vegetation to avoid detection by a ranger, following which they moved back to the urban space: *pers. obs.*). Correspondingly, quantification of other environmental parameters may have provided a better understanding of how baboons move in urban space (Edelaar et al., 2017; Strandburg-Peshkin et al., 2017). For example, information on the ways in which local residents perceive the level of threat posed by individual baboons may have provided more information on individual space-use patterns (Mormile & Hill, 2017). Differences in residents' behaviour towards both baboons and management may influence levels of ranger assertiveness (*pers. obs.*), which is likely to have knock-on effects for baboon movement and space-use. A better understanding of residents' attitudes may thus help in the development of more proactive management strategies (Merkle et al., 2011), including the development of publicly-directed information and educational tools to reduce attractants in urban space.

Another drawback with conducting behavioural research to inform conservation is the mismatch between research and implementation (Jarvis et al., 2015; Jarvis et al., 2020). This is frequently manifested as a discrepancy in the time it takes to publish peer-reviewed articles (due to time needed for data analysis, writing up the manuscript, and the processes involved in publication) and the need for management action, which is invariably immediate. Such a discrepancy reduces the implementation of behavioural knowledge in wildlife conservation (Berger-Tal et al., 2016). For example, about 7 months after data collection in the current study was completed, the beta male in the study troop was euthanised in accordance with "BTTG3 – Guidelines for Categorising and Managing Damage Causing Baboon(s) (DCB) in Urban Areas, Cape Peninsula" (Baboon Technical Team, 2019). My results show that his use of urban space was lower than several other females in the group (i.e. Fig. III-3, Chapter 3; Fig. IV-3, Chapter 4), and these females used urban space without him (i.e. he did not necessarily lead them into urban space). The current research findings were only published in October this year (Bracken et al., 2021), three years after the field work was conducted, effectively making them obsolete for short-term management decisions. The value of this detailed research is not therefore to inform short-term decisions, but rather to provide an independent assessment of the success of management in deterring baboons from urban space and to show how baboons are adjusting to overcome such deterrents and are altering their behaviour once in urban space. Previous research on the Cape baboons has acknowledged the mismatch between research and management timelines, and the authors made recommendations to management ahead of publication on how to improve management (e.g., more consensus in ‘no go’ areas by rangers: Fehlmann, 2017). However, this strategy is risky given that the research findings have yet to be subject to the peer-review process.

The study would have also benefitted from a larger sample size, both in terms of a larger number of collared individuals in the troop, as well as gathering information from other Peninsula troops. As can be seen from the eigenvector centrality scores in Fig. III-S1 (sensitivity analysis, Chapter 3), I am missing information for other socially-connected individuals, particularly the dominant female. Additionally, there were other uncollared baboons that frequently used the urban space (*pers. obs.*) alongside collared baboons. This information would have boosted all analyses, particularly in providing greater insights into individual-level responsiveness to urban space (Chapter 5). In this study 13 out of 21 adults were sampled; it may be the case that sampled individuals were more “trappable” than others due to differences in detection probability (where bold, active, exploratory individuals might be more likely to be sampled) (Carter et al., 2012b; Merrick & Koprowski, 2017), which could potentially influence repeatability estimates. Individual GPS data also uncovered that one female drastically reduced her urban space-use after giving birth (Fig. III-6, Chapter 3), and more data on other individuals may have supported this finding (during the study period another two females without GPS data gave birth and were seen to reduce use of urban space: *pers. obs.*). Since group composition and environment varies greatly across Peninsula baboon troops (Hoffman & O'Riain, 2012b), more information on other groups would complement the major findings of this thesis (i.e. in understanding how other peninsula troops respond to being managed).

Finally, in October 2021, the alpha male of the Da Gama troop was electrocuted while climbing an unprotected electricity pole and died from his injuries, several weeks after the loss of the only other adult male in the troop (who died in the same way). These deaths emphasize the ongoing negative interactions between Cape baboons and urban space, and the need for investment into better infrastructure. These unfortunate events also hint at a potential future research avenue from the results in this thesis. I found in this study that dominant baboons (such as the dominant male) had a large influence on group movement (Chapter 6), making these individuals "keystone" in the group's collective dynamics (King et al., 2018). If, opportunistically, it happened that a follow-up study was possible following the loss of such an important individual from the leadership network, it might reveal how the network reconfigures, or whether social dynamics are permanently changed (King et al., 2018). Though the position of alpha is likely to be filled by another male (either by a subadult or dispersing male), this period of upheaval is likely to result in an increased threat of infanticide (Palombit, 2003) and therefore an increased stress response in the group (Beehner et al., 2005). In terms of management, this may significantly alter individual use of urban spaces.

The results from the current thesis mainly come from individual GPS data. However, the dataset collected in the current study was much wider – including observational, hormonal and environmental data, as well as further data from the tracking collars (acceleration and magnetometry data) (Chapter 2, methods). As part of a larger project, the acceleration data has been used to extract individual baboon behaviour (Christensen, 2022, following Fehlmann et al., 2017c). Using this, it may be interesting to investigate behavioural synchrony (King & Cowlishaw, 2009a) and individual baboon behavioural budgets in and out of the urban space, as previous research has highlighted how human presence can reduce time for affiliative behaviours (Kaburu et al., 2019; Marty et al., 2019) which may have consequences for individual fitness (Silk et al., 2010b) and group-living (Lehmann et al., 2007). I also found that the Da Gama troop breaks into subgroups when in the urban space indicating that, though whole group cohesion breaks down, certain individuals still aggregate together. It would be important for management to know the drivers of this – i.e. whether it is due to patchy food sources, variation in risk, or the physical composition of urban space, etc. Using the quadrat data (perhaps in conjunction with satellite imagery and ad lib data on urban foraging) it may be possible for me to obtain both a representation of food availability across the baboons' environment, as well as an indication of how open different habitat types are in terms of substrate and vegetation structure. Field ranger survey data has allowed me to quantify risk (Chapter 4). Since both habitat and social factors (Strandburg-Peshkin et al., 2017) and risk (Fehlmann et al., 2017a) influence the ways in which baboons navigate their environment, this would help to understand the causes of loss of cohesion (and formation of subgroups) in urban space. Finally, variation in individual baboon energetic status and physiological stress levels may underlie how individuals respond behaviourally to anthropogenic environments (Blickley et al., 2012; Curry et al., 2018; McDonnell & Hahs, 2015). Repeatable measures of individual physiology can be used in conjunction with movement measures (i.e. personality types: Chapter 5) to understand whether individual levels of movement vary with their physiology (i.e. 'behavioural syndromes': Hertel et al., 2020). This individual-level information could be important for management and conservation efforts (Merrick & Koprowski, 2017) in furthering the understanding of why certain individuals are more flexible in response to anthropogenic change.

An interesting future avenue of research from the current study could come from conducting before-and-after comparative studies on the effects of a management intervention (e.g. after implementation of a structural barrier to the landscape such as an electric fence, lethal removal of certain individuals or the onset of a contraception program). Using spatial analyses from tracking collars could show the responses at both inter-individual and group-levels. Combining this with behaviour calculated from acceleration data (from tags on the same tracking collars) would allow for an assessment of space-use as well as fine-scale individual behavioural responses. Additionally, combining behavioural research with sociological research (i.e. understanding human perspectives: Mormile & Hill, 2017) would give a more comprehensive overview relevant to informing management decision-making.

CONCLUSION

Understanding how animals adapt to anthropogenic influence is becoming increasingly important as human populations increase, and the proportion of people living in urban spaces rises (Alberti et al., 2003; Sih et al., 2011). I have quantified how simultaneous high-resolution spatial data on multiple individuals can uncover a wealth of information on animal responses to urban landscapes. I have shown that baboon management in Cape Town is succeeding in limiting the amount of time that baboons spend in urban space, but that low-ranking, socially-peripheral individuals are benefiting from the focus on adult males and the core of the troop. I have shown huge variation in how individuals within a group respond to urban spaces and their associated risks and rewards, and how this translates to changes in individual movement trajectories and collective dynamics. Results from this thesis will be important in management of the Cape baboons, and more widely, in providing a basis to understand how other populations and species cope with human pressure.

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REPRINTS OF PUBLICATIONS

International Journal of Primatology
https://doi.org/10.1007/s10764-021-00247-x

Socioecology Explains Individual Variation in Urban Space Use in Response to Management in Cape Chacma Baboons (*Papio ursinus*)

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Received: 14 October 2020 / Accepted: 27 July 2021/

Abstract

The presence of wildlife adjacent to and within urban spaces is a growing phenomenon globally. When wildlife's presence in urban spaces has negative impacts for people and wildlife, nonlethal and lethal interventions on animals invariably result. Recent evidence suggests that individuals in wild animal populations vary in both their propensity to use urban space and their response to nonlethal management methods. Understanding such interindividual differences and the drivers of urban space use could help inform management strategies. We use direct observation and high-resolution GPS (1 Hz) to track the space use of 13 adult individuals in a group of chacma baboons (*Papio ursinus*) living at the urban edge in Cape Town, South Africa. The group is managed by a dedicated team of field rangers, who use aversive conditioning to reduce the time spent by the group in urban spaces. Adult males are larger, more assertive, and more inclined to enter houses, and as such are disproportionately subject to "last resort" lethal management. Field rangers therefore focus efforts on curbing the movements of adult males, which, together with high-ranking females and their offspring, comprise the bulk of the group. However, our results reveal that this focus allows low-ranking, socially peripheral female baboons greater access to urban spaces. We suggest that movement of these females into urban spaces, alone or in small groups, is an adaptive response to management interventions, especially given that they have no natural predators. These results highlight the importance of conducting behavioral studies in conjunction with wildlife management, to ensure effective mitigation techniques.

Keywords Baboon · Dominance rank · Management · Social cohesion · Urban space use

Introduction

Urban spaces are growing in size and structure and have complex, powerful direct and indirect effects on ecosystems (Alberti *et al.,* 2003). Species-level adaptations to urban landscapes include flexible behaviors (Chapman *et al.,* 2012; Lowry *et al.,* 2013; Sih

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Handling Editor: Joanna M. Setchell.

et al., 2011), tolerance to a wide variety of habitats (Bonier *et al.,* 2007; Ducatez *et al.,* 2015), and generalist diets (McKinney, 2002). At an individual level, urban space use can vary according to phenotype (Lowry *et al.,* 2013), for example, age and sex (Baker *et al.,* 2007; Dowding *et al.,* 2010; Maibeche *et al.,* 2015; Marty *et al.,* 2019; Merkle *et al.,* 2013). Adult male Barbary macaques (*Macaca sylvanus*), living in Gouraya National Park that borders the city of Bejaia in Algeria, eat more human foods than females or juveniles (Maibeche *et al.,* 2015), and male American black bears (*Ursinus americanus*) in Missoula, Montana, use urban spaces more frequently than females and are 1.6 times more likely to be located next to a house (Merkle *et al.,* 2013). Social context and life-history strategies can also drive differences in urban space use (Baranga *et al.,* 2012; Kark *et al.,* 2007). For example, in baboons (*Papio* spp. excluding *Papio hamadryas*), male (but not female) dispersal is common (Altmann & Alberts, 2003; Silk *et al.,* 2003), leading to males being more likely to encounter urban environments (Beamish, 2009). However, detailed investigations of interindividual differences in urban space use are rare, because of the challenges of observing the behavior and movements of many individuals simultaneously (Hughey *et al.,* 2018).

Primates are among the most high-profile species to use urban space (Fehlmann, O'Riain, Kerr-Smith, & King, 2017b; Hoffman & O'Riain, 2012b; Klegarth *et al.,* 2017). As innovative problem solvers (Reader & Laland, 2001) that are adaptable to a variety of environments and diets (Swedell, 2011), they can exploit high-calorie human crops, foods, and waste (Strum, 2010). This urban foraging behavior positively affects time and energy budgets (Fehlmann, O'Riain, Kerr-Smith, & King, 2017b; van Doorn *et al.,* 2010), resulting in improved body condition for individuals (Strum, 2010) and smaller home ranges for groups (Altmann & Muruthi, 1988; Hoffman & O'Riain, 2012a; Strum, 2010). However, use of urban space by primates also has costs and can result in severe injuries or death (Beamish & O'Riain, 2014) and exposure to cross-transmission of pathogens (Drewe *et al.,* 2012) as a result of their proximity to people.

Contacts and negative interactions with humans are most common among adult males within primate groups (Fuentes & Gamerl, 2005; Maibeche *et al.,* 2015; Marty *et al.,* 2019; McLennan & Hockings, 2016; Strum, 2010). It is therefore suggested that management strategies aimed at reducing conflict should focus on adult males (Baranga *et al.,* 2012; Fehlmann, 2017). For example, in the City of Cape Town, South Africa, adult male chacma baboons (*Papio ursinus*) exploit spaces at the periphery of the city that are close to refuges (Fehlmann, O'Riain, Kerr-Smith, & King, 2017b), engaging in brief, high-activity "raids" to forage in urban spaces (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a) and obtain high-calorie human foods (Kaplan *et al.,* 2011). As a result, "baboon rangers" are employed to deter baboons from urban spaces (Hoffman & O'Riain, 2012b) and have been successful in reducing negative impacts to people and property (Fehlmann, 2017; van Doorn & O'Riain, 2020).

Male-focused baboon management can be doubly effective because high-ranking adult males are seen to have a strong influence on group-level movement decisions in different chacma baboon populations (Kaplan *et al.,* 2011; King *et al.,* 2008, 2011; Stueckle & Zinner, 2008; Sueur, 2011), and group-level urban space use can be significantly reduced by focusing on males in this population (Kaplan *et al.,* 2011). Indeed, males appear to exert a strong influence on movement decisions across baboon species. In olive baboons (*Papio anubis*) the highest-ranked male is most likely to determine the direction and timing of group movements (Ransom, 1981), in hamadryas baboons (*Papio hamadryas*), males exclusively initiate group movements (Kummer, 1968), and in Guinea baboons (*Papio papio*), adult males initiate the majority of group departures (Montanari *et al.,* 2019). However, propensity to initiate group movements can be affected by individual, social, and/or environmental factors, and more shared decision-making processes have been observed in olive baboons (Strandburg-Peshkin *et al.,* 2015) as well as female leadership in yellow baboons (*Papio cynocephalus*) (Norton, 1986).

Here, we study urban space use by a group of baboons ranging in the Da Gama Park region of Cape Town. To better understand interindividual variation in patterns of urban space use, we fitted adults with tracking collars that provided information on their location at high-resolution (1-Hz GPS data). Because adult males are the focus of management (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a) and are typically the cause of conflict with people (Beamish, 2009; Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a), we expected that males, rather than females, would spend more time in the urban space. However, at the start of our study, baboon management reports for the focal group indicated that all baboons were entering the urban space, often in small groups without adult males (Richardson, 2018a, 2018b). We therefore explored the influence of baboon identity and social factors on use of urban space.

Methods

Study Site and Subjects

We studied the Da Gama group, which is named after the suburb in which the group ranges: Da Gama Park in the city of Cape Town (Fig. 1a, b). The group comprised 2 adult males, 19 adult females, and approximately 30 subadults, juveniles, and infants. The group's home range includes both urban and natural spaces. Urban spaces encompass two residential suburbs: Da Gama, which is mostly low-income state housing for staff of the South African Navy, and Welcome Glen, a middle-income suburb. The urban environment provides energy-rich food sources (e.g., bread, vegetables, and bird seed) from houses, compost bins, and food waste, as well as from woody plants such as fruiting trees (e.g., guava: *Psidium guajava*) and *Pinus* spp. (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a; Hoffman & O'Riain, 2011). The natural habitat is mostly within Table Mountain National Park and is dominated by indigenous fynbos vegetation (*Protea*, *Erica*, and *Restio* spp.) with smaller patches of exotic vegetation (such as *Pinus*, *Acacia*, and *Eucalyptus* spp.) (Hoffman, 2011; van Doorn *et al.,* 2010; van Doorn & O'Riain, 2020), which comprises the bulk of the baboons' diet when in this habitat (van Doorn *et al.,* 2010). We studied the group from July to November 2018, and here we use data collected mainly during the austral winter (July–September) when our GPS collars were active and when the Peninsula baboons show greater use of urban spaces (van Doorn *et al.,* 2010).

GPS Data

To obtain information on baboons' space-use patterns, we fitted 16 adults (2 males, 14 females) with SHOAL group (Sociality, Heterogeneity, Organisation And Leadership group, based at Swansea University, UK) in-house constructed collars (F2HKv3).

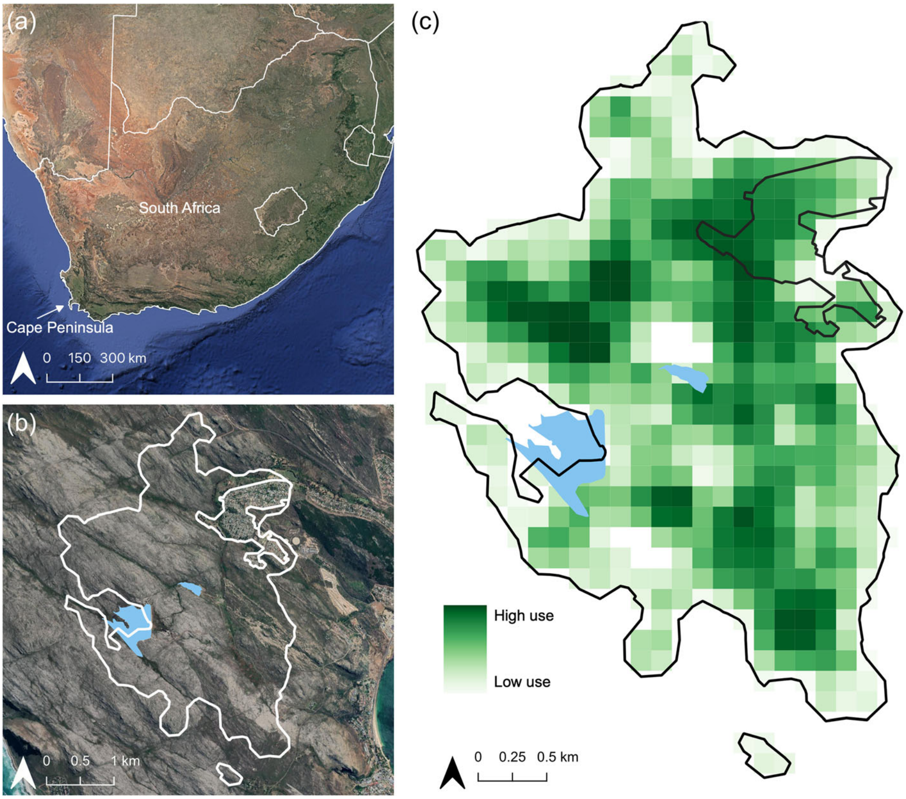

Fig. 1 Study site and baboon group overall space use, between July and September 2018. **a** The location of the Cape Peninsula in South Africa (−34.161, 18.403). **b** 95% kernel home range of the baboon group (outer white outline) and the defined urban space (inner white outline). **c** 95% kernel home range including the intensity of use, presented within 150 m × 150 m grid cells, with urban space indicated. Dams are represented as blue areas.

Collars recorded GPS positions at 1 Hz (1 fix/s) between 08:00 and 20:00 local time (GiPSy 5 tags, TechnoSmArt, Italy). The GPS recording period thus started in the morning after the baboons had left their sleeping site and continued until they had settled at a sleeping site in the evening. Data from 15 collars were retrieved (1 collar was not found after release), and 2 collars failed to record GPS data, resulting in data for 13 baboons (2 males, 11 females), for a mean ± SD of 43 ± 10 days, range = 21–54 days (Electronic Supplementary Material [ESM] Table SI). Data from 13 baboons represented 61% of all adults in the group and so although we are missing information from several adult females, having 1-Hz GPS data for 2 males and 11 females of different rank for this period of time provides us with an excellent dataset to test our predictions regarding individual differences in urban space use. However, these data come from a single group, with only two males, and therefore making inferences about urban space use by baboons more broadly should be cautioned.

We conducted all analyses in R Studio, version 1.0.153 (R Core Team, 2020). *Ad hoc* checks of the GPS positional data compared to known landmark locations at the field site in Cape Town and in Swansea, UK, indicated positional accuracy always within 5 m. Nevertheless, GPS standalone horizontal position will depend on 1) satellites available, 2) how the collar was positioned on the baboon at any time point, and 3) the immediate environment surrounding the collared individual. Therefore, we processed GPS data to remove erroneous fixes 1) by removing relocations outside the study area and 2) by removing successive 1-s GPS fixes between which it would have been impossible for the baboons to travel (i.e., they would have travelled too quickly or would have made an especially large turn). We used two functions as described in Bjørneraas *et al.* (2010) where outliers are identified as being above a predefined distance threshold from surrounding fixes (here, 250 m), or as "spikes" in the trajectory (caused by a high outgoing and/or incoming speed: here, 10 m/s, or sharp turning angle: here, cosine of turning angle set at $\theta = -0.95$) (explained further in Supplementary Methods in the ESM). A median 0.01% of GPS fixes per collar (range 0.00%–0.03%; ESM Table SII) were removed in this manner. Where GPS fixes were missing or had been removed, and where these missing values lasted a time period of less than or equal to 10 s, the path was interpolated using the fixLocNA function in the swaRm package (Garnier, 2016) following O'Bryan *et al.* (2019). A median 0.02% of GPS data was interpolated per collar (range 0.00%–0.07%; ESM Table SII).

Urban Space Use

We investigated baboon urban space use at a resolution of 150 m × 150 m by adding grid cells over the study area in QGIS, version 3.12 (QGIS.org, 2020). We chose this grid cell resolution as the area is larger than the average spread of an individual group in the Cape Peninsula (Hoffman & O'Riain, 2012a) and is consistent with grid-cell sizes used to investigate space use in this population (Fehlmann, O'Riain, Kerr-Smith, & King, 2017b), affording comparisons across groups. We delineated the urban space across these grid cells by drawing a polygon around areas dominated by residential buildings and surfaced roads, using Google satellite imagery and OSM standard maps (Fig. 1b). This resulted in 55 urban grid cells.

We calculated urban space use as the intensity of cell use (between 0 and 100, with 0 indicating no use, to 100 indicating complete use) by each collared baboon for each grid cell in the urban space (resulting in $N = 55$ measures per baboon) using all available GPS data. We determined intensity of cell use using fixed kernel densities and an *ad hoc* method for choosing the smoothing parameter, with the function getvolumeUD from the package adehabitat in R (Calenge, 2006). The baboon group used a variety of sleeping sites throughout their home range, but most frequently slept on top of buildings within the urban space during the period in which GPS receivers were active (52/61 days), particularly on the roof of an apartment block (ESM Fig. S1). This meant that GPS fixes in the urban space during the evening (after the rangers had left) (18:00–20:00, ESM Fig. S2) were associated with the group returning to or being at the urban sleep site. We therefore calculated and reported urban space use based on kernel density estimates using both daytime GPS data (08:00–18:00) and all GPS data (08:00–20:00). We used daytime GPS data when presenting our main results because using all data would overestimate large group sizes in the urban space as all baboons use the sleep site at the same time (ESM Fig. S2). We examined variation in individual baboons' urban space use by subtracting an individual's daytime urban grid cell use from the group mean, the result indicating whether an individual used a given cell more or less than the group mean.

To provide context for urban space use, we calculated the number of times one or more baboons entered (and subsequently exited) the urban space polygon using the function getRecursionsInPolygon, Recurse package, R (Bracis *et al.,* 2018). We investigate recursions to provide information on common urban group size (i.e., how frequently urban space is used by all collared baboons or a subset while the rest of the group is outside of urban space). We considered all entries into the polygon to be a recursion, without placing restrictions on recursion duration or interval length between visits. This may overestimate quick visits to the urban space but is likely to reflect true urban group sizes. We also used the MoveVis package (Schwalb-Willmann *et al.,* 2020) in R to animate examples of baboons entering and exiting urban space (Supplementary Videos).

Dominance Rank

We calculated baboon dominance hierarchies from observations of aggressive interactions (displacements, chases, and aggressive displays) that were decided following the clear submission of one of the individuals. We recorded these *ad libitum* by direct observation over 78 days of group follows. We calculated dominance for the 2 males from 75 observations: M1 won 28 interactions (37%) and M2 won 16 interactions (21%), with 31 interactions undecided (41%). M1 was therefore ranked first. All adult males outrank adult females in chacma baboon groups (Engh *et al.,* 2009; Kitchen *et al.,* 2009). We calculated female rank from 634 interactions (median = 96, range 11–129), using the packages AniDom and Compete in R (Sánchez-Tójar *et al.,* 2018). Full details are provided in Fürtbauer *et al.* (2020). We standardized ranks between 0 and 1 (with 1 being the highest and 0 the lowest ranking individuals) using the function rescale from the scales package in R (Wickham, 2014).

Social Cohesion

To estimate baboon social cohesion, we calculated individual eigenvector centrality scores from proximity-based social networks for daytime minutes during which all collared baboons were outside of the urban polygon, using the package Spatsoc in R (Robitaille *et al.,* 2019). We chose to remove times inside the urban polygon, as proximity to humans is predicted to alter social networks (Morrow *et al.,* 2019). This resulted in 307,977 minutes in total; mean: 23,690, range: 9743–29683 per individual. Spatial proximity networks have been correlated with other affiliative (i.e., grooming) networks (Cheney *et al.,* 2006; Silk *et al.,* 2003) and provide an association network from which social integration can be derived. We calculated spatial networks by grouping GPS locations temporally (1-min intervals) and then spatially (within 5 m, using the chain rule: Castles *et al.,* 2014), where each GPS fix was buffered by 5 m, and two or more individuals were considered in the same group if they shared a common buffer, even if some of those individuals were not within 5 m of one another (Peignier *et al.,* 2019; Robitaille *et al.,* 2019). We then converted the grouped data into a group by individual matrix, from which a proximity-based social network was built, using the package asnipe in R (Farine, 2013). We defined the strength of associations between dyads of baboons (or network edges) using the simple ratio index (SRI) (Farine & Whitehead, 2015). From this proximity-based network, we calculated individual eigenvector centrality scores. Eigenvector centrality measures a baboon's importance in the spatial network, while giving consideration to the importance of its neighbors in this network (Farine & Whitehead, 2015). Because collars recorded data for different lengths of time, we created networks and calculated eigenvector centrality scores for periods during which different numbers of collars (1–13) were recording. We present network analyses using 40 days of synchronous GPS collar data for a time period when >10 collars were active (>75% of the collared individuals) in natural areas. These criteria were chosen following a sensitivity analysis (ESM Fig. S3).

Statistical Analyses

We modeled the difference in urban cell-use by baboons as our response variable, using a Gaussian generalized linear mixed model (GLMM) with a spatial autocorrelation (fitme function in the spaMM package in R: Rousset & Ferdy, 2014; with a Matérn covariance matrix and maximum likelihood method). To test for the influence of baboon identity on urban space use we fitted individual identity as a random effect, allowing for different intercepts (i.e., interindividual differences) and tested the significance of individual ID using maximum likelihood ratio tests. Additionally, we calculated the intraclass correlation coefficient (ICC) across individuals, using the ICCest function in the ICC package in R (Wolak *et al.,* 2012). To test for the influence of social factors, we considered the effects of dominance rank and eigenvector centrality in the proximity network in the GLMM as fixed effects. Because dominance rank and eigenvector centrality in the proximity network showed a moderate correlation (r_S: 0.48, $P = 0.09$) we chose to explore their effects in separate models (Suzuki *et al.,* 2008), while controlling for sex (male, female). We selected the best performing model by Akaike information criteria (AIC) using the function get_any_IC in the spaMM package, R and calculated AIC weights using the function Weights in the MuMIn package, R (Barton, 2009). We checked model fit using graphical procedures (*Q–Q* plot and standardized residuals vs. predicted values) using the package DHARMa in R (Hartig, 2020).

Ethical Note

To fit collars, a veterinarian anesthetized baboons after cage trapping. Cage trapping was organized by Human Wildlife Solutions and conducted according to the Baboon Technical Team's protocols (Hoffman, 2011) as described in the Supplementary Information of Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.* (2017a). The use of the collars was approved by Swansea University's Ethics Committee (IP-1314-5). Collars weighed a mean of 2.2% of baboon body mass (range 1.2%–2.6%). Collars were fitted with a drop-off mechanism (version CR-7, Telonics, Inc.) to avoid the need for a recapture. The authors declare that there are no conflicts of interest.

Data availability Data required to reproduce our analyses are included as the Electronic Supplementary Material.

Results

The urban space represented 13% of the group's home range (Fig. 1b). During daytime hours baboons spent a mean of 11% of their time in the urban space (range: 3%–26%; N = 13 individuals; hours 08:00–18:00; ESM Fig. S4a). If the time baboons were moving to, or were at, their urban sleep site in the evening was included (18:00–20:00), this mean time increased to 21% (range: 14%–34%; n = 13 individuals; 52/61 GPS days; ESM Fig. S4b).

Using information from when all collars were recording (N = 13) during daytime hours (08:00–18:00), we found that baboons entered the urban space alone, or in groups of varying size (median urban group size = 7, range 113; Fig. 2a; see Video S1 and Video S2 for animated GPS tracks) and stayed for short periods (median duration = 288 s, range 1–35,819 secs; Fig. 2b). If we consider daytime hours when any number of collars were recording and explored the proportion of collared baboons visiting urban space, patterns of space use were qualitatively similar (Fig. 2c, d).

Baboons differed in their use of urban space (Fig. 3a), as shown by the effect of individual identity in our model (GLMM: χ^2 LRT = 194.22, $P < 0.001$), and an intraclass correlation coefficient (ICC) of 0.31, 95% CI 0.18–0.55. Both dominance rank and eigenvector centrality in the proximity network (Fig. 3b, c) predicted variation in urban cell use (Fig. 3d, e) with lower ranking, socially peripheral baboons using urban space more compared to groupmates. A model comparison showed eigenvector network centrality and dominance rank to be comparable when using daytime GPS data

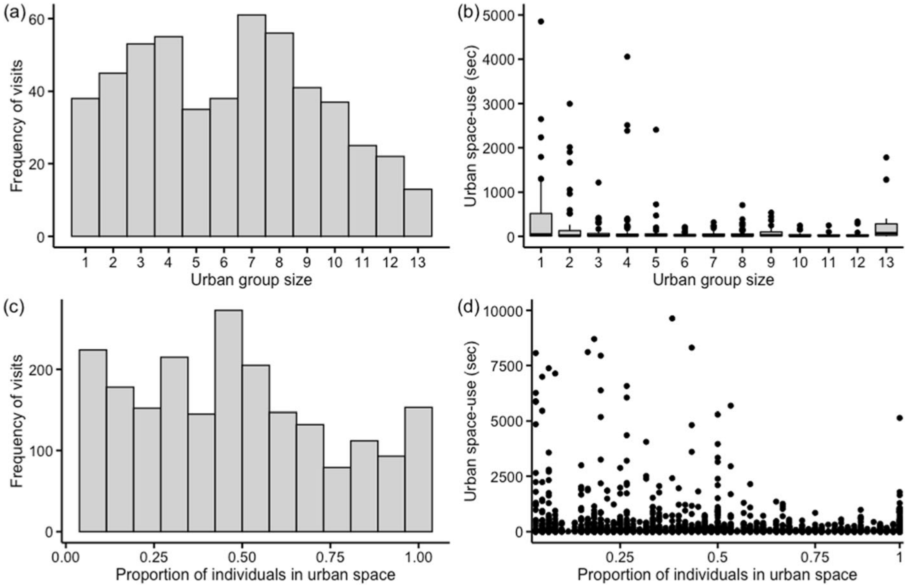

Fig. 2 Urban space use of a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Frequency of visits to urban space. **b** Seconds spent in urban space, for different baboon group sizes. **c** Frequency of visits to urban space as a function of the proportion of collared individuals observed in urban space. **d** Number of seconds spent in urban space as a function of the proportion of collared individuals observed in urban space. Figures **(a)** and **(b)** are based on a time period when all tracking collars (N = 13) were recording GPS; figures **(c)** and **(d)** are based on all available GPS data, as collars recorded for differing lengths of time. In **(b)** boxplots indicate median, upper, and lower quartiles, whiskers indicate interquartile ranges, and filled black circles indicate outliers. Note in **(b)** seven outliers (>5000 s) are not shown.

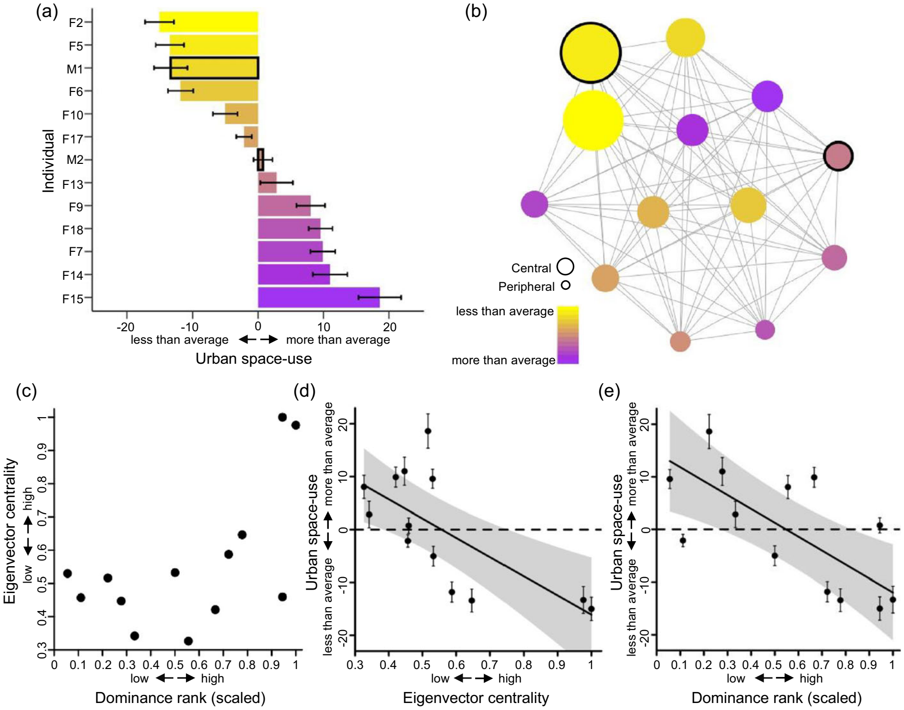

Fig. 3 The influence of social factors on variation in urban space use for a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Individual mean ± SE difference in urban cell use. **b** Baboon social network with increasing circle size indicating higher eigenvector centrality in the group proximity network, and yellow to purple colors representing higher (yellow) or lower (purple) than group mean of urban cell use. M and F denote male or female individuals in **(a)**, and two male baboons are represented with black outline in both **(a)** and **(b)**. **c** Correlation between dominance rank and eigenvector centrality in the group proximity network. **d** The influence of baboon eigenvector centrality in the group proximity network on mean ± SE individual difference from the group mean of urban cell use. **e** The influence of baboon dominance rank on mean ± SE individual difference from the group mean of urban cell use. For **(d)** and **(e)** the black line represents the predicted values, the shaded area represents the confidence intervals using a spaMM model (Rousset & Ferdy, 2014), and the dashed line represents the group mean of urban cell use, which is set to zero.

(network centrality AIC: 6061.93, AIC weight: 0.564; dominance rank AIC: 6062.45, AIC weight: 0.436) and all GPS data (network centrality AIC: 5665.22, AIC weight: 0.393; dominance rank AIC: 5664.34, AIC weight: 0.607) (Supplementary Results). Full model outputs are provided in the Supplementary Information (Table SIII).

Discussion

Baboon management practice on the Cape Peninsula appears to be minimizing temporal and spatial overlap between the Da Gama baboon group and urban spaces. Our GPS data from 13 adult group members estimates that 13% of the group's overall home range is urban, with individuals spending a mean of 11% of their daytime (08:00–18:00) in urban spaces. These data contrast favourably with previously recorded use of urban spaces by baboons in managed groups on the Cape Peninsula (e.g., baboons in urban spaces for 30% of all scans: van Doorn & O'Riain, 2020), but are considerably higher than recent values reported for another Cape Peninsula group, where collared individuals spent a mean of only 1.8% of time in urban spaces (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a). However, this study relied solely on collared adult males; the urban space in which the study was conducted accounted for only 3% of the overall home range and was buffered by extensive vineyards, which reduced the incentives to forage in urban spaces (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a). In contrast, the urban space in the Da Gama group home range transitions abruptly into natural land within Table Mountain National Park. Of concern (from the perspective of baboon management) in the present study is the variation in the way in which individuals use urban spaces during the daytime (range: 3%–26% of total time), because this will mean that different individuals or subgroups of individuals can be in separate places at the same time—both within and outside the urban space—preventing the management of the group as a whole, and consequently splitting the field ranger team into smaller, less effective units.

We found that baboons do not use the urban space equally, adding to the growing evidence that animals adaptively alter their space use in response to human-induced changes to the landscape (Davison *et al.,* 2009; Hamer & McDonnell, 2008; Roth *et al.,* 2008; Šálek *et al.,* 2015). In particular, we found females to use the urban space more often than males. Crop-foraging behavior by females in other baboon populations has been explained by their close association with crop-foraging males (Strum, 2010). In the current study population, and in a population in Namibia, chacma baboon alpha males that hold central positions in spatial and grooming networks are more readily followed by others (Kaplan *et al.,* 2011; King *et al.,* 2011), and especially by close affiliates (King *et al.,* 2008). Baboon management therefore focus on deterring adult male baboons from urban spaces (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a) and, with them, the rest of the group. So why do baboons still enter the urban space, and frequently in small groups? We suggest that baboon socioecology and management practices together drive the patterns we see in the Da Gama group.

We propose that male-focused management has had two consequences for the Da Gama group. First, the successful implementation of this approach has led to lower urban space-use of the males (and especially the alpha). The second, unintended consequence of rangers focusing on the alpha male and the core of the group (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a), in combination with the absence of baboon predators on the Cape Peninsula (Skead, 1980) and the group's relatively large size, is that low-ranking socially peripheral females have been afforded opportunities to temporarily fission and use urban space. Indeed, our analyses show that baboon dominance rank and centrality in the proximity network (which are moderately correlated) both predicted variation in urban space use.

Low-ranked socially peripheral females are afforded more opportunities to use urban space where food rewards are plentiful (van Doorn & O'Riain, 2020). This may be explained by a variety of factors. Because male baboons are being actively managed away from urban spaces (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a), and low-ranked females have weaker affiliation to dominant males (Archie *et al.,* 2014; Palombit *et al.,* 2001), these females are more likely to fission under conflicts of interest (King *et al.,* 2008). Additionally, low-ranked socially peripheral females are often the last to join group movements (King *et al.,* 2011), avoid joining others at foraging patches (King *et al.,* 2009), and are likely to be spatially peripheral, affording exploration of novel areas (Kurihara, 2016), the adoption of "producer" foraging tactics (King *et al.,* 2009), and innovative and risky behaviors (Reader & Laland, 2001). These factors together may drive low-ranked females with low social cohesion to leave the group and access food rewards located in the urban space, rather than remain with the dominant male and his higher-ranking close female affiliates that are generally the primary focus of management (Fehlmann, O'Riain, Kerr-Smith, Hailes, *et al.,* 2017a).

Other case studies also lend support to social factors being important predictors of individuals' use of anthropogenic environments. For instance, the amount of crop foraging by elephants (*Loxodonta africana*) in Amboseli National Park, Kenya, is predicted by sex and age (where older males are more likely to crop forage), but also by having close associates that crop forage (Chiyo *et al.,* 2012). Studies of primates across species and populations similarly highlight the role of sex and sociality in individuals' use of anthropogenic environments. In three macaque species (*Macaca mulatta*, *Macaca fascicularis*, *Macaca radiata*) across India and Malaysia, males and high-ranking individuals of both sexes had more anthropogenic food in their diets than other individuals (Marty *et al.,* 2019). In moor macaques (*Macaca maura*), males and individuals with high betweenness centrality in association networks were more often seen on roads and in close proximity to humans (Morrow *et al.,* 2019). A comparative study on 10 periurban macaque groups across three species found that individuals occupying peripheral spatial positions in the group were more likely to interact with humans (Balasubramaniam *et al.,* 2020). The authors suggest this pattern was driven by reduced access to natural forage and increased exposure to human presence for individuals that are peripheral to the group. Overall, this research across different species and contexts highlights how social and ecological factors can interact in complex ways to influence individual behavior and use of urban environments.

The frequent recursions to urban space by individuals and small groups demonstrates high fission–fusion dynamics in the Da Gama group, and these dynamics can lead to a permanent group fission (Sueur *et al.,* 2011), especially when social relationships are constrained at large group sizes (Lehmann *et al.,* 2007). If a permanent fission occurs, this, in effect, creates two groups where there was previously one, and therefore a greater management challenge. In other baboon populations, the exact group size at which fission occurs depends on several factors (Henzi *et al.,* 1997), and on the Cape Peninsula such fissions have previously been observed for a range of group sizes (termed splinter groups: Forthman-Quick, 1986; Strum, 2010). Management of splinter groups is doubly challenging because there is not enough capacity to manage them (i.e., in terms of budget and/or personnel), resulting in increased time in urban spaces compared to managed groups (Hoffman & O'Riain, 2012b), and urban space use is linked to higher levels of human-induced injuries and death (Beamish, 2009). Further work is therefore needed to investigate potential ways of limiting the time that solitary and small groups of female baboons spend in urban spaces, thereby also reducing the potential for future fission events and formation of splinter groups.

The City of Cape Town invests approximately R14 million (US $800 000) per annum on preventing baboons in 10 Peninsula groups from entering urban spaces. We found that small groups of female baboons are breaking away from the main group and spending time in urban spaces. Though adult males may be more noticeable in urban spaces (as they are perceived to be more threatening to humans: Beamish, 2009), individuals from all age–sex classes may cause damage to residential buildings, vehicles and bins (Anna M. Bracken and Charlotte Christensen), and therefore the increased use of urban spaces by small groups of females heightens the risk of damage to property and causes difficulties for management (van Doorn & O'Riain, 2020). Ways in which group size can be constrained in the longer term should be considered, because smaller groups are predicted to be more cohesive (Sueur *et al.,* 2011) and are less likely to fission under conflicts of interest (King *et al.,* 2008), making them easier to manage. One option would be the routine contraception of females, which has been used in captive settings (Plowman *et al.,* 2005). However, contraception also alters the proportion of females in different reproductive states, which impacts behavioral synchrony within chacma baboon groups (King & Cowlishaw, 2009). Additionally, preliminary data gathered during the current study suggest that females spend less time in urban spaces when they have infants (Bracken *et al.*, unpubl. data.). Constraining group sizes by contraception of females would therefore bring its own management challenges. In the meantime, management should continue to develop other tools to reduce baboon–human conflict, e.g. baboon-proofed fences and baboon-proofing property and bins (see Fehlmann *et al.,* 2020; Hoffman & O'Riain, 2012a; Kaplan *et al.,* 2011 for discussions). Integrating social sciences research to understand perceptions of individual baboons of different size and sex would further inform management of how and why these low-ranking females have greater access to urban spaces; for example, there may be differences in people's perception of the damage caused, and the threat posed, between male and female baboons (Mormile & Hill, 2017). Additionally, because local residents are integral to "baboon-proofing" exercises, understanding residents' perceptions of management will inform and promote their success.

In summary, we show that individual baboons can vary greatly in their use of urban spaces, and this can be predicted by social integration; individuals peripheral in the social network are more likely to fission from the group and to use the urban space. Understanding the ways in which group structure influences urban space use is crucial (Baranga *et al.,* 2012), and our results highlight the importance of examining the responses of wildlife to human landscapes at an individual level (Merrick & Koprowski, 2017). Further work studying individual movement trajectories has the potential to provide greater insight: for example, identifying "keystone" individuals that use urban spaces (King *et al.,* 2018), which may drive an increase (or decrease) in the urban space use of other group members. Additionally, analysis of individual movement can uncover specific behavioral types, such as individuals that are more exploratory or have a higher tendency for risk taking (Merrick & Koprowski, 2017), and flexibility in these behavioral types (Hertel *et al.,* 2020), which may predict propensity to use urban space. Such approaches are likely to aid management (Merrick & Koprowski, 2017) by identifying individuals with a large influence on urban space use (King *et al.,* 2018), and incorporating this individual-level information in the development of flexible management tactics. We hope that this work will assist future management decisions involving the Cape baboons and may provide a basis for understanding urban species elsewhere.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-021-00247-x.

Acknowledgments Fieldwork was approved by the Baboon Technical Team (BTT) in the Cape Peninsula and by Research Agreement with South African National Parks (SANParks). Thanks to Human Wildlife Solutions (service providers employed by the City of Cape Town) and veterinarian Dorothy Breed for organizing baboon cage trapping, and to Esme Beamish, and Human Wildlife Solutions for their assistance.

We thank Lucy Robertson, Charlotte Solman, and Francesca Marshall-Stochmal for assistance with fieldwork. AB thanks Alexis Malagnino for his help and advice with GPS processing and analysis. AJK and IF thank Layla King for support. AB and CC were supported by College of Science/Swansea University PhD scholarships. This research was supported by grants (awarded to AJK) from Swansea University's College of Science and the Association for the Study of Animal Behaviour (ASAB). JO'R was supported by NRF incentive funding. We are grateful to the editor-in-chief Jo Setchell, guest editor Dr Giuseppe Donati, and two anonymous reviewers for constructive feedback during peer review.

Author Contributions AB and AJK conceived the study with advice from MJO concerning data required to improve adaptive management and the independent assessment of baboon management by professional service providers employed by the City of Cape Town. AB, CC, GF, MDH, and PWH constructed the tracking collars. AB and CC collected data in the field. AB processed and analyzed the data with input from AJK and IF. AB led writing of the manuscript with input from all authors, who read and approved the final manuscript.

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Research

Flexible group cohesion and coordination, but robust leader–follower roles, in a wild social primate using urban space

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Cite this article: Bracken AM, Christensen C, O'Riain MJ, Fürtbauer I, King AJ. 2022 Flexible group cohesion and coordination, but robust leader–follower roles, in a wild social primate using urban space. *Proc. R. Soc. B* **289**: 20212141.
https://doi.org/10.1098/rspb.2021.2141

Received: 29 September 2021
Accepted: 10 December 2021

Subject Category:
Global change and conservation

Subject Areas:
behaviour, ecology

Keywords:
cohesion, coordination, urban space-use, leadership, flexibility

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Electronic supplem
online at https://d
c.5762484.

Collective behaviour has a critical influence on group social structure and organization, individual fitness and social evolution, but we know little about whether and how it changes in anthropogenic environments. Here, we show multiple and varying effects of urban space-use upon group-level processes in a primate generalist—the chacma baboon (*Papio ursinus*)—within a managed wild population living at the urban edge in the City of Cape Town, South Africa. In natural space, we observe baboon-typical patterns of collective behaviour. By contrast, in urban space (where there are increased risks, but increased potential for high-quality food rewards), baboons show extreme flexibility in collective behaviour, with changes in spatial cohesion and association networks, travel speeds and group coordination. However, leader–follower roles remain robust across natural and urban space, with adult males having a disproportionate influence on the movement of group members. Their important role in the group's collective behaviour complements existing research and supports the management tactic employed by field rangers of curbing the movements of adult males, which indirectly deters the majority of the group from urban space. Our findings highlight both flexibility and robustness in collective behaviour when groups are presented with novel resources and heightened risks.

1. Introduction

Owing to the challenges involved in tracking the behaviours of many individuals simultaneously, we are only just beginning to understand the collective behaviour of wild social groups [1–3] and know little about whether and how it changes in anthropogenic environments. This is an important gap in

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[9,15]. This management effort reduces the time the baboons spend in urban space [9,17], but can contribute to significant

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expected poorer whole group coordination [24,56,60] in urban space compared to natural space (hypothesis 2), as

alignment in travel speed and direction would be difficult for individuals to maintain over large distances (though

area may be particularly sensitive to missing individuals [68]. To test for differences in spatial association networks, we extracted two commonly used metrics: eigenvector centrality and

[redacted]

see the electronic supplementary material, methods), we bootstrapped all models with 48 repetitions, randomly sampling from the natural dataset for the number of minutes recorded in

the urban dataset. We extracted model coefficients at each iter-

0.718; $Q = 0.429$) compared to the network in natural space (density = 1; $Q = 0.118$), reflecting lower cohesion in urban space (figure 1) where baboons are further apart (figure 1*a*,

Table 1. Results of a non-parametric bootstrap (48 iterations) of a generalized least-squares model for the effect of space (urban, natural) on each of 11 collective parameters of a baboon group living on the urban edge in Cape Town, South Africa. (Estimates, *t*-values and *p*-values are the mean average taken across bootstrap iterations, 95% confidence intervals (CI) indicate the 95% distribution of the estimates, and standard errors represent the error around the estimates. 'Log' indicates

[redacted]

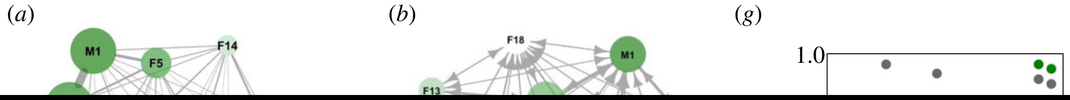
± s.e. = −0.837 ± 0.108, $t = -7.751$, $p < 0.001$; electronic supplementary material, figure S3a). Similarly, polarization increased with increasing standard error in speed (electronic

values in association and leadership networks were not correlated (Spearman's rank correlation: natural: rho = 0.538, $p = 0.061$; urban: rho = 0.032, $p = 0.921$).

[redacted]

significantly reduced in urban space, supporting our first hypothesis. This finding is in line with recent research

spread of the group in urban space had an uneven distribution. Individuals were often seen in dispersed subgroups,



[redacted]

into urban space [11]. High speed in urban space is presumably indicative of high risk, and is probably the result of individuals

tion when moving off independently of one another—resulting in low whole group coordination in movement.

In the case of our third hypothesis, we found that, though leader–follower networks were interrupted, and leadership eigenvector centrality was significantly reduced in urban

[redacted]

leader–follower networks based upon pulls across the whole dataset. It would therefore be informative to compare both datasets at different scales (i.e. different threshold distances with shorter or longer lag times between movement) and for different types of movement events, to examine how collective movement is shaped by differences in context or species.

help and advice with GPS processing, A.J.K. and I.F. thank Layla King for her support. Thanks to two anonymous referees and editors for their constructive feedback which improved the manuscript.

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International Journal of Primatology (2021) 42:589–599
https://doi.org/10.1007/s10764-021-00220-8

The Relationship Between GPS Sampling Interval and Estimated Daily Travel Distances in Chacma Baboons (*Papio ursinus*)

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Received: 9 December 2020 / Accepted: 14 April 2021/

Abstract

Modern studies of animal movement use the Global Positioning System (GPS) to estimate animals' distance traveled. The temporal resolution of GPS fixes recorded should match those of the behavior of interest; otherwise estimates are likely to be inappropriate. Here, we investigate how different GPS sampling intervals affect estimated daily travel distances for wild chacma baboons (*Papio ursinus*). By subsampling GPS data collected at one fix per second for 143 daily travel distances (12 baboons over 11–12 days), we found that less frequent GPS fixes result in smaller estimated travel distances. Moving from a GPS frequency of one fix every second to one fix every 30 s resulted in a 33% reduction in estimated daily travel distance, while using hourly GPS fixes resulted in a 66% reduction. We then use the relationship we find between estimated travel distance and GPS sampling interval to recalculate published baboon daily travel distances and find that accounting for the predicted effect of sampling interval does not affect conclusions of previous comparative analyses. However, if short-interval or continuous GPS data—which are becoming more common in studies of primate movement ecology—are compared with historical (longer interval) GPS data in future work, controlling for sampling interval is necessary.

Keywords Daily travel distance · Day path length · GPS · Movement ecology · *Papio ursinus*

Handling Editor: Joanna Setchell.

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Introduction

Understanding how animals interact with and move through their environment enables researchers to better understand animal behavior, physiology, and ecology (Getz and Saltz 2008; Nathan *et al.* 2008). Modern studies of animal movement use the Global Positioning System (GPS) to estimate animals' travel distance over a given time period. Researchers record GPS fixes at intervals along the journey of a focal animal or group— either using a handheld GPS (Santhosh *et al.* 2015; Schreier and Grove 2010), or by attaching a GPS logger to a focal animal (Hampson *et al.* 2010a,b; Ren *et al.* 2008)—and sum the distances traveled between GPS fixes. More refined estimates of distance traveled are also possible; for example, modeling movement as a continuous-time stochastic process minimizes the effects of position and velocity autocorrelation that are inherent in such data (Calabrese *et al.* 2016).

Recording of GPS at intervals in time (rather than continuously) is common because it saves battery life and allows researchers to increase the time over which data are collected (Mitchell *et al.* 2019; Ryan *et al.* 2004; Sahraei *et al.* 2017). However, this practice underestimates travel distance (McGavin *et al.* 2018; Sennhenn-Reulen *et al.* 2017). For example, a study of Guinea baboons (*Papio papio*) (Sennhenn-Reulen *et al.* 2017) examined differences in travel distance estimates from 2-h periods by subsampling GPS data collected at one fix per second, finding that travel distances were significantly shorter if less frequent GPS fixes were used in calculations. Indeed, extensive theoretical and empirical work has shown that the temporal resolution of GPS fixes needs to match those of the behavior of interest; otherwise estimates are likely to be inappropriate (Borger *et al.* 2006; de Weerd *et al.* 2015; Ganskopp and Johnson 2007; Johnson and Ganskopp 2008; McGavin *et al.* 2018; Mills *et al.* 2006; Mitchell *et al.* 2019; Noonan *et al.* 2019; Postlethwaite and Dennis 2013; Rowcliffe *et al.* 2012; Sennhenn-Reulen *et al.* 2017; Swain *et* al. 2008; Tanferna *et al.* 2012).

Here, we estimate daily travel distances for chacma baboons (*Papio ursinus*) using GPS data collected at one fix per second synchronously for 12 adult individuals over 11–12 days. By sampling different temporal resolutions from this high-frequency GPS data set, we investigate the relationship between estimated travel distances and GPS sampling frequency (Sennhenn-Reulen *et al.* 2017). Then, we use the quantified relationship between estimated travel distance and GPS sampling interval to recalculate published baboon daily travel distances (e.g., Dunbar 1992; Johnson *et al.* 2015) and see how estimates alter when accounting for the relationship between estimated distance and GPS sampling interval found in our own data set.

Methods

Study System

We studied wild adult chacma baboons in the Da Gama group in Cape Town, South Africa (34.1617° S, 18.4054° E). The group's home range includes urban areas comprising residential suburbs and natural areas that fall mostly within Table Mountain National Park which are dominated by indigenous fynbos vegetation with smaller patches of exotic vegetation (Hoffmann and O'Riain 2012). The Mediterranean climate of the Cape Peninsula is characterized by hot dry summers and mild winters with moderate–high rainfall (Hoffman and O'Riain 2012), and in this study we use GPS data collected during winter (August) of a field season lasting from July to November 2018. The Da Gama group comprised 2 adult males, 19 adult females, and *ca*. 30 subadults, juveniles, and infants.

Movement Data

During the field season, we recorded GPS data for 13 individuals (2 males, 11 females) for a mean ± SD of 42.77 ± 9.92 days, range = 21–54 days (Bracken *et al.* in press) using in-house assembled SHOALgroup collars (F2HKv3) containing GiPSy 5 GPS loggers (TechnoSmArt, Italy) recording GPS fixes at 1-s sampling intervals between 06:00:00 and 18:00:00 UTC (Bracken *et al.* in press). Here we use a subset of these GPS data that provide continuous data for 12 baboons (2 males, 10 females) for 11–12 days in August 2018, representing 143 daily travel distances.

Before calculating daily travel distances (below), we removed erroneous GPS fixes outside the study area, or successive GPS fixes between which it would have been impossible for the baboons to travel (Bracken *et al.* in press). These fixes represented a median 0.01% of GPS fixes per collar (range 0.00%–0.01%) and the remaining missing or removed fixes that lasted a time period of less than or equal to 10 s, were interpolated using the fixLocNA function in the swaRm package (Garnier 2016) following O'Bryan *et al.* (2019) and Bracken *et al.* (in press). This resulted in a median 0.01% of each baboon's tracks being interpolated (range 0.00%–0.01%). Remaining missing fixes lasting >10 s represented a median 0.56% per collar (range 0.00%–1.61%).

Daily Travel Distances

To investigate the effect of GPS sampling interval on estimated daily travel distance, we subsampled the high-frequency GPS data and calculated travel distances for each baboon, for each day, using GPS fixes set at 1 s, 30 s, 60 s, 300 s, 1200 s, 3600 s, and 7200 s. We estimated daily distance by summing distances between GPS fixes and used fixed time intervals from the 1 s data set, since we wanted to simulate different programmed sampling intervals used by on-animal GPS loggers.

Because travel distance estimates made using short GPS sampling intervals will be more sensitive to measurement error than estimates made using longer GPS sampling intervals, we also calculated daily travel distances using 1 s smoothed data in an attempt to reduce high-frequency noise (Noonan *et al.* 2019). To smooth data, we used the function TrajSmoothSG from the trajr package in Rstudio (version 1.3.0), which uses a Savitzky–Golay ethod (McLean and Skowron Volponi 2018). We applied a filter order of 2 and a filter length of 7, which approximately corresponds to our maximum level of GPS error and was thus expected to reduce potential noise while retaining track characteristics (McLean and Skowron Volponi 2018). We performed *ad hoc* checks of the GPS data using known landmarks at the field site in South Africa, and in Swansea, UK and these indicated positional accuracy always to be within 5 m.

GPS Sampling Interval and Daily Travel Distances

We investigated how GPS sampling interval affected daily travel distance estimates by fitting a linear mixed-effect model in RStudio using the lme4 package (Bates *et al.* 2015). We fitted daily travel distances (N = 1144) as our response variable and sampling interval (1 s, 1 s [smoothed], 30 s, 60 s, 300 s, 1200 s, 3600 s, and 7200 s) as a fixed categorical effect. We fitted baboon identity as a random effect to control for potential interindividual differences in travel distance, checked model residuals, and used the emmeans package (version 1.4.8; Lenth 2020) for *post hoc* (Tukey method) tests for each combination of sampling interval.

Quantifying the Reduction in Daily Travel Distance

We compared estimated daily travel distance using one fix per second GPS data to different GPS sampling intervals to quantify the reduction in estimated distance when using less frequent sampling intervals and expressed this value as a proportion. We found the reduction in estimated distance traveled was proportional to GPS sampling interval and was best modeled by a logarithmic function. Using this model, we recalculated travel distances for 38 baboon groups (provided by Johnson *et al.* 2015) that provide information on GPS sampling intervals.

Ethical Note

To fit collars, a veterinarian anesthetized baboons using Ketamine (dose adjusted for body mass) after cage trapping conducted by service providers in accordance with local protocols (described by Fehlmann *et al.* 2017a). Collars were approved by Swansea University's Ethics Committee (IP-1314-5), weighed mean 2.2% baboon body mass (range 1.2%–2.6%), and were fitted with a drop-off mechanism (version CR-7, Telonics, Inc.) to avoid the need for recapture (ESM Fig. S1). The authors declare that there are no conflicts of interests.

Data Availability The dataset generated and analyzed during is available in the Electronic Supplementary Material (ESM 3).

Results

The mean estimated daily travel distance across all days and baboons was 10.86 km when calculated using a 1 fix per second sampling interval and 2.71 km when using a 7200 s sampling interval. The estimated daily travel distance becomes progressively shorter with less frequent GPS sampling because fewer GPS fixes do not properly capture the animal’s movement path (Fig. 1; ESM Video S1). As a result, less frequent GPS fixes result in a significant reduction in calculated daily travel distances (Fig. 2a; ESM Table S1; Video S1), and this reduction changes with GPS sampling interval according to a logarithmic function (proportion distance captured = 0.081ln(sampling interval) + 0.9682; r^2 = 0.99; Fig. 2b and c).

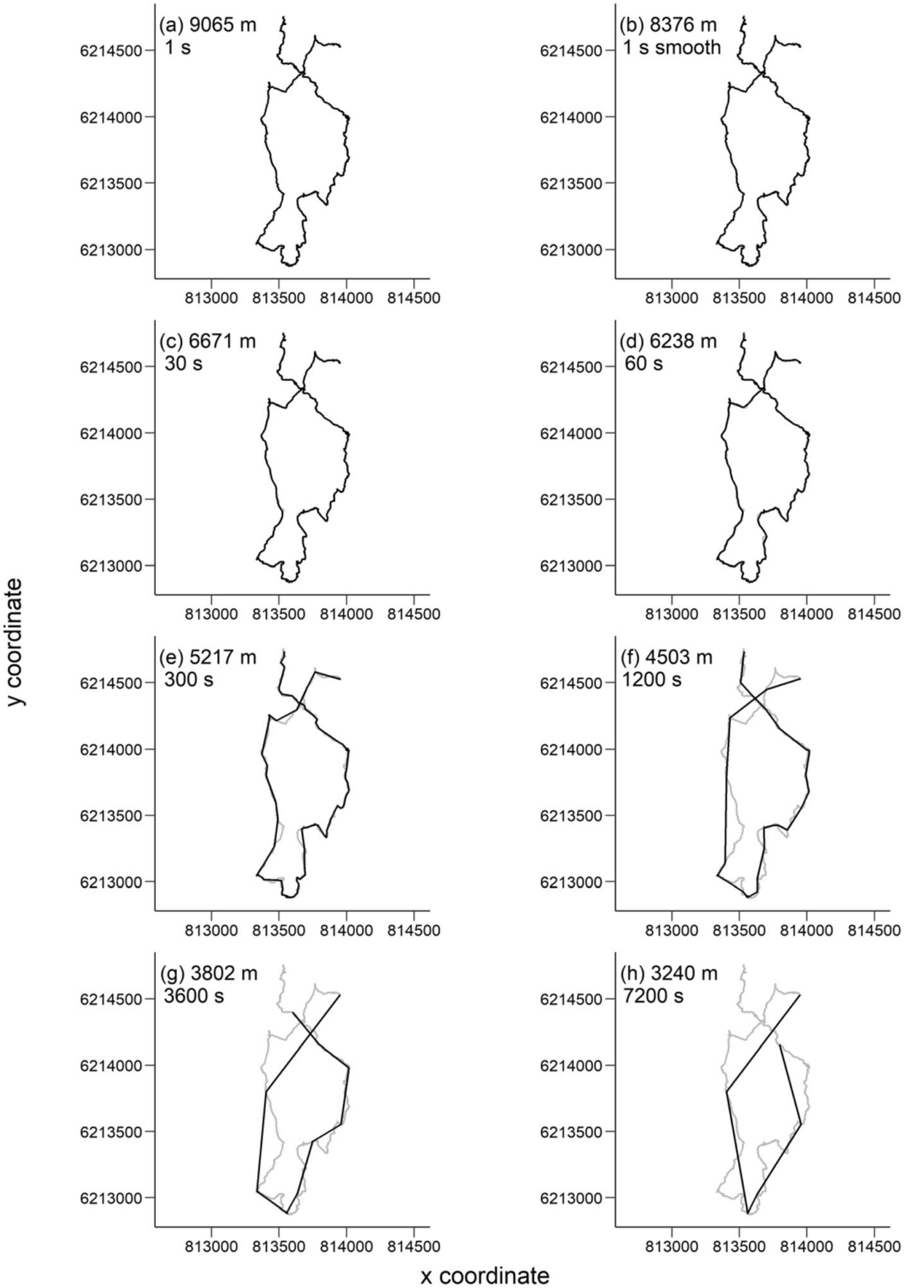

Fig. 1 Path traveled (black line) by one adult female chacma baboon between 06:18 and 18:00 UTC on August 4th, 2018 in Cape Town, South Africa, estimated using a GPS sampling interval of **(a)** 1 s, **(b)** 1 s smoothed, **(c)** 30 s, **(d)** 60 s, **(e)** 300 s, **(f)** 1200 s, **(g)** 3600 s, and **(h)** 7200 s. In **(b)–(h)** an additional green line representing the path estimated using 1-s sampling interval is shown for comparison.

Applying our model to published baboon daily travel distances (Fig. 3a), we found travel distances were ≥50% farther when using one fix per second sampling interval

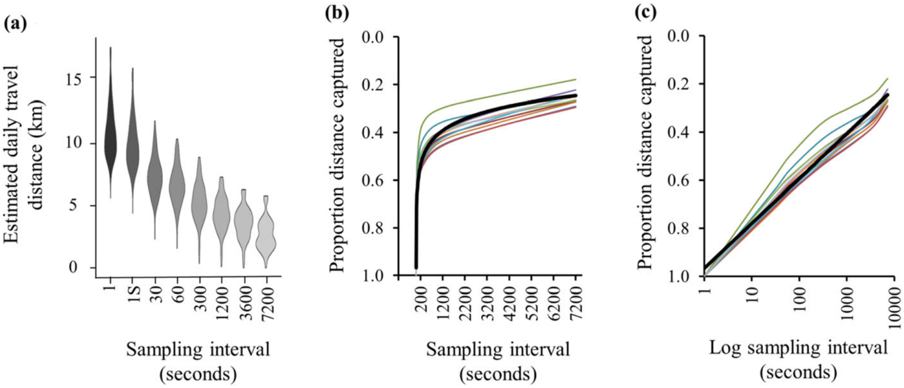

Fig. 2 **(a)** Kernel probability density of daily travel distances by 12 chacma baboons over 11–12 days, in Cape Town, South Africa, measured using GPS sampling intervals ranging one fix per second to one fix per 7200 s; smoothed 1-s data (1S) are also shown. **(b)** Comparison of the estimated distance calculated with one fix per second GPS compared to less frequent GPS sampling intervals, expressed as a proportion. **(c)** Comparison of the estimated distance calculated with one fix per second GPS compared to less frequent GPS sampling intervals (log scale). For **(b)** and **(c)** individual baboon data (*N* = 12) are modeled by colored lines, and the fitted logarithmic function across all data is given by the black line. The vertical axis in **(b)** and **(c)** is reversed to aid interpretation.

(Fig. 3b). We found that the range of GPS sampling intervals used in the published work is small (300–3600 s; Fig. 3a), and the proportion of distance captured did not get larger or smaller for groups that travel farther (Fig. 3b and c).

Discussion

Using less frequent GPS sampling intervals to estimate chacma baboon daily travel distances reduces the opportunity to measure an animal’s deviation from a linear path, resulting in smaller estimated daily travel distances. The reduction in estimated travel

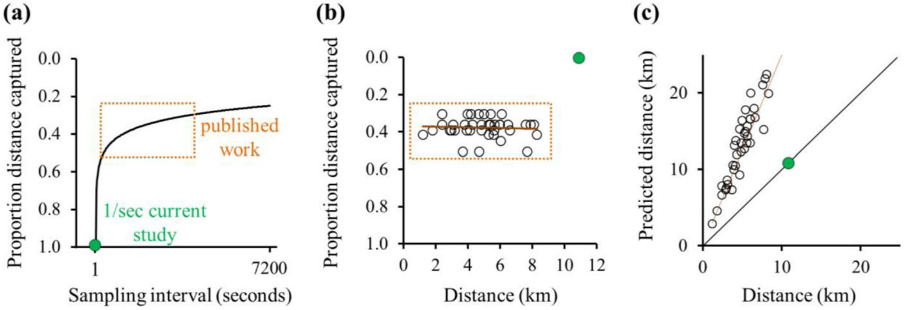

Fig. 3 **(a)** Comparison of the estimated distance calculated with one fix per second GPS (filled circle) compared to less frequent GPS sampling intervals, expressed as a proportion. The dashed box indicates the range of GPS sampling interval (300–3600 s) used in 38 published groups’ daily travel distances (Johnson *et al.* 2015). **(b)** Estimation of the proportion of distance captured for 38 published group daily travel distances (data points given by open circles inside the dashed box) based on their reported GPS sampling intervals, using the relationship modeled in **(a)**. One fix per second GPS data used in the current study is shown by the filled circle data point. **(c)** Predicted daily distance traveled for 38 published groups (Johnson et al. 2015), based on the reported groups’ daily travel distances and their GPS sampling interval, using the model shown in **(a)**. One fix per second GPS data (current study) is shown by the filled circle that falls on a 1:1 line.

distance seen with increasing GPS sampling interval (here, the difference between estimates at one fix per second and other intervals) can be modeled by a logarithmic function. Our findings therefore support empirical and theoretical work showing that the interval at which GPS fixes are taken can systematically change movement distances calculated (Borger *et al*. 2006; de Weerd *et al*. 2015; Ganskopp and Johnson 2007; Johnson and Ganskopp 2008; McGavin *et al*. 2018; Mills *et al*. 2006; Mitchell *et al*. 2019; Noonan *et al*. 2019; Postlethwaite and Dennis 2013; Rowcliffe *et al*. 2012; Sennhenn-Reulen *et al*. 2017; Swain *et al*. 2008; Tanferna *et al*. 2012) and affirm research with Guinea baboons reporting similar findings when estimating travel distances over a shorter time frame (2-h blocks) and with fewer baboons ($N = 4$) (Sennhenn-Reulen *et al*. 2017).

Miscalculation of travel distances can have important implications for studies of movement ecology (Hebblewhite and Haydon 2010; Patterson *et al*. 2008; Schick *et al*. 2008), disease dynamics (Dougherty *et al*. 2018; White *et al*. 2018) and designation of conservation spaces (Cristescu *et al*. 2013; Darnell *et al*. 2014; Douglas-Hamilton *et al*. 2005). For example, distances traveled calculated from GPS data have been used to estimate the energy cost coefficients of locomotion (e.g., Brosh *et al*. 2010) and these will alter substantially if the relationship between estimated distances and sampling interval that we report is typical across species and contexts. Indeed, our baboon case study suggests that moving from a GPS frequency of one fix every second to one fix every 30 s results in a 33% reduction in estimated daily travel distance, while using hourly GPS fixes results in a 66% reduction in estimated daily travel distance.

Future studies should consider the impact of GPS sampling intervals on distance estimates. Assuming that estimated distances change with GPS sampling interval according to a logarithmic function may be informative, but other factors will also need to be considered. In the context of baboon behavior, for example, 1) the tortuosity of the travel path and 2) the speed of travel will affect how much a path is underestimated (Sennhenn-Reulen *et al*. 2017), because while slower movement decreases travel distance, more tortuous movement increases travel distance (Johnson *et al*. 2015). Therefore, while the logarithmic relationship we describe could be a general phenomenon, the effect size (exponent) will change with a myriad of social and ecological factors (Dunbar 1992; Johnson *et al*. 2015). Where high-accuracy estimates of travel distance are needed, researchers should therefore consider continuous-time stochastic process models (Calabrese *et al*. 2016) to minimize confounding effects of position and velocity autocorrelation.

Comparative investigations of daily travel distances between species and populations rely on estimates of travel distances, typically from GPS data (Carbone *et al*. 2005; Dunbar 1992; Johnson *et al*. 2015). Given the significant differences in estimated distances according to GPS sampling interval, this could result in flawed comparisons. Using the relationship described for our data, we calculated daily travel distance for 38 baboon groups (Johnson *et al*. 2015) as if they had used a GPS sampling interval of one fix per second. Published travel distances captured a minimum 50% of the distance predicted if a 1-s sampling interval was used, but because the range of GPS sampling intervals used by baboon researchers to date is small (300–3600 s) the model predicted distances did not systematically vary across groups/sampling intervals. Previous comparisons of daily travel distances in baboons are therefore sound. However, if high-resolution GPS data (as used in the present study) were to be included in such comparisons in future, this would introduce pronounced differences in travel distance estimates. Estimated travel distances using high-frequency GPS data therefore cannot be compared to published distance estimates (that use less frequent sampling intervals) without properly controlling for differences in sampling regimes.

Our case study also highlights an understudied aspect of high-resolution GPS data in animal movement studies: positional accuracy. Because GPS positional error is Gaussian in nature, this error will not tend to systematically alter estimates of interindividual distances (Haddadi *et al.* 2011; King *et al.* 2012) or interaction with features of the environment (Fehlmann *et al.* 2017a; Strandburg-Peshkin *et al.* 2017), or conspecifics (Farine *et al.* 2016, 2017; Strandburg-Peshkin *et al.* 2015), and therefore does not normally need to be accounted for in such contexts. However, calculated distance traveled estimates are sensitive to positional measurement error (McGavin *et al.* 2018; Noonan *et al.* 2019), and these errors are pronounced at short GPS sampling intervals which will affect the estimated travel path. We therefore smoothed our 1-s GPS data in an attempt to reduce the impact of such high-frequency noise, and this resulted in significantly shorter distance estimates (ESM Table SI). Further work is now needed to explore if such smoothing is required because GPS loggers have on-board smoothing algorithms (which typically cannot be accessed by the end-user). These algorithms minimize "jitter" or "drift" when the logger is slow-moving or stationary (see ESM Fig. S2 for an example from our data) making it challenging to determine if *post hoc* smoothing removes "real movement," "noise," or both. Combining aerial video footage and GPS data of moving animals in the wild (e.g., on a beach where tracks are left) would be one way to investigate the relationship between true movement and GPS measured movement. Another would be to match GPS data to acceleration data to distinguish between active and nonactive time periods (Fehlmann *et al.* 2017b).

Finally, our findings highlight the need to choose an appropriate GPS sampling interval. The smaller the sampling interval, the higher the number of GPS fixes taken within a given time frame and the higher the accuracy of any subsequent distance estimate. But this comes at the cost of shorter battery life, and hence a shorter data collection period. This makes high-resolution GPS sampling less practical for longer-term studies in primate spatial ecology because collars need to increase in size and weight to accommodate larger batteries. However, this issue can be overcome if collars use solar cells with rechargeable batteries and dynamically switch between different sampling rates depending on the animal's activity (e.g., Wilson *et al.* 2018). Given these tradeoffs, studies will likely continue to use different GPS sampling regimes, and so our case study provides useful rule-of-thumb for the magnitude of change expected when estimated travel distances with different GPS sampling intervals.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10764-021-00220-8.

Acknowledgments Data were collected during fieldwork approved by the Baboon Technical Team (BTT) in the Cape Peninsula and by Research Agreement with South African National Parks (SANParks). Thanks to Human Wildlife Solutions and veterinarian Dorothy Breed for organizing baboon cage trapping, and to Justin O'Riain, Gary Buhrman, Esme Beamish, and Human Wildlife Solutions for their assistance. We thank Carlo Catoni (TechnoSmArt), Gwenda Kesans (Ride and Drive Equestrian), Gaelle Fehlmann, Mark Holton, and

Phil Hopkins for assistance with collar design and build. AB thanks Alexis Malagnino for advice with GPS processing. AJK and IF thank Layla King for support. AB and CC were supported by College of Science/Swansea University PhD scholarships. Research was supported by grants from Swansea University's College of Science and the Association for the Study of Animal Behaviour (ASAB). We are grateful to Editor-in-Chief Jo Setchell and two anonymous reviewers for excellent and constructive feedback during peer review.

Author Contributions AJK and IF conceived the study. AB and CC constructed the tracking collars and collected data in the field. AB processed the data. RMcC analyzed the data and conducted statistical analyses with input from AJK, IF, and AB. RMcC wrote the first draft of the manuscript, which was revised by AJK with input from all authors, who read and approved the final manuscript.

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General and Comparative Endocrinology 318 (2022) 113985

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Research paper

Simultaneous investigation of urinary and faecal glucocorticoid metabolite concentrations reveals short- versus long-term drivers of HPA-axis activity in a wild primate (*Papio ursinus*)

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ARTICLE INFO

Keywords:
HPA-axis activity
Non-invasive sampling
Glucocorticoid metabolites
Faeces
Urine
Excretion time lags

ABSTRACT

Glucocorticoids (GCs), a class of steroid hormones released through activation of the hypothalamic–pituitary–adrenal (HPA) axis, perform many vital functions essential for survival, including orchestrating an organism's response to stressors by modulating physiological and behavioural responses. Assessing changes and variation in GC metabolites from faecal or urine samples allows for the non-invasive monitoring of HPA-axis activity across vertebrates. The time lag of hormone excretion differs between these sample matrices, which has implications for their suitability for studying effects of different temporal nature on HPA-axis activity. However, simultaneous comparisons of predictors of faecal and urinary GC metabolites (fGCs and uGCs, respectively) are lacking. To address this gap, we employ frequent non-invasive sampling to investigate correlates of fGCs and uGCs in wild chacma baboons (*Papio ursinus*) ($n = 17$), including long-term (dominance rank, season, female reproductive state) and short-term (time of day, daily weather conditions) factors. Correlated with increasing day length, fGCs gradually decreased from winter to summer. No seasonal effect on uGCs was found but 'rain days' were associated with increased uGCs. Pregnant females had significantly higher fGCs compared to cycling and lactating females, whereas uGCs were not statistically different across reproductive states. A circadian effect was observed in uGCs but not in fGCs. Dominance rank did not affect either fGCs or uGCs. Our study highlights the difference in inherent fluctuation between uGCs and fGCs and its potential consequences for HPA-axis activity monitoring. While uGCs offer the opportunity to study short-term effects, they undergo more pronounced fluctuations, reducing their ability to capture long-term effects. Given the increasing use of urine for biological monitoring, knowledge of this potential limitation is crucial. Where possible, uGCs and fGCs should be monitored in tandem to obtain a comprehensive understanding of short- and long-term drivers of HPA-axis activity.

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https://doi.org/10.1016/j.ygcen.2022.113985
Received 21 June 2021; Received in revised form 7 January 2022; Accepted 24 January 2022

et al., 2000).

Biomedical research has shown that prolonged activation of the HPA-axis can have negative consequences as the physiological mediator

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used fGCs (Palme, 2005), and to understand the potential limitations and advantages of using faeces or urine.

A primary consideration of which matrix to use is that GC excretion lag times differ between faeces and urine (Heistermann, 2010; Touma and Palme, 2005), which spans the time between GC production, metabolism and excretion which, in the case of faeces, also includes gut passage time (Palme, 2019). Time-lags are species-specific (see e.g., Bahr et al., 2000; Heistermann, 2010; Schatz and Palme, 2001), but

and uGCs is driven by the same predictors, and thus can be used interchangeably, a simultaneous investigation is needed.

In the present study, we simultaneously investigate correlates of fGCs and uGCs in wild chacma baboons on the Cape Peninsula, Western Cape, South Africa. Predictors of HPA-axis activity have been robustly documented in long-term field studies of baboons, revealing the effects of reproductive state (Engh et al., 2006; Gesquiere et al., 2008; Weingrill et al., 2004), dominance rank (Bergman et al., 2005; Gesquiere et al.,

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mentary Material). Work was approved by Swansea University's Ethics Committee (IP-1314–5) and local authorities (Cape Nature, permit number: CN44-59–6527; SANparks, permit number: CRC/2018–2019/008 – 2018/V1; CITES, sample export permit: 208683). Weather data was provided by South African Weather Service (SAWS) (https://www.weathersa.co.za), from the Slangkop weather station, approximately 7 km from the field site (Climate number:

Table 1

Details on study animals, including rank, median, range and sample size (n) for fGCs (ng/g) and SG-corrected uGCs (ng/ml). DRScv calculated by SD/mean*100 and corrected for sample size (see Tkaczynski et al., 2019). Samples were

throughout the day and were frozen at −20 °C at the research house until further processing. To remove moisture, faecal samples were freeze-dried at −45 °C for a minimum of 24 h (using a New Brunswick, New Brunswick Scientific Co., Inc., New Jersey USA and Scanvac CoolSafe, LaboGene ApS freeze-dryer) at the University of Cape Town. Samples were stored at −20 °C until ambient shipment to the endocrinology laboratory at Swansea University. For hormone extraction, faecal samples were pulverised using a mortar and pestle and sifted to remove vegetation and seeds (Keay et al., 2006). A sub-sample of 0.09–0.12 g (mean ± SD: 0.103 ± 0.012 g, n = 603) was extracted with 80% watery

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highest standard curve value (>200 ng/ml) were diluted with Standard 0 (1:2–1:10; n = 42 samples) and re-analysed. Sensitivity of the assay was 0.22 ng/ml. High- and low-level quality controls were run in duplicates on each plate (n = 13), and inter-assay coefficients of variation were 9.3% (high) and 7.3% (low). Intra-assay coefficients of variation of

quality controls were 7.3% (high; n = 20) and 7.0% (low; n = 20), according to manufacturer. uGCs concentrations were corrected for specific gravity (SG; measured using a manual handheld refractometer), i.

energetic (e.g., Emery Thompson et al., 2010; Foerster et al., 2012) or psychosocial (e.g., Engh et al., 2006; Weingrill et al., 2004). If increased GCs associated with lactation are driven by increased energetic demands, lactation should be defined as the physiological state in which females are acyclic and still producing milk (hormonal definition, using progesterone criteria described above). If increased GCs are linked to the risk of infanticide, the definition should be based on whether the female

[redacted]

baseline GCs; Touma and Palme, 2005) and urine contamination (n = 55 samples; see Palme, 2005; excluding these 55 samples revealed comparable results for all models), as categorical fixed effects, and standardized dominance rank (between 0 and 1) as continuous fixed effect

(M1 and M2 were assigned the same standardised rank as F1 and F2 respectively, to avoid covariation between sex and rank).

114.29, $p < 0.001$). Baboon ID was highly significant, indicating consistent individual differences in fGCs ($p < 0.001$). Dominance rank and sex had no significant effect on fGCs (Table 2). fGCs did not differ significantly between samples collected in the AM or PM (Table 2;

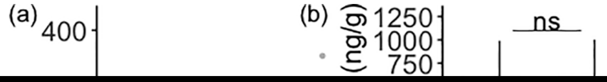

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Fig. 2b). fGCs were significantly negatively correlated with day length (Table 2; Fig. 1). Minimum temperature and rain days did not predict fGCs (Table 2). fGCs were significantly higher in pregnant females

Rain day (Y)	0.249	0.112	2.221	**0.031**
Collection time	−0.115	0.016	−7.044	**<0.001**
Method (Salivette)	−0.223	0.085	−2.607	**0.010**

*Reference category: pregnant.

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Heistermann, 2010), has not been explicitly tested in a comparative study, and therefore the relative merits of either approach was previously only assessed indirectly. To address this gap, we investigated the

effects of long-term, gradually changing factors (seasonal changes, reproductive state) and short-term, acute factors (daily weather parameters, circadian rhythm) on variation in uGCs and fGCs simultaneously in a wild primate. Below, we discuss our findings and

2005), here rainfall was investigated on a daily basis as a potential acute thermoregulatory stressor (e.g., rainfall may compound cold temperatures as has been proposed in baboons and other primates: Chowdhury et al., 2021; Foerster et al., 2012) or a time constraint stressor (similar to day length; see above) as activities such as feeding or grooming are interrupted due to sheltering (Hanya et al., 2018; Majolo et al., 2013). Finally, we found that uGCs were lower in samples collected using

[redacted]

the stressor of interest: if a short-term stressor is severe enough, even a 'muted' fGCs profile will reflect the stressor (with a species-specific time lag: Heistermann, 2010; Palme, 2019). This has been clearly demonstrated in a number of biological validation studies, where fGCs increase

single day, uGCs fluctuate across hours; grey boxes represent ± 4.5 hr time-windows (based on excretion lag for uGCs: Wasser et al. 1994), this means circadian patterns (yellow vertical arrow) and short-term stressors (brown vertical arrow) are captured over the course of hours, while they are not reflected in fGCs which (in baboons) are excreted with a time lag of ± 2 days. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this may be particularly pertinent for a sample matrix with larger inherent fluctuation like uGCs. Studies with low sampling frequencies

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The present study, to our knowledge, provides the first simultaneous investigation into the predictors of variation in fGCs and uGCs, offering empirical evidence for the long-standing assumption that GCs in sample matrices with different excretion time-lags reflect predictors with different temporal profiles. Our findings highlight the difference in inherent fluctuation between uGCs and fGCs and its potential associated consequences for investigating short- versus long-term effects on HPA-axis activity. While uGCs offer the opportunity to study short-term effects, they undergo more pronounced fluctuations, and thus, may be limited in their ability to capture long-term effects. Given the increasing use of urine for biological monitoring, knowledge of this potential lim-

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Hormones and Behavior 126 (2020) 104846

Contents lists available at ScienceDirect

Hormones and Behavior

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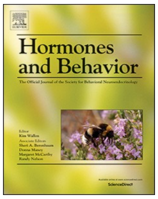

Energetics at the urban edge: Environmental and individual predictors of urinary C-peptide levels in wild chacma baboons (*Papio ursinus*)

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ARTICLE INFO

Keywords:
Baboons
C-peptide
Energy balance
Human-wildlife contact
Pregnancy
Primates
Provisioning
Urine
Season
Salivettes

ABSTRACT

As human-modified landscapes encroach into natural habitats, wildlife face a reduction in natural food sources but also gain access to calorie-rich, human-derived foods. However, research into the energetics of wildlife living within and adjacent to urban and rural landscapes is lacking. C-peptide - a proxy for insulin production and a diagnostic tool for assessing pancreatic function in humans and domestic animals - can be quantified non-invasively from urine (uCP) and may provide a way to investigate the energetic correlates of living in human-altered landscapes. UCP is increasingly used in studies of primate energetics, and here we examine predictors of variation in uCP levels in n = 17 wild chacma baboons (*Papio ursinus*) living at the urban edge on the Cape Peninsula, South Africa. We find that uCP was positively associated with food provisioning and negatively with night fasting. UCP levels were comparable between winter and summer but significantly lower during spring, possibly driven by consumption of energy-rich seeds during summer and more human-derived foods during winter. UCP was elevated in pregnant females and similar for lactating and cycling females. We find no effect of dominance rank on uCP. Samples collected with synthetic Salivettes had significantly lower uCP levels than directly pipetted samples. Overall, our results indicate that uCP is a reliable, non-invasive measure of energy balance and intake in baboons, and suggest potential energetic benefits of living at the urban edge. More broadly, studies of uCP may offer unique insight into the environmental control of hormone-behaviour relationships in species crossing natural and urban environments.

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https://doi.org/10.1016/j.yhbeh.2020.104846
Received 4 February 2020; Received in revised form 23 July 2020; Accepted 21 August 2020

understand energetic correlates of living within and adjacent to urban and rural landscapes therefore requires a physiological measure of energetic condition that is unaffected by psychological stress (see e.g. Dias et al., 2017).

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Cape Peninsula, South Africa where they forage in both natural and urban spaces (e.g. Fehlmann et al., 2017; van Doorn et al., 2010). First, we biologically validate our uCP assay (and assess how uCP responds to intake of high-calorie human foods), and test whether manipulation of food availability affects uCP, and predict baboons will show higher uCP

mediately after urination using Salivettes (Sarstedt Salivette Cortisol

Table 1
Details of study animals, including sex, rank, reproductive state (females), median and range of SG corrected uCP concentrations (see text for details), and number of urine samples collected.

ID	Sex	Rank	Median uCP_{SG} (range; n)

[redacted]

nane-3ß-ol-20-one standard (4.8–625 pg/50 µl) were combined with labelled conjugate (50 µl) and antiserum (50 µl) and incubated over-

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differences), time of day (before/after 9 AM; to account for a potential effect of night fasting; see e.g. Girard-Buttoz et al., 2011; Georgiev, 2012), and season (winter/spring/summer) were included as categorical fixed effects. Winter included the months July and August, spring included the months September and October, and summer included

Fig. 1. Effect of manipulation of food availability on UCP levels in wild chacma baboons. Baboons were provisioned with fruit, vegetables and corn during a 10-day period ("provisioning") and uCP levels compared to the ten days before and after (pre- and post-provisioning). Grey dots represent individual data points.

Table 2
Effects of sex, dominance rank, season, night fasting, and urine sample collection method, on SG corrected urinary C-peptide levels (ng/mg) in male (n = 2)

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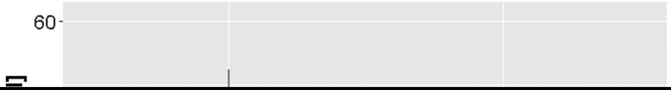
intervals around the median (black line). Grey dots represent individual data points (n = 1 data point for 'Winter' not shown; uCP = 228.9 ng/ml).



Alberts, 2003; Strum, 2010). Interactions between humans and wildlife, however, also carry negative consequences, such as economic losses, disease transmission, and injury and death (Soulsbury and White, 2016; Strum, 2010). While numerous behavioural studies have set out to better understand the causes and consequences of living within and adjacent to urban and rural landscapes (for reviews see e.g. Fehlmann

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Longer-term studies are now required to fully consider effects of reproductive state on uCP, so that researchers can study within-individual variation across states. For example, during our study, just two females conceived, preventing us from linking uCP to changes in energetic condition associated with conception as shown in Sanje mangabeys (*Cercocebus sanjei*) and chimpanzees (Emery Thompson

2004). Similarly, predation of livestock by carnivores increases when natural prey density is low (Khorozyan et al., 2015; Patterson et al.,

2000) and the young of domestic animals are abundant (Nattrass et al., 2020). Previous studies have assessed food availability through comparing both the quality and quantity of food sources in natural and

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trols (Danish et al., 2015; note the small sample size of n = 8 may have prevented an effect from being observed), uCP levels in the present study, on average, were significantly lower in samples collected with synthetic Salivettes than samples collected with pipettes. Given that we can rule out a potential storage effect/degradation (see e.g. Deschner et al., 2008; Higham et al., 2011b) as all urine samples, regardless of the collection method used, were placed in the freezer simultaneously at

We thank the Baboon Technical Team, Cape Nature, and SANParks for authorisation to conduct our research. We also thank Human Wildlife Solutions (in particular Ziggy Rode and Cath Shutte) and their rangers, field assistants Lucy Robertson, Charlotte Solman, and

Francesca Marshall-Stochmal, vets Dorothy Breed and Gary Buhrman, Esme Beamish, and Layla King for their help and support. Many thanks to Andrea Heistermann for help with faecal hormone analysis. We also thank the editors and two anonymous reviewers for their constructive

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