Socio-endocrinology revisited:
New tools to tackle old questions

Charlotte Christensen

BSc Psychology – Zoology, University of Bristol
MSc Behavioural Ecology, University of Bristol

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Thesis summary

Animals' social environments impact their health and survival, but the proximate links between sociality and fitness are still not fully understood. In this thesis, I develop and apply new approaches to address an outstanding question within this sociality-fitness link: does grooming (a widely studied, positive social interaction) directly affect glucocorticoid concentrations (GCs; a group of steroid hormones indicating physiological stress) in a wild primate? To date, negative, long-term correlations between grooming and GCs have been found, but the logistical difficulties of studying proximate mechanisms in the wild leave knowledge gaps regarding the short-term, causal mechanisms that underpin this relationship. New technologies, such as collar-mounted tri-axial accelerometers, can provide the continuous behavioural data required to match grooming to non-invasive GC measures (**Chapter 1**). Using Chacma baboons (*Papio ursinus*) living on the Cape Peninsula, South Africa as a model system, I identify giving and receiving grooming using tri-axial accelerometers and supervised machine learning methods, with high overall accuracy (~80%) (**Chapter 2**). I then test what socio-ecological variables predict variation in faecal and urinary GCs (fGCs and uGCs) (**Chapter 3**). Shorter and rainy days are associated with higher fGCs and uGCs, respectively, suggesting that environmental conditions may impose stressors in the form of temporal bottlenecks. Indeed, I find that short days and days with more rain-hours are associated with reduced giving grooming (**Chapter 4**), and that this reduction is characterised by fewer and shorter grooming bouts. Finally, I test whether grooming predicts GCs, and find that while there is a long-term negative correlation between grooming and GCs, grooming in the short-term, in particular giving grooming, is associated with higher fGCs and uGCs (**Chapter 5**). I end with a discussion on how the new tools I applied have enabled me to advance our understanding of sociality and stress in primate social systems (**Chapter 6**).

Declarations

Declaration 1

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

Signed: [redacted]

Date: 01/04/2022

Declaration 2

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

Signed: [redacted]

Date: 01/04/2022

Declaration 3

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.

Signed: [redacted]

Date: 01/04/2022

Declaration 4

The University's ethical procedures have been followed, and, where appropriate, that ethical approval has been granted.

Signed: [redacted]

Date: 01/04/2022

Ethics statement

To deploy tracking collars, baboons were cage trapped and anesthetised by a veterinarian. Human Wildlife Solutions (HWS; the company in charge of managing baboon-human conflict in 2018) organised the cage trapping following protocols established by the Baboon Technical Team (Hoffman, 2011). Collars were approved by Swansea University's Ethic Committee (IP-1314-5) and weighed a mean of 2.2% of baboon body weight (n=16; range 1.2% - 2.6%). Collars were fitted with a drop-off mechanism (version CR-7, Telonics, Inc.) to reduce the need for recapture. SANParks gave permission to study the baboons in Table Mountain National Park (CRC/2018-2019/008 – 2018/V1) and Cape Nature issued the permit for sample collection (CN44-59-6527). CITES approved export of samples (permit number: 208683).

Health and safety statement

Risk assessments were completed by relevant parties and approved for baboon fieldwork (AB, CC, CS, LR, FMS), collar-building (AB, CC), and laboratory work with baboon samples (CC).

Table of Contents

Acknowledgements

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I would like to thank Gaelle Fehlmann who came out and taught us how to build collars back in 2018 and told us exciting tales of baboon fieldwork to come. Also, for being at the ready with R code advice when it came to processing a large amount of accelerometer data. Thank you to Mark Holton for answering many Daily Diary questions and to Phil Hopkins for helping with designing and assembling the collars; for two engineers in high demand, they always found time for a friendly chat. I would like to thank the members of the SLAM-lab for patiently teaching me the ways of DDMT, particularly Hannah Williams, Baptiste Garde, James Redcliffe and Lloyd Hopkins, who were always willing to take time out of their day to sit down and help. Also thank you to Steve Shaw, lightning-fast IT support and hero of the hour when a connection needed to be set up for remote processing of the accelerometer data at the start of the pandemic. I would also like to thank my progression panel-members, Cindy Froyd and Sofia Consuegra, for taking an interest in my work and asking questions from a different perspective.

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List of Tables & Figures

CHAPTER 1: GENERAL INTRODUCTION

CHAPTER 2: QUANTIFYING ALLO-GROOMING IN CHACMA BABOONS (*PAPIO URSINUS*) USING TRI-AXIAL ACCELERATION DATA AND MACHINE LEARNING

CHAPTER 3: DIFFERENT CORRELATES OF FAECAL AND URINARY GLUCOCORTICOID CONCENTRATIONS IN WILD CHACMA BABOONS (*PAPIO URSINUS*)

CHAPTER 4: ENVIRONMENTALLY IMPOSED TIME CONSTRAINTS AFFECT GROOMING ACTIVITY IN A NON-EQUATORIAL PRIMATE *PAPIO URSINUS*

List of Abbreviations

Hormone-related abbreviations

HPA axis	Hypothalamic-Pituitary-Adrenal axis
GCs	Glucocorticoids
fGCs	Faecal Glucocorticoid metabolites
uGCs	Urinary Glucocorticoid metabolites
uCP	Urinary C-Peptide
CBG	Corticosteroid-Binding Globulin

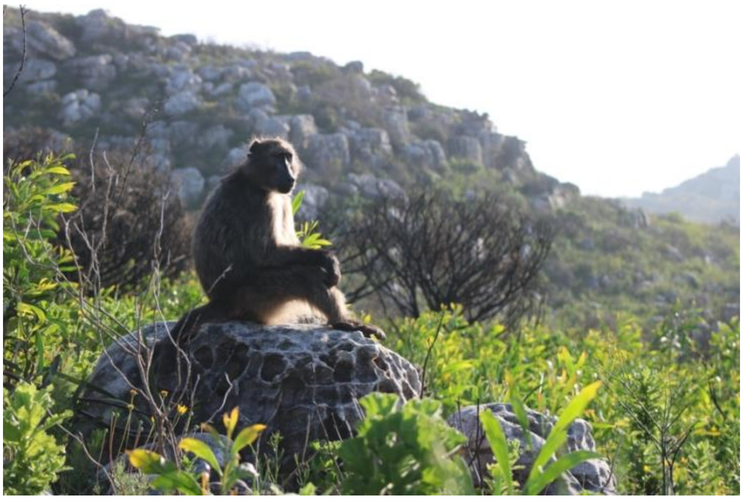
Collar-related abbreviations

ACC	Accelerometer
GPS	Global Positioning System
PDBA	Partial Dynamic Body Acceleration
PDBAX, PDBAZ, PDBAY	Partial Dynamic Body Acceleration along X, Y, Z axes
PSD	Power Spectrum Density
PSD1X, PSD1Z, PSD1Y	Power Spectrum Density associated with the first maximum frequency along X, Y, Z axes
PSD2X, PSD2Z, PSD2Y	Power Spectrum Density associated with the second maximum frequency along X, Y, Z axes
st	Static acceleration
stX, stZ, stY	Static acceleration along X, Y, Z axes
VeDBA	Vectorial Dynamic Body Acceleration
VeDBAs	smoothed Vectorial Dynamic Body Acceleration
MCC	Matthews Correlation Coefficient
TP	True Positive
TN	True Negative
FP	False Positive
FN	False Negative

Other abbreviations

UCT	University of Cape Town
HWS	Human Wildlife Solutions
SAWS	South African Weather Service
SAN Parks	South African National Parks
CITES	Convention of International Trade in Endangered Species of Wild Fauna and Flora

Chapter 1: General Introduction



PC: Charlotte Solman

Social bonds, health, and fitness

Living in a social group presents challenges and opportunities for animals, which impact individuals from the molecular level (Gudsnuk and Champagne, 2012; Snyder-Mackler and Snyder-Mackler, in press) to their ultimate survival (Snyder-Mackler et al., 2020). Individuals in groups both compete for – and facilitate access to – resources, including food, mates, protection, or warmth (Burkart, 2017). Social group stability and slow life histories allow for long-term social bonds to form between members of these groups (Silk, 2007a; Silk and Hodgson, 2021). These bonds provide benefits above and beyond those derived from group-living. Indeed, socially bonded individuals are more likely to show tolerance (Kawazoe, 2021; King et al., 2011), give protection (Micheletta et al., 2012; Nguyen et al., 2009), cooperate (Berghänel et al., 2011), or facilitate access to resources (McFarland et al., 2015; Samuni et al., 2018) compared to non-bonded group members. Ultimately, differentiated social bonds may lead to improved fitness (Ostner and Schülke, 2018), with higher reproductive rates (Cameron et al., 2009; Feldblum et al., 2021; Nuñez et al., 2015; Silk et al., 2003a) and longer life spans (Archie et al., 2014; Barocas et al., 2011; Silk et al., 2010b; Stanton and Mann, 2012). Social bonds may provide fitness benefits not only through access to social favour and material goods (see above) but also by modulating physiological aspects of health and thus survival (Cohen, 2004; Hostinar et al., 2014).

Glucocorticoids: the (mostly) good and the (sometimes) bad

Both human and non-human animal studies suggest that social bonds may impact health by altering the physiological stress response (reviewed in: Hostinar et al., 2014). The vertebrate stress response consists of both behavioural and physiological responses to internal and external challenges (Romero, 2002) and is brought about by the activation of the hypothalamic-adrenal-pituitary (HPA) axis (Sapolsky et al., 2000). This activation triggers, among other endocrine processes, the release of the steroid hormones called glucocorticoids (GCs) (Sapolsky et al., 2000). Before delving into how social bonds may modulate this response, it is important to first consider why modulation of the stress response is relevant to fitness.

Across vertebrates, GCs are part of an adaptive, and highly conserved, physiological response to challenges (Bonier et al., 2009; Sapolsky et al., 2000). Challenges or ‘stressors’ (Nelson, 2005), which can take the form of biotic and abiotic environmental changes (e.g., inclement weather, food shortage, predation pressure) and/or life-history events (e.g., reproduction, migration), require an organism to allocate energy to bodily processes accordingly. GCs facilitate this by mobilizing and diverting stored energy to exercising muscles and increase cardiovascular tone which speeds up this delivery (Sapolsky et al., 2000). GCs also have inhibitory effects on feeding (at least in the short-term) and reproductive physiology and behaviour, which helps prioritise energy use for coping with the stressor (Sapolsky et al., 2000).

Building on the ‘allostasis model’ (McEwen and Wingfield, 2003), the ‘reactive scope model’ (Romero et al., 2009) helps to conceptualise how GCs (and other physiological mediators) maintain stability in life-sustaining internal processes (i.e., homeostasis) and how these physiological mediators operate in different ranges depending on the nature and predictability of a stressor (Romero et al., 2009). When faced with a stressor, physiological mediators (e.g., GCs) are upregulated and, below a certain threshold, this response is considered within the ‘normal reactive scope’. The reactive scope model illustrates how GCs are necessary to sustain life: no circulating GCs would entail homeostatic failure, i.e., death (Romero et al., 2009). It also allows the labelling of the range where physiological mediators exceed the ‘normal reactive scope’, and the organism enters ‘homeostatic overload’. Here, the mediator itself causes disruptions and pathologies ensue. For chronic hypersecretion of GCs, these pathologies include reproductive dysfunction (Kirby et al., 2009), immune suppression (Spencer et al., 2010), neurological damage (Sapolsky, 1999) and cardiovascular disease (Walker, 2007).

A research emphasis on the consequences of homeostatic overload may be the reason that GCs have been inaccurately, and perhaps unhelpfully, labelled “stress hormones” (Higham, 2016; MacDougall-Shackleton et al., 2019), which carries intuitive negative connotations. The inconclusive link between fitness and baseline GCs across wild systems (Bonier et al., 2009) suggests that higher GCs do not necessarily decrease reproductive success or lifespan, sometimes even on the contrary, and that most free-living animals probably have circulating GCs appropriate for the challenges of their environment (Beehner and Bergman, 2017; Bonier et al., 2009; Boonstra, 2013). In fact, the instances in which GCs are linked to deleterious health consequences (see examples above) are usually observed in humans or in animals living in unnatural settings, such as laboratories and zoos, or in areas with high anthropogenic disturbance (reviewed in Dantzer et al., 2014). However, psychosocial stress associated with living in complex and hierarchical social systems is often viewed as a stressor that can lead to chronic GC hypersecretion and deleterious fitness consequences in the wild (Sapolsky, 2021; Tamashiro et al., 2005)

Complex and hierarchical social systems create high levels of conflict and cooperation which can both profoundly influence fitness (Sapolsky, 2005; Silk, 2007b). Potential or realised conflict with others requires individuals to monitor and avoid potential conflict whilst also identifying and investing in relationships that provide social support. This creates a source of psychosocial stress, where the mere anticipation of social threat or perceived lack of support can cause chronically elevated GCs, something which Sapolsky (2021) dubbed “the primate predicament”. It has therefore been proposed that a co-evolution of endocrine responses and behavioural coping mechanisms may act to reduce HPA-axis activity (Spencer, 2017; Walker and McGlone, 2013), and thereby the potential detrimental effects of GCs on immune function (Hoffman et al., 2011), HPA-axis sensitivity (Sapolsky, 1983), and survival (Campos et al., 2021).

Allo-grooming

In many social animals, social bonds are maintained through allo-grooming (Carter and Leffer, 2015; Kutsukake and Clutton-Brock, 2010; Silk et al., 2006a; Wolter et al., 2018) or allo-preening (Morales Picard et al., 2020; Radford and Du Plessis, 2006), which involves picking through and cleaning the fur or feathers of a conspecific. Grooming relationships of primates, in particular, are extensively studied (McFarland, 2018; Sparks, 1967). While grooming serves hygienic (Hutchins and Barash, 1976; Pfoh et al., 2021) and thermal (McFarland et al., 2016) functions, it also serves a social purpose, namely to create or maintain social bonds, which may be enduring (Kalbitz et al., 2016; Mitani, 2009; Silk et al., 2010a) or ephemeral (Henzi and Barrett, 1999).

Grooming is a key component of determining social bond strength. For instance, the composite sociality index (CSI) (Silk et al., 2006a) has been widely adopted (e.g., Ellis et al., 2019; Johnson et al., 2014; Kalbitz et al., 2016; McFarland et al., 2017; Young et al., 2014) and considers the frequency and duration of grooming interactions (as well as spatial proximity) between dyads. Using an affiliative behaviour such as grooming as a part of the proxy for social bonds is necessary, as the study of animal behaviour requires just that: a behaviour that can be measured. However, it does present a complication: social bonds are not tangible (Dunbar and Shultz, 2010) and unlike human studies where questionnaires can be used to disentangle the construct (social bonds) from the observable manifestation (prosocial interactions) (e.g., "feeling close" vs. "behaving close": Aron et al., 1992), animal studies inherently require behavioural criteria to infer mental processes (Shettleworth, 2001). As a result, there often is a ‘mechanistic black box’ (Hofmann et al., 2014; Rubenstein and Hofmann, 2015) when it comes to trying to understand the proximate mechanisms that underpin social interactions such as grooming, all the while relying on grooming as a measure of social bonds.

Proximate mechanisms underlying social bonds

To fully understand the benefits of social bonds, an investigation of both the ultimate (why?) and proximate (how?) questions (Tinbergen, 1963) is needed (Ostner and Schülke, 2018). Both exist in parallel, but the mechanism that elicits the behaviour is unlikely to be the same as the ultimate aim, i.e., grooming is not driven by the knowledge of their future fitness benefits (Massen et al., 2010), but rather is sustained by some closer cost-benefit trade-off (Russell and Phelps, 2013). Without a proximate mechanism to understand what the short-term causes and consequences of grooming are, we are left with the ‘phenotypic gambit’ assumption (Grafen, 1991) – that understanding the ultimate function of a behaviour eliminates the need for investigating proximate mechanisms, such as how grooming may modulate HPA-axis activity, even if this modulation is not its ultimate aim (Brent et al., 2014; Higham, 2016). An integration of proximate and ultimate causes is valuable, as it can reveal more mechanistic details (Zuk and Balenger, 2014) as well as offer a more feasible way to study fitness-relevant behaviours without necessarily measuring survival (Russell and Phelps, 2013), but it is hard to achieve (Hofmann et al., 2014). For the sociality-fitness link specifically, it means that we would have a better understanding regarding which aspects of social behaviour would be selected for within a given socio-ecological context (Ostner and Schülke, 2018). Studies on the ultimate benefits of grooming in the wild have the benefit of being ecologically valid, but have left open questions about the short-term drivers (Hofmann et al., 2014). In contrast, controlled captive and laboratory studies are informative for the mechanisms that underpin grooming, but lose biological validity as they might not translate to natural environments where the costs-benefit trade-offs likely differ (Calisi and Bentley, 2009; Hofmann et al., 2014). Studies in the wild where proximate mechanisms are investigated would thus be a valuable step towards bridging this gap.

One of the short-term consequences of grooming may be the modulation of HPA-axis activity. As mentioned above, maintaining circulating glucocorticoids within a healthy range (i.e., ‘normal reactive scope’: Romero et al., 2009) likely has positive fitness consequences and having social support/strong social bonds may contribute towards achieving this (Hostinar et al., 2014). For instance, in female chacma baboons, individuals that concentrate their grooming around a small number of stable social bonds have lower GCs than females with diffuse, unstable grooming networks, both under stable conditions (Crockford et al., 2008) and when faced with external stressors, such as infanticide risk (Wittig et al., 2008). Male Barbary macaques with strong social bonds show a smaller increase in GCs when faced with external stressors (aggression, inclement weather) compared to males with weak social bonds (Young et al., 2014).

The question is: how does having strong social bonds reduce HPA-axis activity and what potential role does grooming play in this? Having strong social bonds may afford individuals access to fitness-relevant resources (see examples above). Strong social bonds may also reduce HPA-axis activity by changing the perception of the stressor (social buffering: Crockford et al., 2017; Hostinar et al., 2014) or by ‘micro-management’ of the HPA-axis in neutral situations (main effect: Cohen and Wills, 1985; Wittig et al., 2016). Thus, the link between grooming and HPA-axis modulation may be indirect, i.e., via social bonds. However, grooming and social bonds are intertwined measures (see above), which leaves the question of whether grooming directly contributes to the modulation of HPA-axis activity, or whether grooming serves a means-to-an-end, open. While the literature on direct endocrinological consequences of grooming is sparse, there are some other indicators that grooming in primates has tension-reducing properties in the short-term. For instance, recipients of grooming had reduced heart rates in rhesus macaques (Aureli et al., 1999), pigtail macaques (Boccia et al., 1989), crested black macaques (Aureli and Yates, 2010) and Japanese macaques (Ueno et al., 2015) show reduced behavioural indicators of tension after grooming. Moreover, human studies suggest that there are short-term changes in HPA-axis activity after receiving physical touch, whether this was from close social bond partner (Ditzen et al., 2007; Grewen et al., 2005), or a stranger (e.g., massages: Field et al., 2005).

Neuroendocrine pathways are proposed to be involved in creating the ‘psycho-pharmacological’ environment in which social bonds can develop (Dunbar, 2010). Particularly, oxytocin, a neuropeptide which is key in the formation of social bonds (Crockford et al., 2017) and has been found to down-regulate HPA-axis activity (Heinrichs et al., 2003; Szczepanska-Sadowska, 2008), may be a proximate mechanism by which grooming could reduce circulating GCs directly. Some evidence from correlative studies suggests absolute grooming time may indeed be important. For instance, in chacma baboons, females increased both the number of grooming partners, but also their overall grooming rate after the loss of a close relative (Engh et al., 2006a). Similarly, in Barbary macaques, more giving grooming was associated with lower GCs, as was the a larger number of grooming partners (Shutt et al., 2007). Such studies suggest that there may be a link between the amount of grooming and lowered GCs, but they could also be indicative of individuals maintaining or expanding their social bonds which may indirectly lower GCs. These two possibilities are not mutually exclusive, but without direct links between grooming and subsequent endocrine measures, it is not possible to establish or rule out a direct causal mechanism.

Traditional versus new approaches in socio-endocrinology

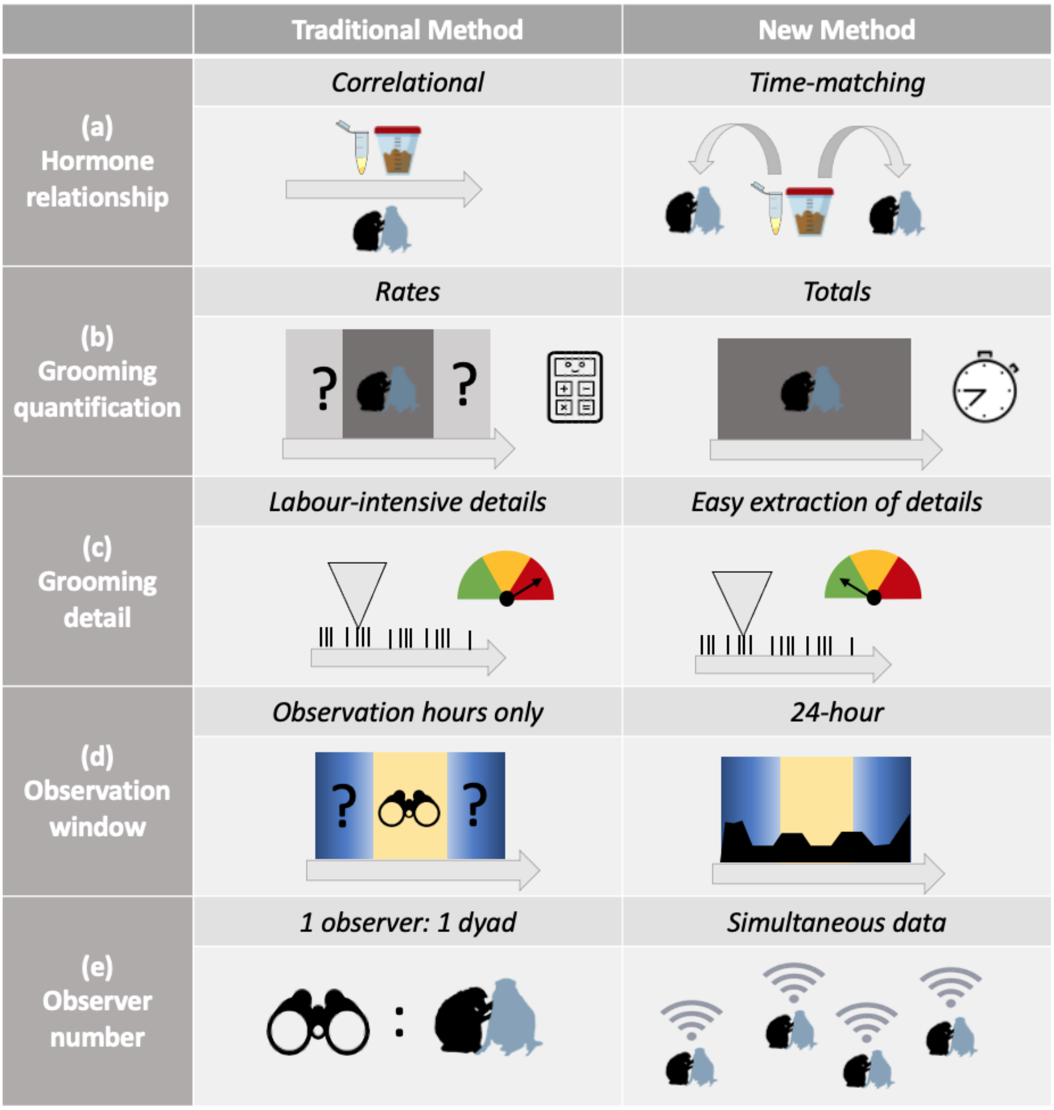
> *“In order to time a [grooming] bout, I had to see it begin, then watch nothing else until it ended, but usually I came upon monkeys already grooming and had no idea how long the bout already had lasted.”*
>
> Sade, 1971, pg. 9 observing Rhesus macaques in Puerto Rico.

To date, most studies linking grooming data to GCs test for correlations between grooming patterns and GCs averaged across time periods of one to several months (Beehner et al., 2005; Bergman et al., 2005; Crockford et al., 2008; Ellis et al., 2011; Engh et al., 2006a; Fürtbauer et al., 2014; Gust et al., 1993; Shutt et al., 2007), with most studies finding evidence for a negative association between grooming and GCs (Crockford et al., 2008; Fürtbauer et al., 2014; Gust et al., 1993; Shutt et al., 2007; Wittig et al., 2008). To my knowledge, only two studies have directly matched grooming data to subsequent GC-measures. First, Edwards et al. (2013) time-matched several social behaviours to faecal glucocorticoids (fGCs) in Barbary macaques but did not find an effect of grooming on fGCs (Edwards et al., 2013). Second, Wittig et al. (2016) found that chimpanzees who groomed with, or were in proximity to, a social bond partner had lower urinary glucocorticoids (uGCs) in the following hours compared to when they were engaging in the same activities with a non-bond partner. Notably, Edwards et al. (2013) pointed out that results found using the time-matching approach (direct link) were not always comparable to the results using long-term averages (correlational) which were also collected. For instance, rates of self-grooming were negatively associated with fGCs when using the time-matched approach but were positively correlated with fGCs over the study period (Edwards et al., 2013). This further highlights the value of investigating short-term changes in endocrine state in response to grooming, as it may differ from broad-scale patterns. Investigating short-term effects of grooming on GCs in the wild using direct observation is difficult because the resolution required to do so is labour-intensive, requires planning for opportunistic samples, and is not conducive to collecting large amounts of data in synchrony as researchers must focus on single individuals (Altmann, 1974).

Animal-mounted tracking devices, such as accelerometers, have opened up new ways to study animal behaviour in high resolution and address unresolved questions (Brown et al., 2013; Kays et al., 2015). Tri-axial accelerometers have been used to identify behaviours (by their unique acceleration signals) in a range of animals (Jeanniard-du-Dot et al., 2017; Lagarde et al., 2008; Lush et al., 2016; Pagano et al., 2017), including primates (Fehlmann et al., 2017a). While allo-grooming has not yet been identified with high accuracy (but see: Fehlmann et al., 2017a), self-grooming has (Graf et al., 2015; Wang et al., 2015; Watanabe et al., 2005). Below I lay out the potential advances of using accelerometer-identified grooming to investigate short-term physiological consequences of grooming, compared to using traditional observation methods.

Traditional data collection methods rely on direct, systematic observation, such as focal follows (Altmann, 1974), from which rates of behaviours are calculated (Altmann, 1974). Many studies have used this approach (Beehner et al., 2005; Bergman et al., 2005; Crockford et al., 2008; Ellis et al., 2011; Engh et al., 2006a; Fürtbauer et al., 2014; Gust et al., 1993; Shutt et al., 2007), calculating grooming rates over a given period and correlating it with average GCs (Fig. I - 1a), but this does not allow for causation to be established. Moreover, observational data is usually rather sparse (e.g., 10-30 minutes per individual per week: Beehner et al., 2005; Wittig et al., 2008). Rates of grooming are thus suitable for monitoring changes across larger time scales, however, when time-matching grooming to endocrine measures, high-resolution grooming data is necessary. Collecting high-resolution grooming data using traditional methods is challenging: in order to collect grooming data the right amount of time before the GC-measure using direct observation, particularly when working with opportunistically collected non-invasive samples (Behringer and Deschner, 2017), requires a study design tailored to this goal (e.g., see: Edwards et al., 2013; Wittig et al., 2016). Indeed, researchers would have to concentrate their efforts on a single individual for a substantial amount of time (6 hours; Edwards et al., 2013; Wittig et al., 2016) to ensure that all relevant grooming interactions and samples were collected. There are also more basic issues with data collection by direct observation. First, direct observation requires daylight (Fig. I – 1d), meaning grooming data at the sleep site (Anderson, 1998; Noser and Byrne, 2007) and potentially throughout the night (Ayers et al., 2020), is likely impossible to collect, and can therefore not be matched to GCs. Second, one observer can obtain detailed grooming data from just one individual at a time, which means the number of observers determines the number of individuals from which data can be collected at any given time (Fig. I - 1e).

In contrast to direct observation, animal-attached accelerometers can be programmed to collect data continuously (Brown et al., 2013), offering several advantages. First, continuous grooming data allows to retrospectively match grooming to each opportunistically collected sample and test direct links between grooming and GCs (Fig. I - 1a). Second, continuous high-resolution data may be important as even relatively short amounts of grooming could affect GCs. For instance, human studies have found that physical touch lasting for as little as 10 minutes (Ditzen et al., 2007) or even short embraces (Berretz et al., 2021) can reduce cortisol concentrations. Hence, high resolution grooming data would be valuable for investigating short-term effects on GCs (Fig. I - 1b). Third, the ‘quality’ of grooming, such as grooming bout length and frequency may also be important in modulating HPA-axis activity. Longer grooming bouts are generally considered more valuable (Fruteau et al., 2011; Fruteau et al., 2009; Manson et al., 2004), while more frequent, short grooming bouts may be indicative of more interrupted grooming (Kaburu et al., 2019). Frequencies and lengths of (self-)grooming bouts have been investigated in relation to anxiety-related behaviours in laboratory rodents (Estanislau, 2012; Kalueff and Tuohimaa, 2004), but to my knowledge never in relation to primate grooming and HPA-axis activity modulation. This information is straightforward to extract from continuous grooming data (Fig. I - 1c). Fourth, collecting data on grooming continuously throughout day- and night-time would allow to investigate night-time grooming, which has not been investigated to date. It would also maximise the use of all collected samples, particularly urine-samples where the GC-metabolite excretion time-lag is relatively short (a few hours: Behringer and Deschner, 2017; Heistermann, 2010), as uGCs can be time-matched to grooming that took place before researchers started data collection (Fig. I - 1d). Finally, the number of individuals from which grooming data can be collected is dictated by the number of collars (Fig. I - 1e), which in group-living primates has reached up to 25 individuals at a time (Strandburg-Peshkin et al., 2017). This means simultaneous grooming data can be collected and compared between individuals in response to the same environmental conditions. It also substantially increases the sample size and thereby the opportunity for matching opportunistically obtained GC-measures to grooming.



	Traditional Method	New Method
(a) Hormone relationship	*Correlational*	*Time-matching*
(b) Grooming quantification	*Rates*	*Totals*
(c) Grooming detail	*Labour-intensive details*	*Easy extraction of details*
(d) Observation window	*Observation hours only*	*24-hour*
(e) Observer number	*1 observer: 1 dyad*	*Simultaneous data*

Figure I – 1: Traditional versus new method Comparison of grooming data obtained from either direct observations ('Traditional Method') or from accelerometers ('New Method'), highlighting the advantages of the latter in the field of socio-endocrinology (see Traditional versus new approaches in socio-endocrinology for more details). **(a) Hormone relationship**: Correlating grooming with concurrent GCs measures vs. time-matching past and future grooming to GCs. **(b) Grooming quantification**: Grooming recorded within short time-windows to calculate rates vs. grooming collected continuously to obtain total grooming time **(c) Grooming detail**: Intensive observations required to obtain detailed grooming data (e.g., frequency and durations of grooming bouts) vs. pulling these metrics easily from continuous grooming data. **(d) Observation window**: Grooming data collection limited by observer time-window (during the day) vs. 24-hour grooming data **(e) Observer number**: One observer: one focal individual/grooming dyad vs. multiple individuals being tracked.

*Clipart for Fig. I – 1 obtained from public domain sources. Baboon figures traced in PowerPoint from baboon photograph.

Study system

Baboons (genus *Papio*) offer an excellent study system for investigating the proximate physiological consequences of grooming. They devote more time to grooming than any other genus (Dunbar, 1991) and have proven to be a tractable system to study the exchange of grooming for commodities such as reduced aggression and tolerance (Barrett et al., 2002), infant handling (Henzi and Barrett, 2002), alliance support (Cheney et al., 2010) or for grooming itself (Barrett et al., 1999b). Changes in grooming budgets have been linked to environmental factors (Hill et al., 2003; van Doorn et al., 2010), reproductive state (Frank and Silk, 2009; Rowell, 1968) and dominance rank (Barrett et al., 1999b; Silk et al., 1999), showcasing that grooming is an integral part of baboon life, but also flexible depending on the socioecological context. Moreover, there is substantial literature on the various drivers of GCs in baboons, including environmental factors (Chowdhury et al., 2021; Gesquiere et al., 2008; Weingrill et al., 2004), reproductive state (Engh et al., 2006b; Gesquiere et al., 2008; Weingrill et al., 2004) and dominance rank (Bergman et al., 2005; Gesquiere et al., 2011b; Levy et al., 2020). Most relevant to this thesis is the work demonstrating the link between grooming and GCs in baboons (Crockford et al., 2008; Engh et al., 2006a; Wittig et al., 2008, but see: Beehner et al., 2005). Female baboons who focussed their grooming network on fewer individuals, both during periods of social upheaval (Wittig et al., 2008) and social stability (Crockford et al., 2008), had lower fGCs compared to females who had more diffuse grooming networks. However, in the context of losing a close relative, it was the females who expanded their grooming rates and networks who had lower fGCs (Engh et al., 2006a). This again highlights how grooming activity is flexible, but also how different aspects of grooming may be important in modulating HPA-axis activity in different contexts. So far, no one has investigated the short-term physiological consequences of grooming in baboons.

In this thesis, I use chacma baboons (*Papio ursinus*) as a model system. Chacma baboons omnivorous, predominantly terrestrial primates, who live in multi-male, multi-female groups in southern Africa (Fischer et al., 2019). Males disperse when they reach maturity

(Beehner et al., 2006a), while females remain in their natal troop, affording them the opportunity to form long-term bonds with both kin and non-kin females (Silk et al., 2010a), although bonds need not be long-term, and can reflect short-term optimal strategies (Barrett et al., 1999b; Barrett and Henzi, 2002; Henzi et al., 2009). Chacma baboons exhibit steep dominance hierarchies (Johnson, 2003), with female rank being matrilineal, resulting in related females assuming adjacent ranks (Cheney, 1977). Conversely, males compete for dominance and dominance-rank is rarely maintained for longer than six months (Kitchen et al., 2003; Palombit, 2003). Compared to the other five baboon species, infanticide rates in chacma baboons are relatively high (Fischer et al., 2019; Palombit, 1999). Male-male alliances are absent, but females do form bonds with males (Moscovice et al., 2010), which likely affords protection for their infants from infanticide by immigrant males (Palombit et al., 1997).

Study troop and field season

I collected data between June and November 2018, data was collected on a troop of wild chacma baboons, named the “Da Gama troop”, situated in Da Gama Park on the Cape Peninsula, South Africa (-34.15562°N, 18.39858°E; Fig. I – 2a). The troop consisted of approximately 50 baboons, with 19 adult females and two adult males. Their home-range encompassed both natural areas and urban space (Bracken et al., 2021; Fig. I - 2b-d) and a team of field rangers employed by local service providers HWS (Human Wildlife Solutions) herded the baboons throughout the day to reduce human-baboon overlap (Bracken et al., 2021; van Doorn and O'Riain, 2020).

The field season can be roughly divided in three phases: (i) orientation and preparation, (ii) main data collection and (iii) collar-retrieval and sample export. The data collection was led by me and another PhD student (Anna Bracken), and we were assisted by three research assistants from Swansea University (Charlotte Solman, Lucy Robertson and Francesca Marshall-Stochmal). Below I briefly outline each phase of fieldwork (‘we’ refers to Anna Bracken and myself).

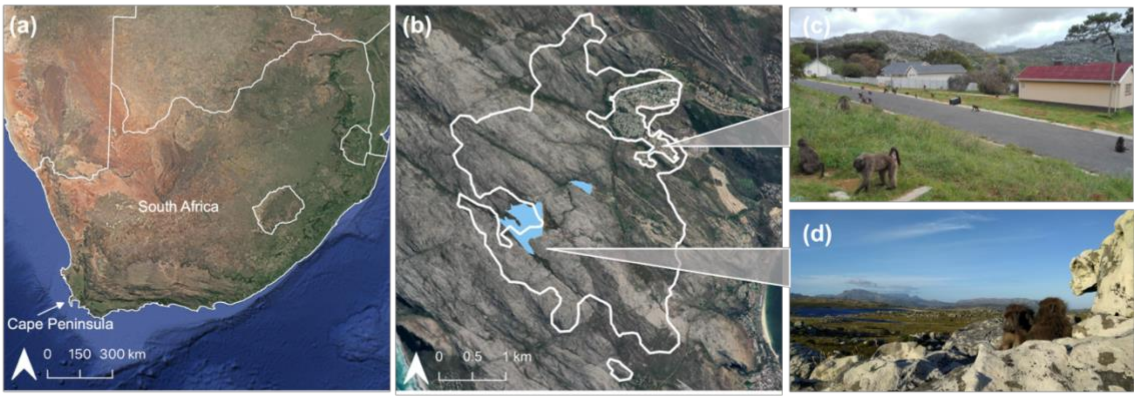


Figure I – 2: Study site (a) Location of the Cape Peninsula, South Africa, **(b)** home-range of the 'Da Gama' troop between July and September 2018, outer white line denotes the 95% kernel home range of the baboons, inner while line defines the urban space, blue areas are dams, **(c)** 'Da Gama' troop in the residential urban space **(d)** two females grooming in the natural space within Table Mountain National Park, with the large dam pictured in the background. Panel **(a)** and **(b)** are originally from Bracken et al., 2021 and are re-used here with permission. Photo credits: **(c)** Charlotte Solman; **(d)** Charlotte Christensen

Orientation & preparation *June – July 2018*: During the initial period, we met with Human Wildlife Solutions (HWS) and discussed the logistics and protocols of conducting research on the baboon troops on the Cape Peninsula, which are managed by HWS. We visited several troops on the Cape Peninsula to establish which troop would be most suitable in terms of size, habituation, habitat, sample collection feasibility and capture logistics. We received training in baboon behaviour observations from experienced baboon researchers from the University of Cape Town (UCT) and practiced collecting focal, scan and ad lib data. We set up an 'at home' lab in our house near the baboon troop (± 15-minute drive), so that samples could be immediately processed after returning from the field. We sourced lab consumables, a centrifuge (to extract urine from the Salivettes) and chest-freezer (to store the samples) from UCT for the 'at home' lab.

We selected the 'Da Gama' troop as our study troop. To learn the identities of the troop members, we created ID charts based on distinguishing features (Fig. I – S1). When the field assistants arrived from Swansea University, we trained them in the tasks of collecting urine and faecal samples and video data (see below). Towards the end of this period, we prepared collars for deployment, which involved calibrating them in the baboon home-range (see Chapter 2 for details), programming drop-offs and taping up the collars (Fig. I – 3a).

Figure I – 3: Collar and observational data (a) taped-up collars after calibration, ready for deployment, **(b)** direct focal observations in the field. Photo credits: Charlotte Solman.

Main data collection *August – October 2018*: Baboon capture and collar deployment took place between 25/07/18 and 02/08/18. Once collars were deployed, the main data collection started. This involved collecting urine and faecal samples from identifiable individuals for hormone analysis (Fig. I – 4a-d; see Chapter 3). Time-stamped video data were collected from collared individuals, which would be used for making a labelled dataset of all behaviours for machine learning training and validation purposes (see Chapter 2). Behavioural data was collected (Fig. I – 3b), including *ad libitum* data for dominance rank calculations (see Chapter 3) and focal and scan data for behavioural budgets (see Chapter 2). Baseline data on troop sleep site, weather conditions and female reproductive state were also recorded on every observation day. Management data on herding was recorded *ad libitum* as well as during focal and scan data. Periodically, faecal samples were driven to UCT to be freeze-dried (see Chapter 3; Fig. I – 4e), in preparation for sample export.

Collar-retrieval & sample export *November 2018*: Collars (n=11) were retrieved on drop-off date (16th October 2018) and were brought back to the house to download GPS and Daily Diary (accelerometer) data. N=3 collars dropped off later, necessitating several days of collar search (2 collars were retrieved, 1 collar is still missing to date). N=2 female baboons had to be re-trapped (20th November 2018) due to the drop-off not triggering.

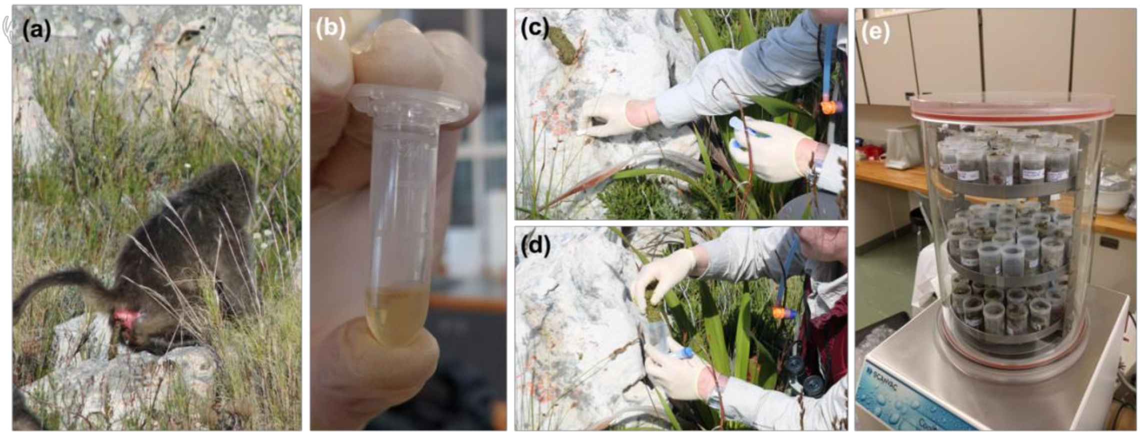


Figure I – 4: Baboon faecal and urine sample collection (a) female baboon defecating, **(b)** 2-ml safe-lock Eppendorf containing baboon urine, **(c)** urine sample collection in the field using a synthetic swab (Starstedt Salivette Cortisol), **(d)** faecal sample being transferred to a 40ml screw-top plastic pots **(e)** faecal samples being freeze-dried at UCT in a Scanvac CoolSafe (LaboGene ApS) to remove the moisture. Photo credits: **(a)**, **(b)**, **(e)**: Charlotte Christensen; **(c)**, **(d)**: Charlotte Solman.

Aims & Objectives

The overarching aim of this thesis is to develop and apply the methods to study proximate endocrinological consequences of grooming, using high-resolution accelerometer data and non-invasive measures of GCs obtained from urine and faecal samples. This allows to test whether grooming directly contributes to lowering HPA-axis activity, an important aspect of the widely documented health benefits of social bonds. The thesis comprises four data chapters which I outline below.

In **Chapter 2**, I identify giving and receiving grooming from collar-mounted tri-axial accelerometers using a supervised machine learning approach. Thus far, allo-grooming has not been successfully identified from accelerometers (but see: Fehlmann et al., 2017a). Accelerometer-derived grooming provides the continuous data stream needed to time-match grooming to glucocorticoid-measurements (Fig. I - 1a).

In **Chapter 3**, I establish general predictors of glucocorticoid variation (both urinary and faecal GCs) in the study troop. I test the effect of dominance rank, reproductive state and abiotic environmental conditions which have previously been found to predict HPA-axis activity in baboons generally, and Western Cape baboons specifically. These analyses lay the foundation for future analyses, as they establish which factors to control for when testing the effect of grooming on fGCs and uGCs. Moreover, because both urine and faecal samples were collected simultaneously, testing whether the same predictors are reflected in both sample types is important.

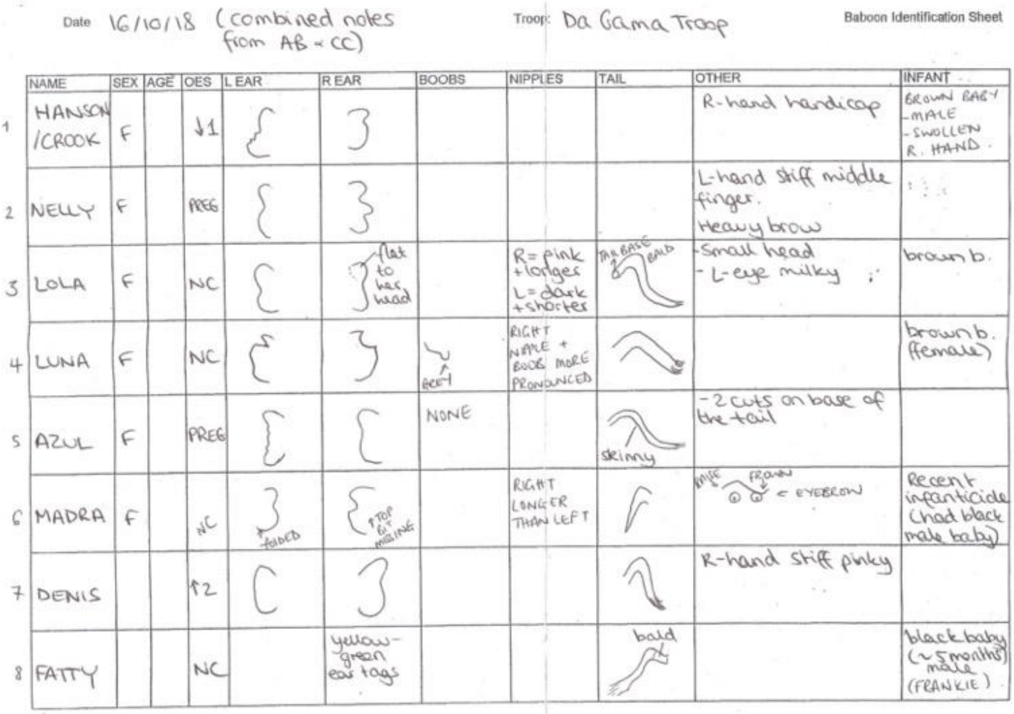
In **Chapter 4**, I test what socio-ecological factors drive grooming patterns, with a focus on day length and rain which were found to predict fGCs and uGCs respectively (Chapter 3). Establishing what factors dictate total grooming time, bout frequencies and average grooming bout length as well as the temporal distribution of grooming across 24-hours, allows to hypothesise how temporal bottlenecks may affect the time available to engage in grooming and service social bonds, which may consequently affect HPA-axis activity.

In **Chapter 5**, I realise the overarching aim of the thesis and establish whether there is a direct effect of grooming on uGCs and fGCs. This chapter draws upon the continuous grooming data obtained in Chapter 2, the predictors of uGCs/fGCs established in Chapter 3, and the predictors of grooming patterns established in Chapter 4. Using a time-matching approach, I link giving and receiving grooming to uGCs and fGCs to investigate the direct role of grooming in HPA-axis modulation.

In **Chapter 6**, I contextualise the findings of the thesis within the broader literature and discuss whether grooming may pose a short-term, psychosocial stressor in certain socio-ecological contexts. I end with discussing how new tools can advance our knowledge regarding the sociality-health-fitness link.

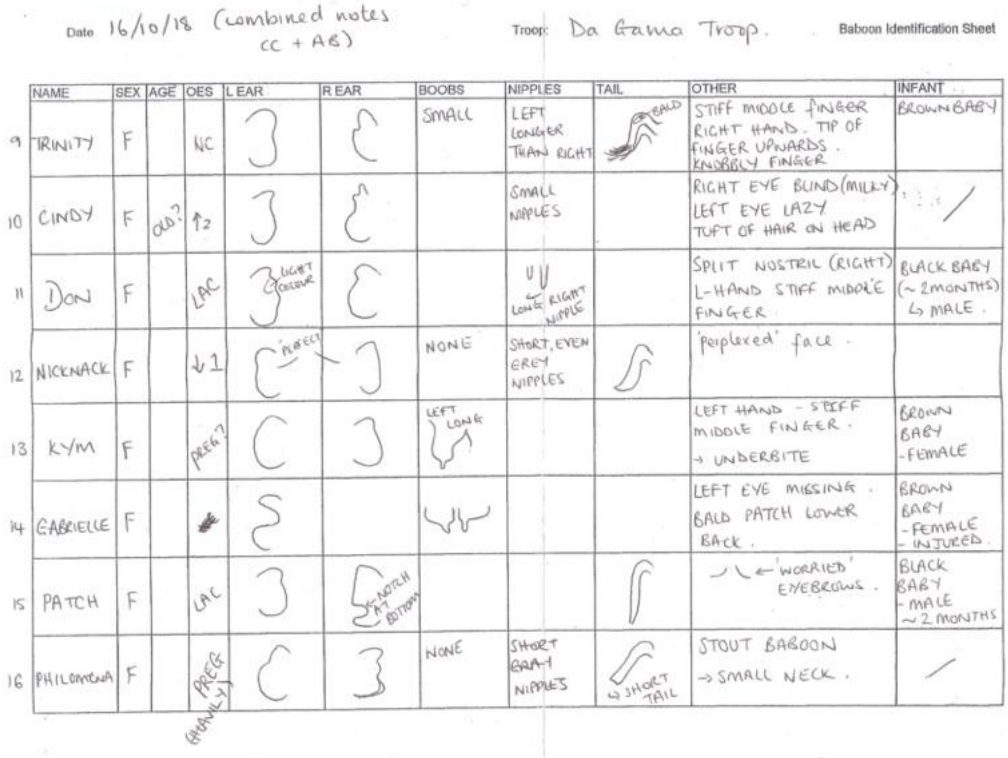
In "*Reprints of Publications*", I provide papers that I have contributed to as part of the larger baboon research project. These include work on environmental predictors of energetic condition (Fürtbauer et al., 2020), individual variation in urban space use (Bracken et al., 2021), group coordination in urban space (Bracken, 2022) and the effect of GPS-sampling interval on daily travel length estimations (McCann et al., 2021).

Appendix



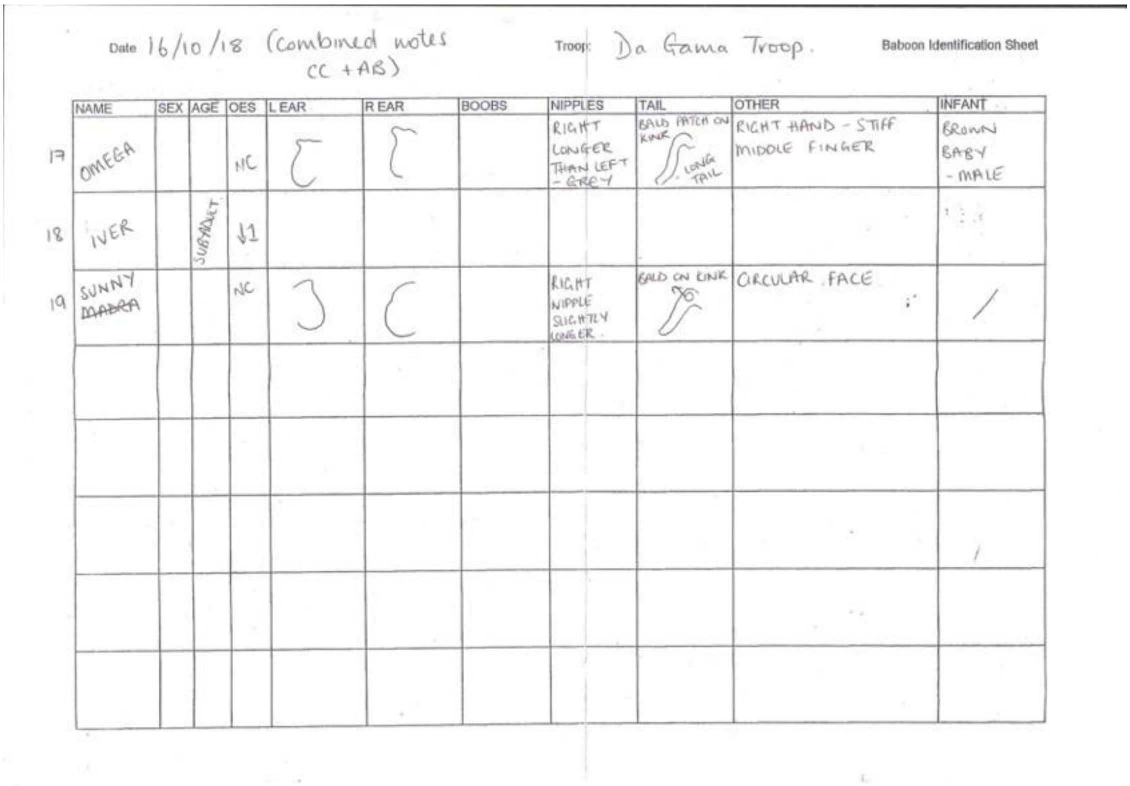
Date 16/10/18 (combined notes from AB + CC) Troop: Da Gama Troop Baboon Identification Sheet

	NAME	SEX	AGE	OES	L EAR	R EAR	BOOBS	NIPPLES	TAIL	OTHER	INFANT
1	HANSON /CROOK	F		↓1						R-hand handicap	BROWN BABY -MALE -SWOLLEN R. HAND.
2	NELLY	F		PREG						L-hand stiff middle finger. Heavy brow	
3	LOLA	F		NC		flat to her head		R= pink + longer L= dark + shorter	TAIL BASE BALD	-Small head -L-eye milky	brown b.
4	LUNA	F		NC			BEEFY	RIGHT NIPPLE + BOOB MORE PRONOUNCED			brown b. (female)
5	AZUL	F		PREG			NONE		skinny	-2 cuts on base of the tail	
6	MADRA	F		NC	FOLDED	TOP BIT MISSING		RIGHT LONGER THAN LEFT		RAISE FROWN ← EYEBROW	Recent infanticide (had black male baby)
7	DENIS			↑2						R-hand stiff pinky	
8	FATTY			NC		yellow-green ear tags			bald		black baby (~5months) male (FRANKIE)



Date 16/10/18 (combined notes CC + AB) Troop: Da Gama Troop. Baboon Identification Sheet

	NAME	SEX	AGE	OES	L EAR	R EAR	BOOBS	NIPPLES	TAIL	OTHER	INFANT
9	TRINITY	F		NC			SMALL	LEFT LONGER THAN RIGHT	BALD	STIFF MIDDLE FINGER RIGHT HAND. TIP OF FINGER UPWARDS. KNOBBLY FINGER	BROWN BABY
10	CINDY	F	OLD?	↑2				SMALL NIPPLES		RIGHT EYE BLIND (MILKY). LEFT EYE LAZY TUFT OF HAIR ON HEAD	/
11	DON	F		LAC	LIGHT COLOUR			LONG RIGHT NIPPLE		SPLIT NOSTRIL (RIGHT) L-HAND STIFF MIDDLE FINGER	BLACK BABY (~2MONTHS) ↳ MALE.
12	NICKNACK	F		↓1	PERFECT		NONE	SHORT, EVEN GREY NIPPLES		'perplexed' face.	
13	KYM	F		PREG?			LEFT LONG			LEFT HAND - STIFF MIDDLE FINGER. → UNDERBITE	BROWN BABY -FEMALE
14	GABRIELLE	F								LEFT EYE MISSING. BALD PATCH LOWER BACK.	BROWN BABY -FEMALE -INJURED.
15	PATCH	F		LAC		NOTCH AT BOTTOM				← 'WORRIED' EYEBROWS.	BLACK BABY -MALE ~2 MONTHS
16	PHILOMENA	F		PREG (HEAVILY)			NONE	SHORT GRAY NIPPLES	↳ SHORT TAIL	STOUT BABOON → SMALL NECK.	/



Date 16/10/18 (combined notes CC + AB)

Troop: Da Gama Troop.

Baboon Identification Sheet

	NAME	SEX	AGE	OES	L EAR	R EAR	BOOBS	NIPPLES	TAIL	OTHER	INFANT
17	OMEGA			NC				RIGHT LONGER THAN LEFT - GREY	BALD PATCH ON KINK LONG TAIL	RIGHT HAND - STIFF MIDDLE FINGER	BROWN BABY - MALE
18	IVER		SUBADULT	↓1							
19	SUNNY ~~MABRA~~			NC				RIGHT NIPPLE SLIGHTLY LONGER.	BALD ON KINK	CIRCULAR FACE	/

Figure I – S1: Baboon identification sheet Identifying features of the n=19 adult female chacma baboons of the Da Gama troop.

Chapter 2: Quantifying allo-grooming in chacma baboons (*Papio ursinus*) using tri-axial acceleration data and machine learning

Charlotte Christensen[1], Anna M. Bracken[1], M. Justin O'Riain[2], Gaëlle Fehlmann[3], Mark D. Holton[1], Phil W. Hopkins[1], Andrew J. King[1], Ines Fürtbauer[1]

Affiliations:
[1]Biosciences, School of Biosciences, Geography and Physics, Faculty of Science and Engineering, Swansea University, SA2 8PP Swansea, United Kingdom
[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch, 7701, South Africa
[3]Present address: Cognitive and Cultural Ecology Group, Max Planck Institute of Animal Behaviour, Radolfzell, Germany

Statement of contributions:

CC and IF designed the study. CC and AB conducted the fieldwork and built the collars with help from GF, MDH and PWH. JOR provided logistical support in the field. CC compiled the data and conducted the analysis with advice from IF and AJK. CC wrote the chapter with critical review, edits, and discussion from IF and edits from AJK.

PC: Charlotte Solman

Chapter 2: Quantifying allo-grooming from tri-axial acceleration data

Abstract

Accurate quantification of activity budgets is pivotal for understanding how animals respond to changes in their physical and social environment. Allo-grooming has been extensively studied in non-human primates and has important health and fitness consequences. To understand the causal relationship between grooming and fitness, accurate grooming estimates over time are required. Traditional methods use direct (focal) observations to calculate rates of grooming activity, which provide systematic but sparse data. Animal-mounted collars, in contrast, provide a new way of quantifying activity budgets continuously but have thus far not been used to quantify allo-grooming. Here, I test whether grooming (giving and receiving) can be accurately identified and quantified using tri-axial acceleration data obtained from n=12 wild chacma baboons (*Papio ursinus*). Using a machine learning (random forest models) trained on ~23 hours of labelled data, giving grooming and receiving grooming were identified with high precision (81% and 91%) and recall (87% and 79%) using ~10 hours of labelled data. Applying this model across n=680 collar days (16,319 hours), it was estimated individuals spend on average 19% giving and 15% receiving grooming during daytime hours (07:00-17:00). I further compared the suitability of random forest models built using individual specific labelled data versus labelled data pooled across all individuals. Individual data resulted in higher precision for certain behaviours (including giving and receiving grooming) but models built using data pooled across all individuals likely yielded more robust predictions; the relative merits of each method are discussed. Finally, rates of behaviours obtained from remote (acceleration data) and direct (focal data) observation are compared and shown to be significantly and positively correlated for giving but not for receiving grooming. Continuous behavioural data from collars opens many new avenues for investigation. For instance, in the field of socio-endocrinology, it will allow to time-match hormone measures to fine-scale grooming data, a key step in understanding the physiological basis of the grooming-health-fitness relationship, which thus far has been addressed almost exclusively through correlative data in the wild.

Chapter 2: Quantifying allo-grooming from tri-axial acceleration data

Introduction

How animals allocate time and energy to different activities has important fitness consequences (Boyd and Hoelzel, 2002). As behavioural states are mutually exclusive, the observed activity budgets can be seen as the result of a context-dependent trade-off, reflecting environmental (e.g., climatic conditions: Hill, 2006; food availability: Kurup & Kumar, 1993, predation pressure: Cowlishaw, 1997), demographic (e.g., group-size: Isbell & Young, 1993) and physiological (e.g., lactation: Dias, Rangel-Negrín, & Canales-Espinosa, 2011; Hamel & Côté, 2008, pregnancy: Silk, 1987) constraints. Moreover, individual characteristics such as sex (Alberts et al., 1996; Baldellou and Adan, 1997), age (Sierra-Marques and udia Calegaro—Marques, 1994), or dominance rank in group-living species (Gilbert-Norton et al., 2013) may dictate what activities require more time investment.

One of the core activities in the time budgets of many social animals is "allo-grooming" (hereafter: "grooming"), a prosocial behaviour found across multiple taxa (Kern and Radford, 2018; Kimura, 1998; Lazaro-Perea et al., 2004; Radford and Du Plessis, 2006; Rathinakumar et al., 2017) and extensively studied in non-human primates (Dunbar, 1991; Silk et al., 2006b). Grooming conspecifics has benefits that reach beyond the hygienic function of removing debris from fur or skin (Hutchins and Barash, 1976), taking up a significant portion of daily activity budgets (Dunbar, 1991). Grooming plays an important role in the maintenance of social bonds (Lehmann et al., 2007), and has been linked to ultimate fitness benefits such as increased life-spans and reproductive outputs (Silk et al., 2003a; Silk et al., 2010b). Grooming can also be exchanged for coalition support or tolerance from more dominant individuals (Barrett et al., 1999a; Henzi and Barrett, 1999; Tiddi et al., 2012). On a physiological level, grooming has been linked to reduction in glucocorticoids (GCs) through modulation of hypothalamus-pituitary-adrenal (HPA) axis activity (Fürtbauer et al., 2014; Wittig et al., 2016). Chronically elevated GCs can have detrimental health consequences (Ebrecht et al., 2004; Sapolsky et al., 2000) and high exposure to GCs is linked to reduced survival (Campos et al., 2021). Therefore, accurately quantifying grooming is crucial for our understanding of the grooming-health-fitness relationship.

Direct behavioural observations are limited by how much data can be recorded, which is affected by e.g., the habitat the animal lives in, the times the animal is active, or simply the number of animals in a social group that a single observer can observe at any given time (Brown et al., 2013; Caravaggi et al., 2017). Traditional behavioural observation methods, i.e., focal and scan sampling (Altmann, 1974), allow researchers to approximate activity budgets by calculating rates of behaviour. This generally precludes addressing questions which require behavioural data which can be temporally matched to other measures of interest (e.g., physiological state) (Edwards et al., 2013), particularly in cases where the measure of interest can only be collected opportunistically (e.g., non-invasive hormone sampling). For instance, many studies which link physiological measures (e.g., GCs) to grooming, match grooming rates to average GCs measured across the same time span (Crockford et al., 2008; Fürtbauer et al., 2014; Shutt et al., 2007; Sonnweber et al., 2015), hereby establishing correlation but not necessarily causation. Moreover, even when grooming data is matched to subsequent, rather than concurrent, physiological measures (Engh et al., 2006a; Wittig et al., 2008), observer-collected grooming data is still relatively sparse (e.g., 10 to 30 min per day). Human studies have shown that even brief periods of physical touch can attenuate cortisol (Ditzen et al., 2007; Feldman et al., 2010; Field et al., 2005), but similarly high-resolution data on grooming which can be directly matched to GCs are challenging to collect in wild systems (but see: Wittig et al., 2016). To investigate detailed aspects of social touch, such as total duration (Taylor et al., 2015) and frequency (Light et al., 2005), which may be important in modulating the link between grooming and HPA-axis activity (Boccia et al., 1989; Shutt et al., 2007), continuous, high-resolution data is required.

The advances in animal-mounted tracking devices have allowed researchers to gain insights into animal movement and behaviour that would have been impossible to record through direct observations (Brown et al., 2013; Kays et al., 2015). Tri-axial accelerometers, in particular, allow to identify behaviours through the unique acceleration patterns associated to them (Brown et al., 2013). In a first instance, accelerometers might simply provide information on whether the animal is “active” or “inactive” (Gervasi et al., 2006; Papailiou et al., 2008; Van Oort et al., 2004). However, recent studies have identified specific behaviours (Fehlmann et al., 2017a; Pagano et al., 2017) and some have used accelerometers to estimate activity budgets of their study animals, e.g., northern fur seals *Callorhinus ursinus* and Antarctic fur seals *Arctocephalus gazella*

(Jeanniard-du-Dot et al., 2017), Greek tortoises *Testudo graeca* (Lagarde et al., 2008) and brown hares *Lepus europaeus* (Lush et al., 2016). In an extensive review on the use of accelerometers in behavioural studies, Brown et al. (2013) showed that the identified behaviours typically fall under the categories of “locomotion”, “resting”, and “feeding/foraging”, but highlighted the general scarcity of measurements of social behaviours, with exceptions such as mating (Lagarde et al., 2008; Whitney et al., 2010), parent-offspring interactions (Shuert et al., 2018), aggressive interactions (Lagarde et al., 2008) and territorial or courtship displays (Ismail et al., 2012). The limited use of acceleration data to estimate social behaviours is likely because such behavioural “events” occur less frequently and for shorter time periods than “state” behaviours (Brown et al., 2013).

Allo-grooming has not yet been identified using tri-axial acceleration data, but self-grooming has (with varying levels of accuracy) in a number of species (Graf et al., 2015; Iwata et al., 2013; Lush et al., 2016; Pagano et al., 2017; Shamoun-Baranes et al., 2012; Wang et al., 2015; Watanabe et al., 2005), suggesting the identification of allo-grooming should be possible. Primates dedicate a substantial time to allo-grooming and thus, present an ideal study system to collect accelerometer data on social interactions. In fact, the first study to produce an acceleration ethogram for a primate included grooming (Fehlmann et al., 2017a). This study was conducted on male chacma baboons and successfully identified foraging, locomotion and resting with high precision (ability to minimise false positives/type 1 error) and recall (ability to minimise false negatives/type 2 error) (precision: 88.3%; recall 70.7%) (Fehlmann et al., 2017a). However, due to the low number of grooming events in this study (male chacma baboons have to my knowledge never been reported to groom one another: Clarke et al., 2010; King et al., 2011; Saayman, 1971; Weingrill, 2000), identification of grooming was less exact (>60% precision and recall for receiving grooming, and ~20% for giving grooming). The accurate identification of allo-grooming would allow for the incorporation of this behaviour into activity-budgets, in a species where grooming interactions underpin social bonds, with ultimate fitness consequences (see above).

This study aims to identify allo-grooming (giving and receiving) in wild chacma baboons using tri-axial acceleration data and machine learning. *Papio* are an ideal study genus as they spend between 5.7 and 18.9% of the day grooming (Dunbar, 1991). The present study focusses on females who, unlike males, are philopatric, maintain long-term female-female bonds within the group (Lehmann et al., 2007), and spend larger proportions of their time grooming than males (Hill, 1999). First, I used a random forest model (Breiman, 2001) to identify behaviours from tri-axial acceleration, with a particular focus on grooming, following the “end to end” methods described in Fehlmann et al. (2017). Second, because collared females in our study troop differed in weight (between 17.7 - 23.7 kg; unpublished data), ages (veterinary estimate: ± 5 - 18 years old), reproductive states (e.g., n=7 females had infants that would ride on back or belly; Fig. II - S8a) and handicaps (Fig. II - S8b), a host of factors could potentially affect individual accelerometer measurements, which arise from morphological or behavioural differences (Campbell et al., 2013; Dickinson et al., 2021; Jeantet et al., 2018; Laich et al., 2008; Shuert et al., 2018). I therefore explore the performance of random forest models based on individual datasets compared to models based on data pooled across all individuals. Third, I applied these two models to estimate and compare activity budgets. Fourth, studies of primate socioecology estimate activity budgets using traditional methods (Altmann, 1974) to investigate how environmental (Hill, 2006; Marty et al., 2019; Zhou et al., 2007), reproductive (Akbar et al., 2019; Dunbar and Dunbar, 1988; Fürtbauer et al., 2014), demographic (Canteloup et al., 2019; Li et al., 2014; Slater et al., 2009) and social (Guo et al., 2020; Isbell and Young, 1993) factors affect grooming rates. I therefore compare accelerometery-based rates of behaviours to direct (focal) observations.

Methods

Study site and troop

The study was conducted on the “Da Gama” troop which consisted of approximately 50 individuals, including 2 adult males and 19 adult females. The troop was studied in Da Gama Park, in the Western Cape, South Africa (-34.15562° N, 18.39858° E) between June and November 2018.

Collars and acceleration data

Collars were built at Swansea University. Each collar contained a Daily Diary (Wilson et al., 2008) containing a tri-axial accelerometer (recording at 40 Hz). Collars were fitted to the baboons between 25/07/18 and 02/08/18 in collaboration with Human Wildlife Solutions (HWS) by a local certified veterinarian under anaesthetic after baboons entered food-baited cages. Baboons were anesthetized using Ketamine (dose adjusted for body mass) 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 reduce the need for recapture. No baboons died or sustained injury during the capture and no injuries from wearing the collars were witnessed during the period the collars were deployed (Isbell et al., 2019). Sixteen adults (n=2 males, n=14 females) were fitted with tracking collars. One collar was not retrieved at the end of the study period (F1), one collar did not collect accelerometer data (F13), one collar only collected 2 days of acceleration data (F17, before any video data was collected) and one collar collected faulty data (F18, as confirmed by matching accelerometer to GPS to estimate 'active' time; Fig. II - S6). Together this resulted in a final sample size of n=12 individuals (n=10 females, n=2 males; see *Appendix* Table II – S2 for individual acceleration data details), and a total of n=680 collar days (mean±SD = 53±23 full days of accelerometer data; the first day of trapping and the last, not full day of data collection were discarded).

Video collection and processing

Baboons were habituated to observer presence (10 m distance) which allowed for the collection of video data using hand-held video-recorders (Sony HD Handycam HDR-CX190). During a video-follow, the observer (myself, Anna Bracken, Lucy Robertson, Charlotte Solman, Francesca Marshall-Stochmall) would dictate date and time and narrate behaviours. In total, 29.4 hrs of video were recorded (mean±SD = 2.3±0.8 hrs per individual, range 1.3-3.5 hrs) from which I extracted baboon behaviours at time-steps of 1 second, generating a labelled data set of 38 behaviours (see *Appendix*: Table II – S3 for full ethogram; Table II – S4 for ethogram sample sizes).

If the baboon was shifting from one behaviour to another (e.g., from sitting to walking), the adjustment period (typically less than 2 sec) was assigned to whichever behaviour most closely matched the transitionary behaviour. Some videos contained multiple collared individuals (particularly videos of grooming dyads), meaning that some video footage was used to label behaviours of more than one individual. During preliminary analysis some behaviours (receiving grooming, resting, foraging) were sub-classified by posture (lying, sitting, standing). However, fewer behavioural categories have been found to improve model accuracy (Dickinson et al., 2021) and here, I collapsed behavioural categories into a single category (without posture) to improve the overall accuracy of the random forest model (analyses not shown).

From these labelled video data, six main "state" behaviours: "giving grooming", "receiving grooming", "resting", "foraging", "walking" and "running" were taken forward for analyses, following Fehlmann et al. (2017). "Standing" was not included due to its low accuracy (Fehlmann et al. 2017) and where state behaviours occurred at the same time as "event" behaviours (e.g., body-shakes, self-scratching, baby-pulling, lip-smacking, etc. see Table II – S2) those seconds were removed to obtain a "pure" behavioural data set. This resulted in 83,243 s, i.e., 23.1 hrs (on average 3.9 ± 2.5 hrs per behaviour; and 1.9 ± 0.7 hrs per baboon; Table II - 1) for use in the random forest models. I also extracted the number of independent events (Table II - 1). A new event was classified when a change occurred in main activity (e.g., transition from receiving grooming to giving grooming). Additional behaviours (e.g., self-scratching, adjusting body position, lip-smacking) and changes in posture (lying, sitting, standing) were incorporated into the main activity and counted towards the same event so as to maintain a conservative estimate of number of events.

Table II – 1: Sample sizes for random forest model training and validation Number of seconds and independent events per behaviour recorded for each baboon (n=12). For details on behaviour labelling see main text. S = number of seconds, E= number of independent events, T.S. = number of training seconds, V.S. = number of validation seconds.

Baboon ID	Resting		Giving Grooming		Receiving Grooming		Foraging		Walking		Running		T.S.	V.S.
	S	E	S	E	S	E	S	E	S	E	S	E	S	S
M1	2666	51	1268	6	336	2	3349	67	505	83	160	34	5749	2535
M2	563	14	364	6	1151	2	377	4	267	25	28	6	1932	818
F2	1146	22	734	3	1307	6	1357	33	383	58	70	20	3527	1470
F4	1642	32	2352	17	3054	15	2535	98	867	110	45	8	7366	3129
F5	776	36	4238	23	1094	9	2769	89	840	107	0	0	6760	2957
F6	1120	24	3079	22	1359	15	1557	45	836	71	47	14	5605	2393
F7	1224	11	292	7	0	0	2416	40	415	53	16	4	3082	1281
F9	831	27	1578	15	1690	8	429	17	226	40	33	6	3335	1452
F10	707	39	3257	30	2868	27	3160	96	1009	130	77	22	7771	3307
F14	1322	25	1870	17	1241	17	811	27	262	34	18	5	3870	1654
F15	287	20	2677	19	1007	10	2062	78	961	103	9	3	4869	2134
F19	1900	40	319	5	436	10	2983	74	602	87	7	2	4388	1859
Total	**14184**	**341**	**22028**	**170**	**15543**	**121**	**23805**	**668**	**7173**	**901**	**510**	**124**	**58254**	**24989**

Data preparation in DDMT and R

The analysis of accelerometer data detailed below closely follows the workflow and code provided by Fehlmann et al. 2017 and used Daily Diary Multi Trace (DDMT; http://www.wildbytetechnologies.com) software. Before baboons were fitted with the collars, sensors were calibrated at the field site to create offsets in DDMT, providing the time-reference used to match video to accelerometer data. The position of the daily diary in the collar was specified to correct the position of acceleration channels (X = surge, Y = sway, Z = heave) relative to the ground. Datasets containing the labelled behaviours with associated timestamp were imported into DDMT as "bookmarks". Timestamps were verified visually to ensure the DDMT timestamp matched the video timestamp. Accelerometer data and associated behaviours were exported out of DDMT using Bookmark Multisession. In R, the labelled data set from all 12 baboons was divided in 70% (58,254 seconds, 16.2 hrs) training set and 30% (24,989 seconds and 6.9 hrs) validation set (to test the precision and recall of the random forest model prediction), allowing for a "supervised algorithm" approach (Fehlmann et al., 2017a; Nathan et al., 2012; Shamoun-Baranes et al., 2012). The same procedure was followed for models using individual-level baboon data, rather than data pooled across all individuals resulting in 12 individual random forest models (see Table II – S6 in *Appendix* for sample size of training and validation set for individual models).

Computing variables from acceleration data

All analyses (computation of variables, random forest models, comparison of models, and calculation of activity budgets) were conducted in R studio (version 3.6.1). Tri-axial acceleration allows the identification of behaviours through deriving information about the posture of the animal (static acceleration) and the movement of the animal (dynamic acceleration). Calculations combining the signal along the three axes can provide further metrics that can be used to differentiate behaviours from one another. To match the labelled behaviours (1 Hz) to the acceleration signal (40 Hz), the mean values for each metric were calculated for 16 acceleration variables per second. Acceleration variables were computed using the methods described in (Fehlmann et al., 2017a), excluding the variables that were found to have low predictive power (tri-axial PDBA-to-VeDBA ratio and first and second maximum frequencies associated with tri-axial power spectrum densities (PSDs)). This resulted in the following 16 variables being included in the model: (1-3) tri-axial static acceleration (X, Y, Z), (4-5) pitch and roll, (6) vectorial dynamic body-acceleration (VeDBA), (7) smoothed VeDBA, (8-10) tri-axial partial dynamic body acceleration (PDBA) and (11-16) tri-axial power spectrum density (PSD) for the first and second associated maximum frequencies. See Fehlmann et al. (2017a) for a comprehensive description of these variables and associated R script.

In brief, (1-3) acceleration along each channel (surge, sway, heave or X, Y, Z respectively) is associated with a static (st) component which results from the position of the sensor relative to the earth's gravitational field. For each channel, static acceleration ranges from 1 to -1 *g*, with a measure of 1 *g* indicating that the sensor is facing upwards (directly opposite to gravity's pull). Static acceleration provides information on the posture of the animal (Shepard et al., 2008b). The tri-axial static acceleration (stX, stY and stZ) was calculated by taking a running mean of 3 seconds from the raw acceleration (Shepard et al., 2008a) as used for other terrestrial mammals (Lush et al., 2016). To calculate body pitch and roll (4-5) the arcsine from the static acceleration channels stZ (heave) and stY (sway) was calculated (Shepard et al., 2008b). VeDBA (6) was calculated using the dynamic acceleration along X, Y, Z using the following equation:

$$VeDBA = \sqrt{\mathrm{X}^2+\mathrm{Y}^2+\mathrm{Z}^2}$$

and smoothed VeDBA (7) was obtained by taking the 3s running mean of VeDBA. PDBA (8-10) was calculated by taking the absolute dynamic acceleration value for each axis. Using Fast Fourier analysis, which decomposes the signal into amplitude and frequency, the PSDs were extracted by taking the first (11-13) and second (14-16) maximum power spectral density for each axis across 3 second intervals (Watanabe et al., 2005). This captures the dominant power spectrum, hereby revealing periodicities created by cyclic large body movements while ignoring smaller ones.

Random forest model fitting

Random forest models have been employed for many accelerometer-derived behaviour identification studies and have been found to outperform other machine learning approaches (Jeantet et al., 2018; Ladds et al., 2016; Mansbridge et al., 2018; Tatler et al., 2018). To run the random forest models, I used the R package ‘random forest’ (Liaw and Wiener, 2002). Random forests are a machine learning method based on building classification trees (Breiman, 2001). It operates using two “layers of randomness” by first using a random subset of the data each time a tree is grown, and second by using a random subset of variables (here the 16 variables computing from tri-axial acceleration) for each classification step (Nembrini et al., 2018). By running this repeatedly the model finally obtains the final classification trees. Each classification tree contains a set of hierarchical decision rules which aims to split the data into subsets which represent a given behaviour. To achieve “purity” in the subset (pure = a subset which only contains one behaviour), decision rules aim to maximise the impurity reduction at each split. Some variables may contribute more to the decrease in impurity at each split than others, and this can be represented by the Gini index: the difference between the impurity at a split and the sum of the weighted impurity of the two splits that follow averaged across all trees (Breiman et al., 1984). The Gini index can be used to rank the variables used to build the random forest in order of importance. Similar to Fehlmann et al. (2017), I ran the random forest model with 500 iterations. To test at how many iterations the model stabilises (i.e., obtains the final classification rules), I ran a post hoc test which revealed that error rates level out after 100 iterations (Fig. II - S3 in *Appendix*).

Model validation

Using the random forest model generated using the training set, I predicted the behaviours from the validation set running 500 trees (Fehlmann et al., 2017a) where the most frequently predicted behaviour across 500 trees is the presented as the final prediction. To assess recall and precision, I compared the output from the predicted behaviours to the observed behaviour in a confusion matrix (Table II - 3) using the calculations below.

$$\text{Precision} = \text{TP} / (\text{TP} + \text{FP})$$

$$\text{Recall} = TP / (TP + FN)$$

(TP = true positive, TN = true negative, FP = false positive, FN = false negative).

Individual versus pooled data model comparison

The objective of accelerometer derived behaviours is usually to make behaviour identification from accelerometer data “generalisable”, e.g., to identify behaviours in captivity which can be applied to animals in the wild (Dickinson et al., 2021; Ismail et al., 2012; Iwata et al., 2013; Jeantet et al., 2018) or across closely related species (Ferdinandy et al., 2020). Indeed, pooling data from multiple individuals to train random forest models is the norm (e.g., Fehlmann et al., 2017a; Ladds et al., 2016; Tatler et al., 2018). However, individual differences in acceleration profiles are likely due to morphological or behavioural differences (Campbell et al., 2013; Dickinson et al., 2021; Jeantet et al., 2018; Laich et al., 2008; Shuert et al., 2018). For instance, accelerometery studies in human athletes show that individual differences translate to distinct acceleration profiles (Mizuike et al., 2009; Schelling and Torres, 2016; Staniak et al., 2018). Considering that baboons show behavioural and morphological differences between sexes (Barrett and Henzi, 2008) and across age-groups (Alberts et al., 2014) and can sustain permanent injuries (Beamish, 2009), it is likely that these translate to different acceleration profiles. Work on walking kinematics in chacma baboons found substantial differences between fore- and hind-limb posture between males of different weights and ages (Patel et al., 2013), which would likely affect locomotion and hence accelerometer measurements. Thus, obtaining models that are fine-tuned to the individual could be beneficial.

In order to compare the performance of models generated using all data, or individual baboon data, I calculated the Matthew’s correlation coefficient (MCC) (Matthews, 1975), which allows for the comparison of predictive models which have been calculated using data sets of different sizes and has been previously used in accelerometery studies for this general purpose (Pagano et al., 2017; Tatler et al., 2018). MCC is expressed as a number between -1 and 1 (-1 indicating total disagreement between model prediction and observation, 1 indicating perfect agreement between model prediction and observation) and is proposed to be superior to harmonic means (e.g., F-measures, which do not account for TN) as it takes into account all four categories of the confusion matrix (FP, FN, TP, TN) and generates a score which is reflective of the number of both true positives and true negatives (Chicco and Jurman, 2020; Jurman et al., 2012).

$$\mathrm{MCC} = \mathrm{TP} * \mathrm{TN} - \mathrm{FP} * \mathrm{FN} \,/\, \surd\, (\mathrm{TP} + \mathrm{FP}) * (\mathrm{FN} + \mathrm{TN}) * (\mathrm{TP} + \mathrm{FN}) * (\mathrm{FP} + \mathrm{TN})$$

To compare the precision, recall, and MCC of individual models compared to pooled data models, I used Wilcoxon signed-rank tests.

Activity budgets based on acceleration data

To obtain activity budgets for each baboon across their respective collar periods, the model output from all baboons was applied to the 'unlabelled' accelerometer data to estimate the total number of seconds engaged in each behaviour (see above). To allow for the comparison of activity budgets from collars to those obtained from focal observations in the field, a subset of the accelerometer data was made for the time window covering direct observation hours (between 07:00 and 17:00 local time). Of the total 58,747,636 seconds (16,319 hrs; 680 days) of accelerometer data, 316,654 seconds (88 hrs, 0.54%) could not be classified as one of the 6 behaviours (mean±SD: 28,786 ± 76,359 seconds, 8±21 hrs per individual (n=11); median 3,176 seconds, 0.9 hrs). N=1 individual had 0 non-classified behaviours. As these points cannot be definitely assigned to any behaviour, they were removed from the daily budget calculations. Further investigation into the characteristics of non-classified acceleration datapoints is provided in the *Appendix* ('*Non-classified behaviours*'; Fig. II – S5). The activity budget for one individual (F18) was also found to be an outlier and presumed to be erroneous based on activity obtained from simultaneously recorded GPS-data, which indicated a discrepancy between accelerometer and GPS identified activity for F18. This individual was excluded from further analysis and removed from the pooled data training data set (see *Appendix*; Fig. II – S6).

Activity budgets based on focal data

Focal observations (Altmann, 1974) were conducted for all collared individuals (n=16, of which n=12 which have acceleration data) between August and November 2018 (observers: myself and Anna Bracken) and included an instantaneous and a continuous part. Instantaneous data were collected on activity (grooming, resting, foraging, walking, running, or engaged in other social behaviour) every minute for 30 min, resulting in 31 scans (Rose, 2000). All social interactions (including giving and receiving grooming) were recorded in detail in the continuous part of the focal observation to the nearest second. If the grooming interaction was still ongoing by the end of the 30-min focal period, the focal observation was continued until the end of the grooming bout (following: Chancellor and Isbell, 2009). Focal observations were carried out within five time-blocks (07:00-09:00, 09:00-11:00, 11:00-13:00, 13:00-15:00, 15:00-17:00; Fig. II – S1 *Appendix*). Each collared individual was observed within each block (median = 5 per block) throughout the study period in a randomised order.

All focals collected up to the collar drop-off date (16/10/2018) and of a minimum of 3 minutes in length were included in subsequent analyses. In total, n=323 focal follows were conducted (mean±SD = 27±4 per individual), the equivalent of 154 hours (mean±SD = 13 ± 2 hrs per collared individual, n=12). I used a Spearman's correlation to establish whether these rates were correlated with those obtained when only using the focals collected while the collars were recording data (i.e., a "true time match"), where the focal data window was adjusted for each baboon's collar duration; n= 208 focals, mean±SD = 17±9 per individual, n= 97 hours, mean±SD = 8±4 hrs per individual). As the correlation was strong and highly significant ($p \leq 0.005$ for all behaviours; *Appendix* Fig. II – S2), the focal data up to the collar drop-off date was included to maximise the amount of data used in the final analysis. To calculate the rates of behaviour, the number of scans engaged in each behaviour was divided by the total number of scans. For grooming, the total number of seconds engaged in either receiving grooming or giving grooming was divided by the total number of seconds of observation. To test whether the activity budgets obtained from the collars (see '*Activity budgets based on acceleration data*') were correlated with the rates collected using focal data, I used Spearman's correlation tests. To test whether rates of behaviours were over- or underestimated when using focal or collar data, I used Wilcoxon signed-rank tests.

Results

Acceleration ethogram

Smoothed VeDBA (VeDBAs) was the most important variable for distinguishing among behaviours (Fig. II – 2b). VeDBAs during running (median [1st and 3rd quartile]: 0.85 *g* [0.62 *g* -1.09 *g*] showed no overlap with any other behaviours, and foraging and travelling had medians that fell outside the interquartile ranges of all other behaviour (Fig. II – 1a; Table II – S7 in *Appendix*). Conversely, the three 'inactive' behaviours, giving grooming, receiving grooming and resting showed substantial overlap in VeDBAs ranges (Table II – S7; Fig. II – 1b). Counter to intuition, median VeDBAs for resting (0.031 *g*) was slightly higher than for receiving grooming (0.027 *g*) (Table II – S7), which may have led to the overestimation of receiving grooming during the night (see '*Activity budgets*' below).

Static acceleration along the heave and surge axes (both provide information on posture) were also important, with stZ and stX ranked 2nd and 5th, and pitch (forward/backward rotation) ranked 4th (Fig. II – 2b). Static acceleration channels interquartile ranges overlap for all behaviours, but the interquartile range for receiving grooming is consistently largest followed by resting (see *Appendix* Table II – S7; Fig. II – S4 for distribution of mean stZ), suggesting, as would be expected, that a large range of postures is adopted during these behaviours.

Three of the power spectrum densities (PSDs), specifically PSD2X, PSD1Z, PSD2Z were in the top ten most important variables. Notably, PSD2X was important for identifying giving grooming with a median that did not fall within the interquartile ranges of other behaviours (median [1st and 3rd quartile]: 0.0001 *g* [0.00007 *g* – 0.0002 *g*]; Fig. II – 1b), suggesting that giving grooming occurs on a regular low-amplitude frequency (with lower values than the aforementioned 'active' behaviours but higher than the two other 'inactive behaviours', i.e., resting and receiving grooming).

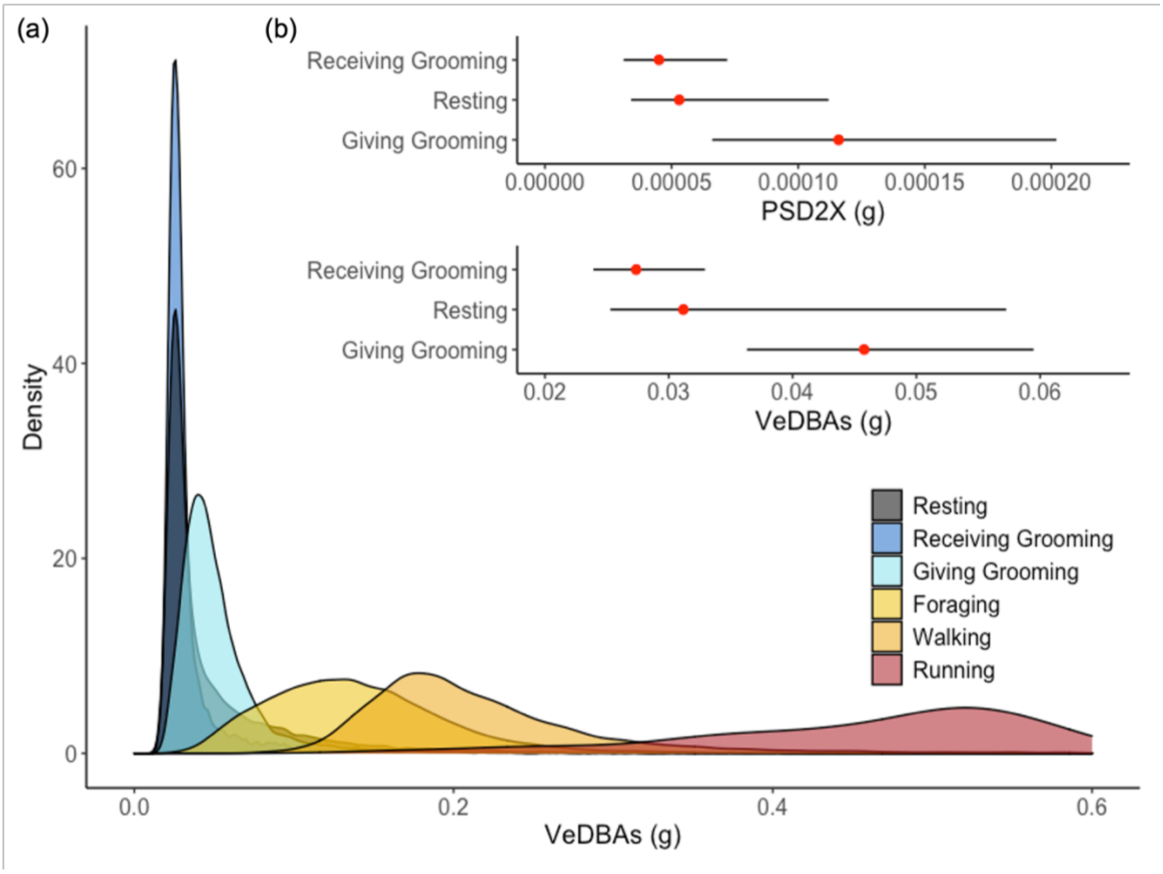


Figure II – 1: Acceleration ethogram (a) Density plots of smoothed VeDBA (VedBAs; most important predictor variable for random forest model) for the six state behaviours. Note that the "Running" density plot extends beyond 0.6 *g* but was cropped for better visualisation of the other behaviours. **(b)** Interquartile ranges for PSD2X and VeDBAs with median (red dot) for the three stationary behaviours: resting, receiving grooming, and giving grooming. Median VeDBAs for the three behaviours fall within the interquartile ranges of another stationary behaviour. Conversely, median PSD2X for giving grooming falls outside the interquartile ranges of resting and receiving grooming (Table II – S7).

Model performance

The model using pooled data reached a precision of mean±SD = 83.8±0.4% and a recall of mean±SD = 82.5±0.5% (Fig. II – 2c; Table II – 2). Receiving grooming had 91% precision and 79% recall, while giving grooming had 81% precision and 87% recall. Resting had the lowest precision (79%) and recall (77%) and was mostly confused with the two grooming behaviours (Table II – 3). Walking, foraging and running had high precision and recall (>80%). The slightly lower recall for walking compared to other active behaviours was primarily due to instances misclassified as foraging (Table II – 3), likely caused by the intermittent nature of walking and foraging.

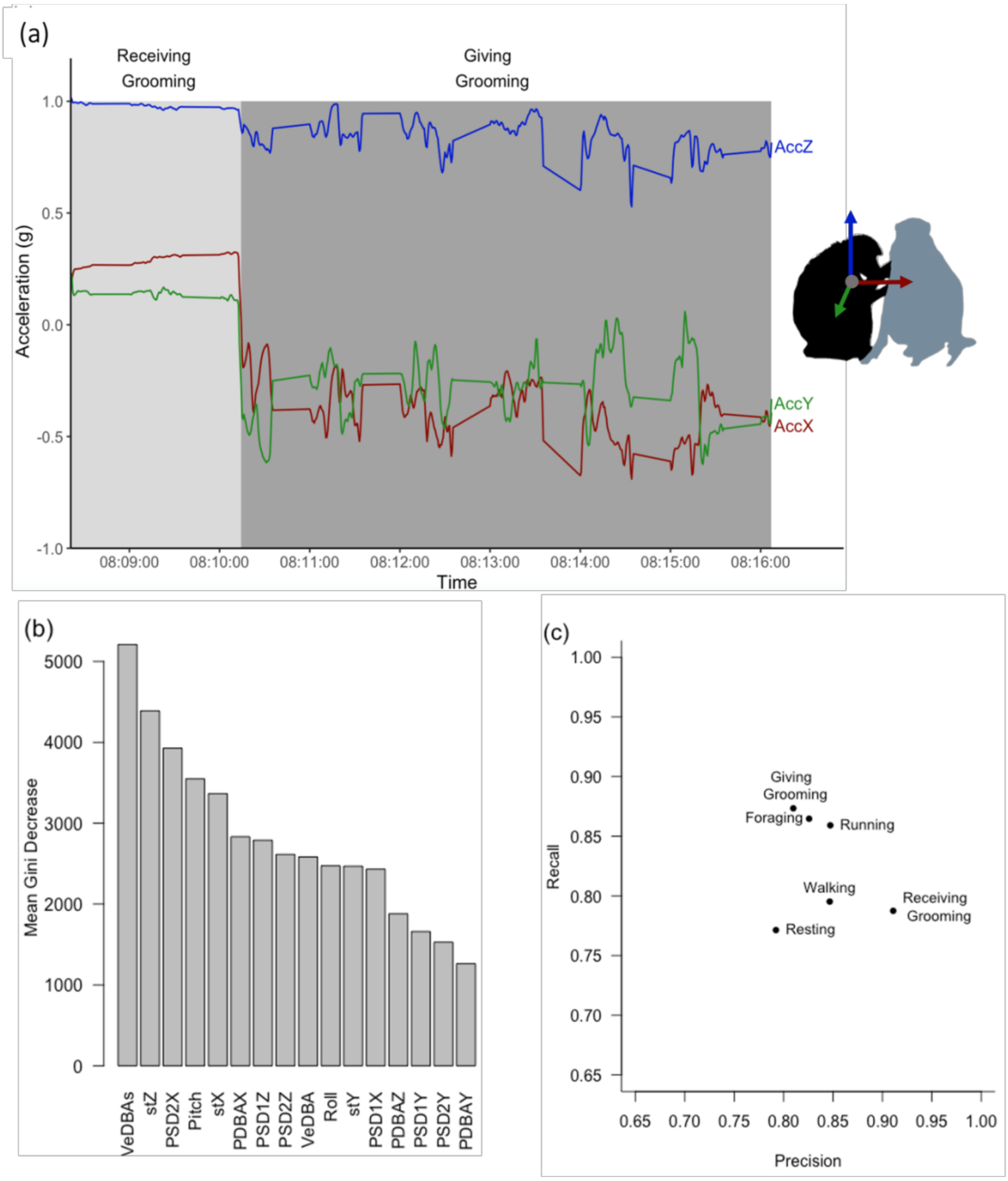


Figure II – 2: Random forest model results (a) Example of labelled tri-axial acceleration data from a female baboon switching from receiving grooming to giving grooming (AccX = surge (red), AccY = sway (green), AccZ = heave (blue)) over an 8-minute period. **(b)** Mean Gini Decrease, ranking the variables in order of importance for identification of baboon behaviours in the pooled data random forest model. **(c)** Precision and recall for six identified behaviours in the pooled data random forest model.

Table II – 2: Performance of random forest model MCC, precision and recall of the pooled data random forest model (n=12 chacma baboons). MCC = Matthews Correlation Coefficient.

	MCC	**Precision**	**Recall**
Resting	.74	.79	.77
Receiving Grooming	.82	.91	.79
Giving Grooming	.78	.81	.87
Foraging	.78	.82	.86
Walking	.83	.85	.80
Running	.85	.85	.86

Table II – 3: Confusion matrix for the pooled data random forest model. Comparison of the predicted behaviour and observed behaviour (based on labelled data set from videos). Observed behaviours are in columns and predicted behaviours are in rows. Values in bold represent the true positives (TP). Instances where the behaviour was incorrectly classified by the model (FP) are in rows, instances where the behaviour was missed by the model (FN) are in columns.

Behaviour	**Resting**	**Receiving grooming**	**Giving grooming**	**Foraging**	**Walking**	**Running**	**Total predicted**
Resting	**3243**	416	246	180	9	9	4094
Receiving Grooming	182	**3243**	158	14	0	0	3953
Giving Grooming	438	429	**5816**	500	0	0	7183
Foraging	331	122	435	**6151**	411	3	7453
Walking	18	3	4	266	**1701**	17	2009
Running	0	0	0	4	18	**122**	144
Total observed	4212	4569	6659	7115	2139	142	

Comparing individual data versus pooled data models

Predictions from individual-level models had significantly higher precision than pooled data for the following behaviours: resting (Wilcoxon signed rank-test: Z=-3.10, $p < 0.001$, n=12), receiving grooming (Wilcoxon signed-rank test: Z=-2.58, p=0.005, n=11), giving grooming (Wilcoxon signed-rank test: Z=-2.70, p=0.003, n=12) and foraging (Wilcoxon signed-ranked test: $Z=-2.25$, $p=0.012$, n=12). Precision for running and travelling were not significantly better for individual data models compared to pooled data models ($p>0.05$; see Table II – S8 in *Appendix*). Individual models had higher recall for receiving grooming ($Z=-1.79$, $p=0.037$, n=11), but the pooled data model had higher recall for running (Wilcoxon signed-rank test: $Z=-0.12$, $p=0.037$, n=11). Recall did not differ between models for the other behaviours ($p>0.05$; see Table II – S8 in *Appendix*). MCC was significantly higher for giving grooming (Wilcoxon signed-rank test: $Z=-2.41$, $p=0.016$, n=12) and receiving grooming (Wilcoxon signed-rank test: $Z=-2.35$, $p=0.020$, n=11) in individual models, but not for any other behaviours (Table II – S8).

Table II – 4: Precision and recall of pooled versus individual random forest models: Precision (**P**) and Recall (**R**) for six behaviours obtained from the pooled data random forest models and the individual data random forest models for n=12 baboons.

		Resting		**Receiving Grooming**		**Giving Grooming**		**Foraging**		**Walking**		**Running**	
		P	**R**	**P**	**R**	**P**	**R**	**P**	**R**	**P**	**R**	**P**	**R**
Pooled	**All baboons**	**0.79**	**0.77**	**0.91**	**0.79**	**0.81**	**0.87**	**0.83**	**0.86**	**0.85**	**0.80**	**0.85**	**0.86**
Individual	**M1**	0.89	0.89	0.93	0.63	0.92	0.91	0.87	0.92	0.74	0.68	0.92	0.81
	M2	0.93	0.88	0.93	0.93	0.79	0.89	0.86	0.89	0.86	0.93	0.67	0.80
	F2	0.90	0.92	0.99	0.97	0.89	0.86	0.87	0.90	0.80	0.81	0.80	0.53
	F4	0.83	0.78	0.91	0.90	0.85	0.87	0.85	0.89	0.84	0.84	0.92	0.86
	F5	0.76	0.67	0.99	0.87	0.88	0.93	0.83	0.85	0.86	0.81	NA*	NA*
	F6	0.85	0.86	0.93	0.83	0.92	0.96	0.84	0.86	0.88	0.85	0.83	0.71
	F7	0.95	0.94	NA*	NA*	0.95	0.75	0.90	0.72	0.79	0.72	0.80	0.80
	F9	0.88	0.88	0.95	0.88	0.85	0.93	0.82	0.72	0.70	0.78	0.86	0.67
	F10	0.85	0.54	0.91	0.86	0.83	0.90	0.85	0.90	0.85	0.82	1.00	0.79
	F14	0.88	0.91	0.96	0.82	0.87	0.95	0.81	0.90	0.84	0.78	0	0.88
	F15	0.88	0.42	0.96	0.92	0.87	0.95	0.81	0.80	0.84	0.81	0	0
	F19	0.86	0.85	0.96	0.77	0.79	0.64	0.84	0.90	0.82	0.76	1.00	1.00
	Mean	**0.87**	**0.80**	**0.95**	**0.85**	**0.87**	**0.88**	**0.85**	**0.85**	**0.82**	**0.80**	**0.71**	**0.71**

**NA: no data was available for this behavioural category for this individual.*

Activity budgets

Activity budgets were calculated by applying the pooled data model to the data set (24 hrs/day, total collar days = 680; Table II - S1). Baboons spent on average (mean±SD) 21.4±9.0% of their time resting, 18.8±6.3% giving and 30.0±8.1% receiving grooming (n=12; Table II - 5). When restricting the collar data to direct observation hours (07:00 to 17:00) the baboons spent 19.0±9.6% of their time resting, 18.7±6.6% giving grooming, 15.2±6.5% receiving grooming (n=12; Table II - 6). For active behaviours see Table II - 5 and Table II - 6.

Based on the results of the accelerometer identified activity budgets, which suggested receiving grooming may be confused for resting, particularly during the night, I calculated whether VeDBAs (the most important predictor variable; Fig. II - 2b) associated with resting overlapped more with receiving grooming during the night relative to the overlap in VeDBAs during the day, which it did (see '*Night vs. Day: Resting vs. Receiving grooming VeDBAs'* in *Appendix* for details).

Table II – 5: 24-hour activity budgets Percentage of time (mean±SD) each individual was engaged in the six identified behaviours based on acceleration data collected continuously for 24hrs/day. For details on total days of data per individual, see Table II – S2 in *Appendix*.

☾/☀	Resting	Receiving Grooming	Giving Grooming	Foraging	Walking	Running
M1	22.6±4.2	28.5±5.8	21.0±3.9	19.0±3.2	7.8±1.8	1.0±0.4
M2	29.2±4.3	31.7±4.5	13.8±4.0	14.5±1.8	8.5±1.4	1.6±0.5
F2	15.2±5.0	28.7±4.6	26.9±5.9	19.4±3.1	8.5±2.1	1.1±0.4
F4	18.8±5.7	33.8±5.3	17.1±4.7	18.6±3.7	10.9±2.4	0.6±0.3
F5	20.9±4.3	27.0±4.1	22.0±4.9	19.1±3.2	10.4±2.3	0.7±0.2
F6	18.1±5.1	25.1±3.7	26.9±7.3	18.9±3.2	10.2±2.2	0.8±0.4
F7	27.9±7.6	23.1±8.3	13.6±4.1	22.6±4.4	6.8±1.8	1.4±0.4
F9	16.5±4.5	35.7±6.0	20.1±4.7	17.0±2.5	9.3±2.3	1.5±0.5
F10	12.2±3.6	36.8±4.8	18.8±4.4	21.0±3.1	10.3±2.2	0.8±0.3
F14	33.4±8.4	23.5±5.4	14.9±5.0	18.3±2.5	9.1±2.1	0.8±0.3
F15	12.2±4.0	43.5±5.2	15.5±3.2	18.1±2.9	9.2±2.3	1.2±0.4
F19	34.6±6.7	25.4±3.6	15.0±3.2	16.5±3.1	7.7±2.0	0.8±0.2
Mean	**21.4±9.0**	**30.0±8.1**	**18.8±6.3**	**18.6±3.1**	**9.1±2.1**	**1.0±0.4**

Table II – 6: Observation hour activity budgets Percentage of time (mean±SD) each individual was engaged in the six identified behaviours based on acceleration data collected between 07:00 and 17:00 (observation hours)/day. For details on total days of data per individual, see Table II – S2 in *Appendix*.

	Resting	**Receiving Grooming**	**Giving Grooming**	**Foraging**	**Walking**	**Running**
M1	25.7±6.8	15.7±6.0	15.2±3.6	29.9±6.9	11.6±3.2	1.5±0.7
M2	34.1±4.4	14.8±4.9	10.6±2.4	23.4±4.3	13.2±2.3	2.6±1.3
F2	13.2±4.5	16.7±5.6	23.4±5.5	32.1±6.6	13.0±3.4	1.5±0.7
F4	15.9±5.1	18.8±6.3	16.1±4.1	31.3±7.5	17.0±4.2	0.8±0.5
F5	13.4±4.4	10.6±4.2	26.2±6.2	32.8±7.3	15.9±4.0	1.0±0.5
F6	15.1±5.2	11.2±4.1	24.5±7.6	31.9±7.3	16.1±4.0	1.2±0.6
F7	25.6±5.9	10.5±5.4	13.1±3.8	35.8±8.7	10.5±3.2	2.0±0.9
F9	14.2±3.3	17.7±6.4	22.6±4.4	28.1±5.3	15.2±4.2	2.2±0.9
F10	8.3±2.8	16.0±5.0	21.1±5.1	36.6±7.1	16.7±4.0	1.3±0.6
F14	25.1±5.5	11.3±3.8	15.5±5.8	32.4±5.8	14.5±4.0	1.2±0.8
F15	10.0±3.2	22.2±6.2	19.5±4.4	31.1±6.0	15.2±4.0	1.8±0.8
F19	30.9±8.9	12.8±4.2	15.6±3.7	27.5±7.0	12.2±3.5	1.0±0.5
Mean	**19.0±9.6**	**15.2±6.5**	**18.7±6.6**	**31.1±6.7**	**14.3±3.7**	**1.5±0.7**

Activity budgets from individual data and pooled data

Estimated behaviours and activity budgets were calculated using models based on individual and pooled data (Table II – S9 & S10 for grooming; Table II – S11 & S12 for all other behaviours). Overall, the activity budgets predicted by the two models did not differ in a consistent manner (i.e., not less or more giving or receiving grooming predicted by either model; Table II – S9 & II – S10). Between-individual variation was larger for individual data models compared to pooled data models, particularly for resting and receiving grooming (Fig. II - 3). For more details see '*Comparing individual vs. pooled data random forest models*' in *Appendix*.

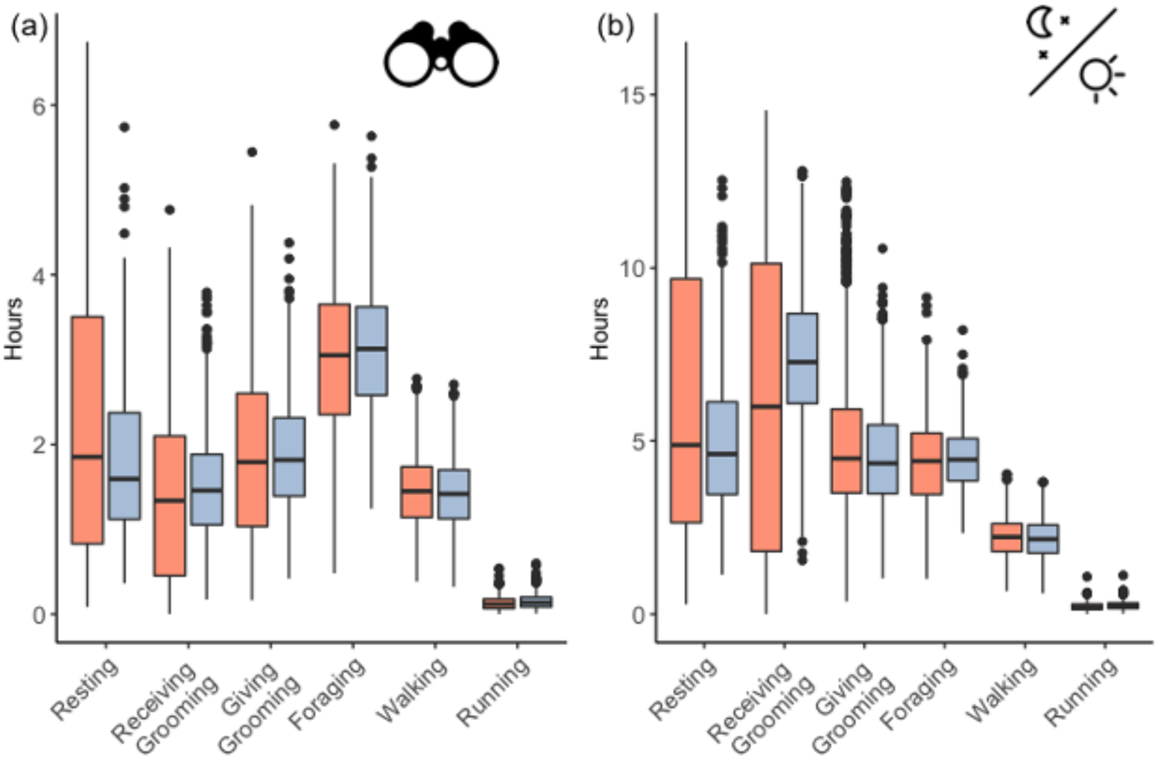


Figure II – 3: Activity budgets from pooled versus individual random forest models Number of hours engaged in each behaviour calculated using individual random forest models (orange boxes) and random forest models built with pooled data (blue boxes) models for n=12 baboons per **(a)** day (direct observation hours) and per **(b)** 24 hours. Boxes show interquartile ranges, lines denote median, whiskers denote maximum and minimum values, outliers are dots.

Comparing acceleration-based rates of behaviours to focal rates

Overall behavioural budgets calculated using focal data and accelerometer (based on pooled data random forest models) during observation hours (07:00-17:00) revealed comparable activity budgets (Fig. II - 4, Table II - S13). Behavioural rates obtained from accelerometer-identified budgets were significantly correlated with the rates obtained from continuous focal data for giving grooming (Fig. II - 5b), but not for receiving grooming (Fig. II - 5c). Rates from accelerometer data and focal data were significantly correlated for resting (Fig. II - 5a) and running (Fig. II - 5f) but not for foraging (Fig. II - 5d) and walking (Fig. II - 5e). Focal sampling resulted in lower rates of receiving grooming (Wilcoxon signed-rank test: Z = -2.31, p =0.021, n=12; Fig. II - 5b) and marginally insignificant lower rates of giving grooming (Wilcoxon signed-rank test: Z=

-1.68, p = 0.092, n=12; Fig. II - 5c) compared to accelerometer-based data. Focal sampling showed higher rates of foraging (Wilcoxon signed-rank test: Z = -3.49, $p <$ 0.001, n=12; Fig. II - 5d), but lower rates of walking (Wilcoxon signed-rank test: Z = -2.70, p = 0.007, n=12; Fig. II - 5e) and running (Wilcoxon signed-rank test: Z = -3.49, p < 0.001, n=12; Fig. II - 5f). There was no significant difference in resting rates between the two methods (Wilcoxon signed-rank test: Z = -1.19, p = 0.233, n=12; Fig. II - 5a).

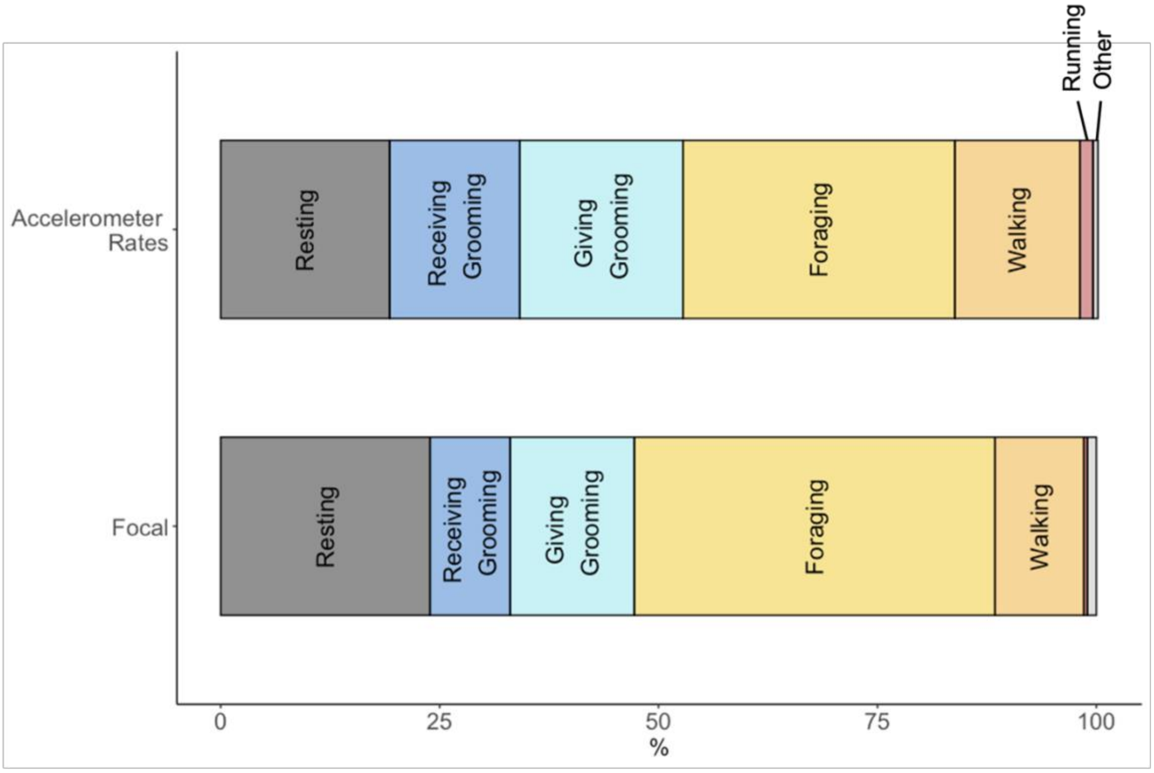


Figure II – 4: Overall accelerometer-identified and focal activity rates Mean rates across n=12 baboons for 6 main behaviours estimated by accelerometer data using the pooled data random forest model (top bar) and focal rates from direct observations (lower bar). Normalised focal rates were used (see Table II - S13).

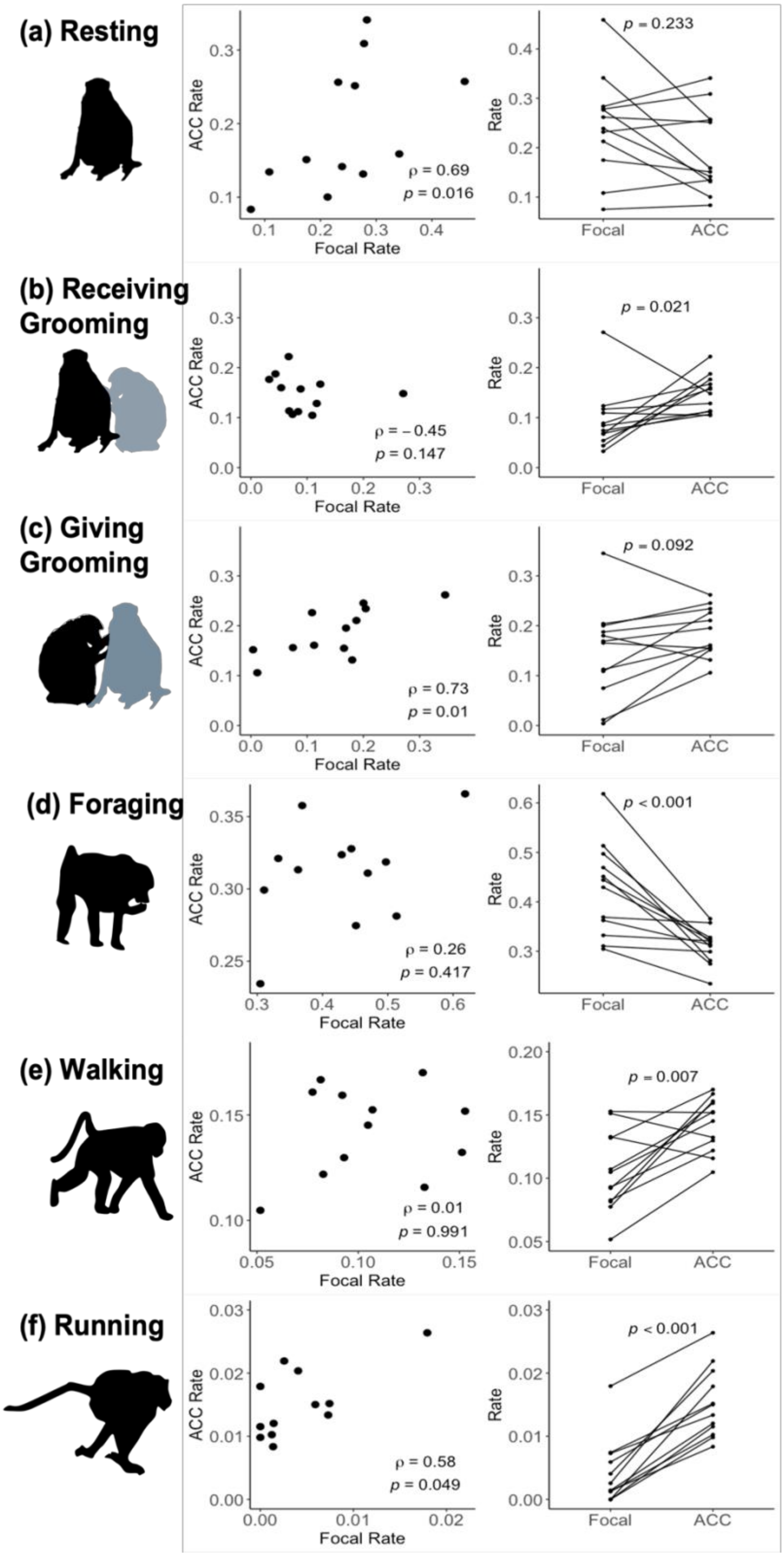


Figure II – 5: Individual accelerometer-identified and focal activity rates Rates of behaviours calculated from focal and acceleration (ACC) data (n=12 baboons) showing the correlation (left column) and difference (right column) between the rates obtained from the two methods for: **(a)** resting, **(b)** receiving grooming, **(c)** giving grooming, **(d)** foraging, **(e)** walking and **(f)** running. Note axes scales differ between behaviours.

Discussion

The overall aim of this chapter was to quantify allo-grooming from accelerometer data using machine learning. I first used random forest models to identify receiving and giving grooming (and other behaviours) from accelerometer data collected from n=12 collared wild chacma baboons. Second, I investigated potential benefits of using individual accelerometer data sets when training random forest models, as opposed to the more common approach of pooling the data for multiple individuals. Third, I applied both models to the full dataset, to calculate activity (grooming) budgets for each individual. Fourth, I compared rates of grooming obtained from focal data (direct observation) to rates obtained from accelerometer data (using the pooled data random forest model). Below, I discuss each objective and associated findings in turn. I also discuss the implications of this methodological advance for the study of allo-grooming and the outstanding questions that can now be addressed.

This study is the first to identify allo-grooming using tri-axial accelerometer data with high precision and recall, for both the actor (precision 81% and recall 87%) and the receiver (precision 91% and recall 79%), allowing me to calculate grooming times for n=12 baboons over n=680 days. Compared to previous work on males only (Fehlmann et al., 2017a), the focus on females (the sex which devotes high proportions of the day to grooming: Hill, 1999) and the larger sample sizes for both grooming behaviours (±6 hrs vs. ±1.5 minutes for giving grooming; ±4.5 hrs vs. ± 4 minutes for receiving grooming in the current versus previous data set, respectively) likely explain this improved detection (see e.g., Pagano et al., 2017). This demonstrates that social behaviours, if performed frequently and when targeted during data collection by the researchers, can be successfully identified and incorporated into activity budgets alongside other key behaviours (Brown et al., 2013). Because machine learning is a 'black box' in terms of its internal decision rules (Nathan et al., 2012), it is important to consider what biomechanical features distinguish grooming from other stationary behaviours in acceleration signals (Chakravarty et al., 2019). Below I describe the findings for giving and receiving grooming in turn.

Acceleration profiles for giving grooming show that sufficient movement takes place to produce a distinctive cyclic pattern, with a median PSD2 along the X axis (surge) which falls outside the interquartile ranges of any other behaviours (*Appendix* Table II - S7, Fig. II - 1b). This surge (back-and-forth) motion makes sense when considering the typical grooming rhythm, in which the actor repeatedly moves their hands forwards and across the recipient in front of them. Power spectra are typically used for identifying locomotion which produces repeated oscillations (Fehlmann et al., 2017a; Sellers and Crompton, 2004; Wang et al., 2015; Yamaguchi et al., 2006), but self-grooming in domestic cats (*Felis catus*) is also associated with differently paced cyclic patterns along the surge axis (Watanabe et al., 2005). In a study on dingoes (*Canis dingo*), "self-grooming" was classified as a 'medium' activity class (repetitive head movement) associated with higher ODBA (overall dynamic body activity) compared to resting behaviours (Tatler et al., 2018). Taken together, the present and previous studies suggest that the act of grooming, while stationary, can still produce a distinct acceleration pattern that is discernible from other stationary behaviours (i.e., resting, receiving grooming). The present study also highlights the value of performing further waveform analyses to obtain descriptive statistics of how signal varies across time (e.g., to detect repetitive patterns), rather than relying on measures of general body activity. For instance, previous work on captive rhesus macaques using omni-directional accelerometers (which provide a general indicator of 'physical activity') successfully differentiated 'active' from 'inactive' behaviours (Papailiou et al., 2008), but these were unaffected by arm and neck movements which would be important for identifying grooming. This corresponds to my findings: VeDBAs (also a general measure of activity based on the dynamic acceleration across the three axes) overlaps between the 3 stationary behaviours: resting, receiving and giving grooming (Table II - S7, Fig. II - 1b). In contrast, the relatively small but repetitive movements made while giving grooming were discernible in the PSDs (Fig. II - 1b).

For receiving grooming, the acceleration profile presents a challenge due to its resemblance to resting (the difference between sitting versus sitting while being groomed is inevitably subtle). Previous studies testing the use of tri-axial accelerometery to differentiate between non-active or slowly executed behaviours suggest that there are limits to what fine-scale changes in movement can be detected using accelerometers alone (Gunner et al., 2020; Williams et al., 2015). As both behaviours are executed in similar body-positions (e.g., sitting, lying), static acceleration which informs posture would not be sufficient to distinguish between these behaviours (e.g., see Fig. II - S4 in *Appendix* for stZ distribution). Nevertheless, the random forest model shows relatively high precision and recall for both behaviours (> 77%). Dynamic acceleration and its derivatives must thus pick up on very small changes in movement. While being groomed may be assumed to be associated with slightly more body-movements due to the manipulation of fur by another baboon, the median VeDBAs is, in fact, lower for receiving grooming than for resting (*Appendix* Table II - S7; Fig. II - 1b). While unintuitive, there are several reasons why resting may generate more overall body movement than receiving grooming. First, based on the labelled data set, resting is a behavioural state that is relatively brief compared to receiving grooming (*Appendix* Table II - S5; resting bouts were on average 4x shorter than receiving grooming bouts). Thus, resting does not necessarily reflect uninterrupted periods of relaxation (which would presumably be associated with very low VeDBAs), but rather takes place as a relatively brief pause between activities. Consequently, when taking a moving average across a 3-second window (as was done to obtain VeDBAs), the calculation will take into account a second of the behaviour that precedes and follows resting. Quick transitions can result in misclassifications of behaviours (Moreau et al., 2009) and considering that transitions have distinct acceleration signatures (Diosdado et al., 2015), it is possible that more noise is introduced into the resting signal due its intermittent nature compared to receiving grooming. Second, from a biological perspective, resting during the daytime (when video footage was collected), may be a more active behaviour than the name suggests. Whilst standing (resting quadrupedally) and secondary behaviours such as self-scratching and body-shakes were removed from the data set to create a “purer” resting category, baboons still move their body during resting when scanning the environment (e.g., vigilance; Cowlishaw, 1998) or as they prepare to start moving (Rose, 1977). Conversely, when being groomed, baboons typically stay still as would be expected when considering the tension-reducing effect of being groomed, which is reflected in lower rates of behavioural indices of stress (e.g., yawning, scratching, body-shaking, auto-grooming; Schino et al., 1988). Furthermore, staying motionless makes the removal of ectoparasites during grooming more effective (Schino et al., 1988). The above notwithstanding, receiving grooming and resting are very similar from an accelerometery perspective with a difference in VeDBAs of less than 0.1 g (Fig. II – 1b). Essentially, this reduces the distinction to: was the baboon ‘still’ or ‘very still’? Based on the results from the random forest model, ‘still’ corresponds to ‘resting’ and ‘very still’ corresponds to ‘receiving grooming’ in a relatively reliable way. However, relying on this very small difference make these two behaviours more prone to confusion, which should be borne in mind when interpreting the results going forward (Chapter 4 and Chapter 5).

The ability to measure grooming continuously (as made possible by using collars) opens a wealth of potential questions that can be investigated, for instance in the field of socio-endocrinology in humans and other animals. In primates, long-term studies have demonstrated that stronger social bonds – measured by grooming interactions (Lehmann et al., 2007; Silk et al., 2006a) – are linked to longer life spans and higher infant survival Grooming has been associated with reduced levels of glucocorticoids (GCs) (Engh et al., 2006a; Fürtbauer et al., 2014; Shutt et al., 2007; Wittig et al., 2008), a class of steroid hormones which is linked to negative health consequences when levels are chronically elevated (Campos et al., 2021; Sapolsky, 2004). Little is known about the mechanism that links grooming to lowered GCs, which is likely important for the maintenance of grooming in the short-term (Russell and Phelps, 2013) and cumulatively could affect fitness in the long-term (Campos et al., 2021). This knowledge gap is, at least partly, due to methodological limitations, as traditional observations provide rates of behaviour which are then matched to average GCs for the same period, allowing only correlative relationships to be established (but see: Wittig et al., 2016). As non-invasive sample collection from animals is opportunistic by nature (e.g., urine and faeces: Palme, 2019), it is unlikely that grooming data (collected the right amount of time before or after the voiding of the sample: Behringer and Deschner, 2017; Heistermann, 2010) will be available using traditional methods. This problem is circumvented by using continuous collar data, as each collected sample can be time-matched to grooming data retrospectively or to grooming data recorded following the hormone measurement; allowing to address both how grooming affected GCs, as well as how GCs may affect grooming (e.g., in the context of social buffering: DeVries et al., 2003). Moreover, the quantitative relationship between hormones and behaviour are not well understood and could manifest in different ways, potentially following a linear relationship or a step-function (on/off) (Hau and Goymann, 2015). To put this into a GC-grooming context: do gradually increasing GCs lead to gradually more time spent grooming? Or do GCs need to fall below a certain threshold to prompt an increase in grooming? To address these questions, details such as length and frequency of grooming time are needed.

The second objective of this chapter was to investigate whether random forest models built using individual accelerometer data sets could outperform the model built using pooled data (here n=12 baboons), considering that individual differences may affect accelerometer signatures (see Introduction, Jeantet et al., 2018; Laich et al., 2008). I investigated this using the commonly used metrics (precision, recall, MCC) and by applying the two types of models to the entire dataset to calculate activity budgets (the third objective of this Chapter). A substantial number of studies have used animal-borne accelerometers and machine learning methods to identify behaviours from observer-verified datasets (Alvarenga et al., 2016; Fehlmann et al., 2017a; Ladds et al., 2016; Mansbridge et al., 2018; Pagano et al., 2017; Tatler et al., 2018; Wang et al., 2015). However, relatively few studies present the next step alongside: using the machine learning model to calculate the occurrence of behaviours from large, unverified data sets to obtain activity budgets over a certain period (but see Lagarde et al., 2008; Lush et al., 2016; Nathan et al., 2012 for exceptions). The present study provides a good example of why this is not only informative from a biological perspective, but why it may also be useful for quality control of the performance of the random forest model (in this case, indicating that random forest models built from pooled data are likely more robust than those built using individual data sets).

I found that giving and receiving grooming, as well as resting and foraging, had higher precision in models built using individual data sets compared to models using pooled data sets, suggesting that accuracy can be improved by using individual datasets. This finding may be particularly relevant for studies using neck-collars like the present and many others (Dunford et al., 2020; Fehlmann et al., 2017a; Heurich et al., 2012; Martin et al., 2016; McClune et al., 2014; Pagano et al., 2017; Soltis et al., 2012; Tamura et al., 2019; Tatler et al., 2018). While neck collars offer benefits, such as ease of deployment and drop-off mechanisms which eliminate the need for re-capture, the less rigid attachment (some rotation is needed to ensure animal welfare) increases the chance of noise being introduced in accelerometer signals (movement not originating from the animal moving but from movement of the tag) (Shepard et al., 2008b; Wilson et al., 2020). As such, accelerometer data collected by neck-collars may benefit from reducing noise which inevitably is introduced by pooling acceleration-data from multiple individuals and is the usual approach (Fehlmann et al., 2017a; Ladds et al., 2016; Tatler et al., 2018). Even when built in a consistent way, slight differences in tilt of the accelerometer tag inside the collar housing can affect the returned acceleration signals (Laich et al., 2008). Recent work has shown that a narrow operational range for VeDBA (e.g., in the case of slow-moving animals) makes the relative noise introduced by differences in tag placements larger (Gunner et al., 2020). This is relevant for behaviours like grooming, which is executed while stationary (low VeDBA range). While individual differences in accelerometery signatures are acknowledged in the biologging literature, they have to my knowledge not been tested in this way (although see Dickinson et al., 2021 and Ferdinand et al., 2020 who test machine learning model performance when removing specific individuals from training data).

The third objective was to apply the random forest models to calculate activity budgets, which revealed a potential caveat to using individual random forest models, despite these having higher precision for four out of six behaviours, including giving grooming and receiving grooming (Table II – S8). Compared to the pooled data random forest models, individual models produced approximately twice the variation in daily estimates between baboons for receiving grooming and resting compared to other behaviours (Fig. II - 3; Table II - S9-S12). While it is possible that individuals vary substantially in how much they rest and receive grooming, the larger variation in daily estimates (±10 hours) could also suggest a less consistent ‘search image’ for receiving grooming and resting. This could be for two reasons: (1) Unbalanced data sets during random forest model training can result in predictions favouring the dominant class (Chen et al., 2004). For individual models, the relative amounts of data available for resting and receiving grooming differed between individuals (Table II - 1) and may have caused biases towards identifying one over the other behaviour. As imbalance increases, so does classification error (Mellor et al., 2015). While random forest models are generally robust to imbalanced data sets (Dittman et al., 2016; Mellor et al., 2015), imbalance could play a significant role when classes are already hard to identify (Mellor et al., 2015; in our case resting and receiving grooming). (2) When using machine learning to recognise behaviours, a representative sample of the behaviour of interest is needed (Liu and Ziebart, 2014; Valletta et al., 2017). When a machine learning model is trained using a biased testing data set, it can appear to function well in the first phase (e.g., when precision and recall are calculated using the same biased data set; see above) but, once applied to a new independent dataset, make predictions that are comparable to random guesses (Valletta et al., 2017). For baboon behaviours, part of what constitutes a representative sample is to have the different postures in which a behaviour can be executed represented in the data. This is particularly pertinent for individual models as they will contain a more limited sample (n=1 individual), compared to the pooled data (here: n=12 individuals). For example, receiving grooming can take place in three general body-positions: standing, sitting, or lying down (n=9/11 baboons adopted all three postures; Table II - S4), while resting can take place sitting or lying down (n=8/12 baboons adopted both possible postures; Table II - S4). Even if all postures are present in the individual data set, the same posture may look slightly different every time (e.g., leaning left/right/forward/backward). With repeated independent events of the same behaviour, the full range of postures is more likely to be captured. A total of 291 independent grooming events were used in the pooled random forest model compared to a median of 10 independent grooming events in the individual data sets, which likely makes the former more robust when calculating activity budgets.

On balance, while the use of individual datasets holds potential, a more representative sample of the different ways in which behaviours can be executed would be needed in the training data (particularly for receiving grooming and resting). Finally, statistical analyses which balance the sample sizes in individual models (e.g., down-sampling majority classes) or statistically control for less represented classes (e.g., weighted random forest models) (Chen et al., 2004) could help answer the questions whether individual models could outperform pooled random forest models. For the remainder of the thesis, I use the pooled random forest model identified activity budgets as these are the ones that have been widely used (Fehlmann et al., 2017a; Lush et al., 2016; Nathan et al., 2012; Pagano et al., 2017; Tatler et al., 2018) and, for reasons outlined above, are likely more robust.

The third objective (calculating activity budgets based on random forest models) revealed a second important caveat. The accelerometer-identified activity budgets suggest that overall baboons spent on average 30% of time engaged in receiving grooming, 19% giving grooming, and 21% resting. When restricting the time-window to direct observation times (07:00 – 17:00), baboons spent on average 15% receiving grooming, 19% giving grooming, and 18% resting. The steep increase in receiving grooming (± 15%) when including night-time hours, compared to a modest increase in resting (±2%), strongly suggests that resting during the night is misclassified as receiving grooming. As discussed above there is considerable overlap between accelerometer variables between resting and receiving grooming, but receiving grooming has the lower median VeDBAs

(Table II - S7; Fig. II - 1b). This raises the question whether receiving grooming is more prone to confusion with resting during the night compared to the day, which may be the case if resting during the night is more still (due to sleeping) compared to resting during the daytime (where brief resting is more typical; Table II - S5). Indeed, other studies treat resting and sleeping as separate behaviours due to the difference in energetic demands (Key and Ross, 1999; Leonard and Robertson, 1997) and a recent study investigating baboon sleep patterns using accelerometers likewise distinguished between 'sleep' and 'resting wakefulness' (Loftus et al., 2022). The median/range VeDBAs calculations for resting during day vs. night in the present study are in line with this, showing more overlap in VeDBAs between resting and receiving grooming at night (Fig. II - S7). When considering direct observation hours only, the activity budgets are biologically more likely (see above; the discrepancy of 4% in favour of giving grooming could be explained by 7 out of 12 collared baboons having infants who they would likely regularly groom but not be groomed by). Thus, to be conservative in future analyses/chapters, receiving grooming will only be considered for daytime (between 07:00 – 19:00) periods.

As a final and fourth objective, this study offered an opportunity to compare acceleration-based activity budgets to direct observations, i.e., focal sampling (Altmann, 1974). Usually, this is not possible because the primary motivation for using collars is to reconstruct activity budgets of animals that are not readily observable in their natural habitat (e.g., Brown et al., 2013; Jeanniard-du-Dot et al., 2017). Focal data may over- or underestimate behaviours depending on the visibility of the behaviour or observer bias to start (or stop) focal follows during certain behaviours (e.g., stationary) over others (e.g., running) (Rose, 2000). Moreover, focal data can be collected using both continuous (here: giving and receiving grooming) or instantaneous (all other behaviours) sampling methods (Altmann 1974; Rose, 2000), with the latter method being prone to underestimation of rare behaviours (Rose, 2000) which accelerometer data collected at 1 second resolution is likely not.

The relative breakdown of behaviours was comparable between the two methods, with baboons spending the predominant portion of the day foraging, followed by resting, giving grooming, receiving grooming, walking, and running (Table II - S13; Fig. II - 4). I found positive correlations for giving grooming and resting rates but not receiving grooming (Fig. II - 5). Moreover, I found that receiving grooming rates were significantly lower using direct observation, while giving grooming and resting were comparable between the two methods (Fig. II - 5). These findings suggest focal data is returning both different and relatively lower individual rates for receiving grooming, but not the other two stationary behaviours. The lack of correlation might be due to the relatively small range in individual rates of receiving grooming (between 3-12%, when ignoring the outlier (M2) visible in the Fig. II - 5b), compared to giving grooming and resting ranges (0-35% and 8-46% respectively) in the focal data, which could make it harder to detect individual differences in receiving grooming and thus correlate to accelerometer-identified rates. Receiving grooming was also the rarest of the three stationary behaviours, both in focal and collar identified rates (Table II - S13; Fig. II - 4), and thus could be subject to lower estimations in focal data despite being easy to observe. Finally, accelerometer-identified receiving grooming, while more distinct from resting during the day (Fig. II - S7), could still be confused with day-time resting if VeDBAs is low (Fig. II - 1). This could potentially inflate the 'true' receiving grooming rate returned by the accelerometers relative to focal data, causing the significantly higher rates identified in accelerometer data (Fig. II – 5b). Foraging rates were significantly higher in focal data, while travelling and running were both lower using focal data. Foraging and walking occur intermittently, and it is possible that the amount of walking between foraging patches is estimated to be lower through instantaneous sampling (i.e., even if a few steps are taken between foraging patches, the behaviour would still be labelled 'foraging' during scan sampling). Moreover, active behaviours such as walking and running are likely underestimated as the focal individual is more easily lost (Rose, 2000; pers. obs.). Finally, sample collection (faecal and urine) often resulted in termination of observations if the focal animal moved off, which could result in less walking/running being recorded. Taken together, these findings suggest that while overall activity budgets are comparable (Fig. II - 4), individual receiving grooming rates are lower and not correlated with accelerometer-identified rates.

Future directions

Social environments have profound impacts on health and fitness in human and non-human animals (Snyder-Mackler et al., 2020). Many animals use grooming to form and maintain social bonds, with primates being the most widely studied taxa (Dunbar, 1991;

Silk et al., 2006b; Silk et al., 2010b). Grooming has been linked to a reduction in the release of glucocorticoids by the HPA-axis in a range of primates (Fürtbauer et al., 2014; Shutt et al., 2007; Wittig et al., 2008; Wittig et al., 2016), a physiological modulation with potentially far-reaching fitness consequences, as life-long exposure to GCs negatively predicts survival (Campos et al., 2021). Even though it is generally acknowledged that the relationship between hormones and behaviour is bidirectional, where changes in hormones can be both the cause and the consequence of behaviour (Oliveira, 2004; Packard et al., 2011), the link between grooming and GCs has remained mostly correlative to date. In part, this is due to methodological restrictions, where observational grooming data is usually too sparse to be time-matched with GCs. To establish causal relationships and study which aspects of grooming are important for modulating HPA-axis activity, high-resolution, continuous grooming data would be needed. In this chapter I identified giving and receiving grooming from tri-axial accelerometer data from n=12 collared chacma baboons, allowing me to calculate total time spent receiving and giving grooming across n=680 days. Continuous grooming data will allow to address the aforementioned knowledge gap, by enabling the investigation of the dynamic relationship between grooming and GCs (Chapter 5) and of the finer resolution details of grooming interactions themselves. This will give insights into the temporal patterns, frequency, and duration of grooming bouts (Chapter 4), which may be important for the modulation of GCs (Chapter 5).

Methodological conclusions

This chapter highlights some methodological considerations for the use of random forest models to predict behaviours from accelerometer data in wild systems, where the dataset used to train the model may differ from the larger dataset from which the model is expected to predict behaviours (Valletta et al., 2017). Calculating activity budgets could serve as a 'quality control' step for random forest model performance beyond the commonly used metrics (e.g., precision, recall and MCC), as highlighted in these two instances:

(1) For the comparison between individual versus pooled data random forest models, I found that while the former had significantly higher precision for four out of six

behaviours (~89%) compared to the latter (~84%), the returned activity budgets showed implausibly high between-individual variation, suggesting individual random forest models were not as robust when applied to larger datasets (Fig. II - 3; Table II - S9-S12). This was likely due to the individual datasets used to train the random forest models being smaller, more unbalanced, and less representative of the postures each behaviour could be executed in.

(2) For receiving grooming and resting, I found that while both had relatively high precision and recall (>77%), the 24-hour activity budgets revealed confusion during the night when both behaviours were associated with low and overlapping VeDBAs (Fig. II – S7; Table II - S7). Resting may be executed differently during video follows compared to outside observation hours (i.e., ‘active’ resting vs. sleeping), which likely exacerbated the confusion with receiving grooming at night. Thus, it is important to not only consider the range of acceleration-signals (Table II – S7) associated to the behaviour of interest (receiving grooming) but also to the behaviour with which it is most likely to be confused (resting) and how this confusion may change across contexts.

Appendix

Table II - S1: Overview of supplementary material for Chapter 2

Content	**Tables & Figures**
S1: Methods	
S1.1: Collar details	
ACC recording periods	Table II - S2
S1.2: Labelled video data	
Behaviour descriptions	Table II - S3
Behaviour sample sizes	Table II - S4
Behaviour bout lengths	Table II - S5
Individual training and validation sample sizes	Table II - S6
S1.3: Observational data	
Focal observation distribution	Fig. II - S1
Focal observation full data vs. collar-adjusted data correlation	Fig. II - S2
S2: Results	
S2.1: Random Forest Model	
Error rate in models over 500 iterations	Fig. II - S3
Variable descriptives	Table II - S7
stZ distribution for each behaviour	Fig. II - S4
S2.2: Activity budgets	
Non-classified behaviours	Fig. II - S5
F18 Activity budget: GPS vs. ACC	Fig. II - S6
Night vs. Day: Resting vs. Receiving grooming VeDBAs	Fig. II - S7
S2.3: Individual vs. Pooled Random Forest Models	
Individuals from study group	Fig. II - S8
Metric comparisons of individual vs. pooled data random forest models	Table II - S8
Activity budget comparisons of individual vs. pooled data random forest models	Table II - S9; S10; S11; S12
S2.4: Focal vs. Pooled Random Forest Model	
Activity budget comparison of focal data vs. pooled data random forest models	Table II - S13; Fig. II - S9

S1.1: Collar details

Table II - S2: Details of ACC recording period for each collared baboon. F1's collar was never retrieved. F17's collar collected 2 days of ACC data before video were collected and was not included in the analysis. F13 did not collect any ACC data. F18's ACC data was found to be erroneous after ground-truthing activity estimates against GPS-obtained activity estimates (Fig. II – S6).

Collar	Baboon ID	Names	ACC start	ACC stop	Full
1	M1	Khangela	31/07/2018	14/10/2018	76
2	M2	Shebeleza	31/07/2018	03/09/2018	35
3	F1	Fatty	NA	NA	NA
4	F2	Hanson	26/07/2018	11/09/2018	48
5	F4	Gabrielle	26/07/2018	12/10/2018	79
6	F5	Luna	27/07/2018	27/09/2018	63
7	F6	Kym	27/07/2018	27/09/2018	63
8	F7	NikNak	27/07/2018	29/09/2018	65
9	F9	Nelly	27/07/2018	26/09/2018	62
10	F10	Trinity	31/07/2018	10/09/2018	42
11	F13	Don	NA	NA	NA
12	F14	Lola	03/08/2018	26/08/2018	24
13	F15	Azul	27/07/2018	15/10/2018	81
14	F17	Sunny	03/08/2018	05/08/2018	2
15	F18	Cindy	27/07/2018	25/09/2018	61
16	F19	Patch	31/07/2018	10/09/2018	42

S1.2: Labelled video data

Table II - S3: Ethogram of labelled behaviours (definitions adapted from: Rose, 1977 and based on personal observations). Behaviours observed in the 29.4 hrs of footage for n=12 baboons. The behaviours in bold were the main behaviours of interest used in the random forest model.

Behaviour	**Description**
Social behaviours (n=16)	
Giving Grooming	Picking through and inspecting fur of conspecific
Receiving Grooming	Being groomed by conspecific
Mating (actor)	Bipedal stance, male mounting female and copulating
Mating (receiver)	Quadrupedal stance, female being mounted by male and copulating
Mounting (actor)	Greeting conspecific in bipedal mount position
Mounting (receiver)	Quadrupedal position being mounted by conspecific
Darting	Post-copulation run by females, often accompanied by copulation-call
Infant grabbing (actor)	Female handling and pulling the young infant of another female, often accompanied by lip-smacking
Infant grabbing (receiver)	Female of whom the infant is being grabbed by another female
Presenting	Displaying rear in quadrupedal stance to other conspecific (typically female to male, but also within sexes as subordinate display)
Inspecting female	Male inspecting genitals of female
Lip-smacking	Greeting conspecific with rapid lip movement
Aggressive display	Threatening body posture accompanied by direct eye-contact, eye-flashing and ground-slapping
Threat yawn	Aggressive display specific to males, during which they display their canines during wide-gaped yawn
Attacking (actor)	Chasing, biting and pinning down conspecific to the ground
Attacking (receiver)	Being attacked by conspecific
Vocalisations (n=3)	
Copulation call	Female call during and immediately following copulation
Bark	Wa-hu by males during aggressive display/interactions
Long-distance bark	Call made when conspecifics are separated, often from elevated post
Self-directed (n=3)	
Auto-grooming	Picking through and inspecting own fur
Self-scratching	Scratching body in rapid motion using hindlegs or forelimbs
Body-shake	Rapid side-to-side full body movement
Locomotion (n=6)	
Walking	Travelling on the ground in walking gait

Table II - S3 *continued*

Running	Travelling on the ground in galloping gait
Climbing up	Travelling up a structure (rock, fence), using arms to pull body up
Climbing down	Travelling down a structure (rock, fence), perching body downward
Jumping	Jumping between or off tall structures
Complex locomotion	Pivoting/spinning/shuffling while walking
Inactive (n=3)	
Resting (sit)	Stationary in seated position
Resting (lie)	Stationary in lying position (lateral and ventral)
Standing	Stationary in quadrupedal position
Foraging (n=4)	
Foraging (sitting)	Extracting, manipulating and consuming food in seated position
Foraging (standing)	Extracting, manipulating and consuming food in quadrupedal position
Drinking	Bending head down to drink water with rear sticking up
Bin manipulation	Pushing and pulling bin, prying items through bin cracks
Other (n=3)	
Adjust collar	Manipulating collar position with forelimbs
Sneezing	Sneezing
Jolt	Sudden rapid movement prompted by approaching conspecific

Table II - S4: Breakdown of the number of seconds and events recorded for each behaviour (n=38). The column "Baboons" shows the number of baboons (max = 12) for which this behaviour was recorded. The number of events reflects the number of times the behaviour was recorded continuously. If a behaviour was interrupted by scratching/shaking/body-posture adjusting and then resumed, the behaviour would still be scored as the same event. However, in this table, changes in postures were scored as new events (to be able to report events for behaviours in different postures (i.e., standing/sitting/lying during receiving grooming, resting and/or foraging). Therefore, for those behaviours the total number of events is higher than reported in Table II - 1, where posture changes were not scored as new events.

Behaviour	**Seconds**	**Events**	**Baboons**
Social behaviours (n=16)			
Giving grooming	**22028**	**170**	**12**
Receiving grooming (sit)	**7188**	**93**	**11**
Receiving grooming (lie)	**5371**	**33**	**11**
Receiving grooming (stand)	**2984**	**38**	**9**
Mating (actor)	98	6	1
Mating (receiver)	130	12	4
Mounting (actor)	24	6	5
Mounting (receiver)	13	5	3
Darting	4	2	2
Baby-grabbing (actor)	311	23	7
Baby-grabbing (receiver)	51	9	2
Presenting	59	9	4
Inspecting female	12	5	1
Lip-smacking	69	27	8
Aggressive display	35	9	5
Threat yawn	21	7	2
Attacking (actor)	18	5	4
Attacking (receiver)	10	3	2
Vocalisations (n=3)			
Copulation call	34*	12*	3*
Bark (Wa-hu)	8*	2*	2*
Long-distance bark	1	1	1
Self-directed (n=3)			
Auto-grooming	1035	45	10
Self-scratching	1462	257	12
Body-shake	56	17	7

Table II – S4 *continued*

Locomotion (n=6)			
Walk	**7173**	**901**	**12**
Run	**510**	**124**	**12**
Climbing up	139	55	11
Climbing down	71	30	11
Jumping	58	49	8
Complex locomotion	63	16	8
Inactive (n=3)			
Resting (sit)	**13769**	**359**	**12**
Resting (lie)	**415**	**15**	**8**
Standing	959	173	12
Foraging (n=4)			
Foraging (sitting)	**8262**	**252**	**12**
Foraging (standing)	**15543**	**576**	**12**
Drinking	35	4	4
Bin manipulation	149	14	3
Other (n=3)			
Adjust collar	52	6	4
Sneezing	1	1	1
Jolt	3	3	1

Table II - S5: Average length of independent behavioural bouts in video recordings (n= 12 baboons). A new behaviour bout was classified when a change happened in main activity (e.g., transition from receive grooming to give groom). Additional behaviours (e.g., self-scratching, adjusting body position, lip-smacking) and changes in posture were incorporated into the main behaviour that was taking place.

	Giving Grooming	**Receiving Grooming**	**Resting**	**Foraging**	**Walking**	**Running**
Bout length (seconds, mean±SD)	129(±158)	126(±169)	29(±67)	36(±59)	8(±9)	4(±3)

Table II - S6: sample size for training set and validation set for the n=12 individual random forest models.

Baboon ID	Training (seconds)	Validation (seconds)	Total (seconds)
M1	5749	2535	8284
M2	4388	1859	6247
F2	3527	1470	4997
F4	7366	3129	10495
F5	6760	2957	9717
F6	5605	2393	7998
F7	3335	1452	4787
F9	2299	944	3243
F10	1932	818	2750
F14	3870	1654	5524
F15	4869	2134	7003
F19	3082	1281	4363

S1.3: Observational data

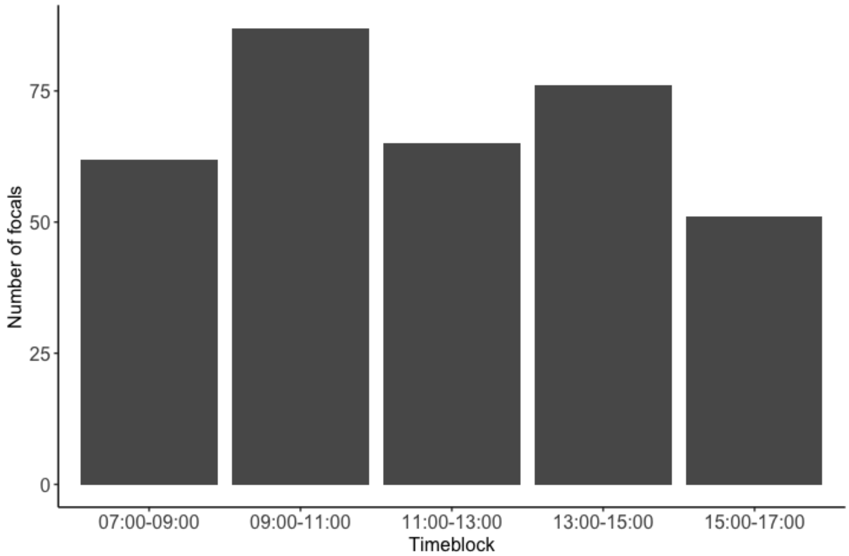


Figure II - S1: Number of focal follows conducted in each 2-hour time block on n=12 collared baboons by two observers (CC and AB) between 17/07/18 and 16/10/18.

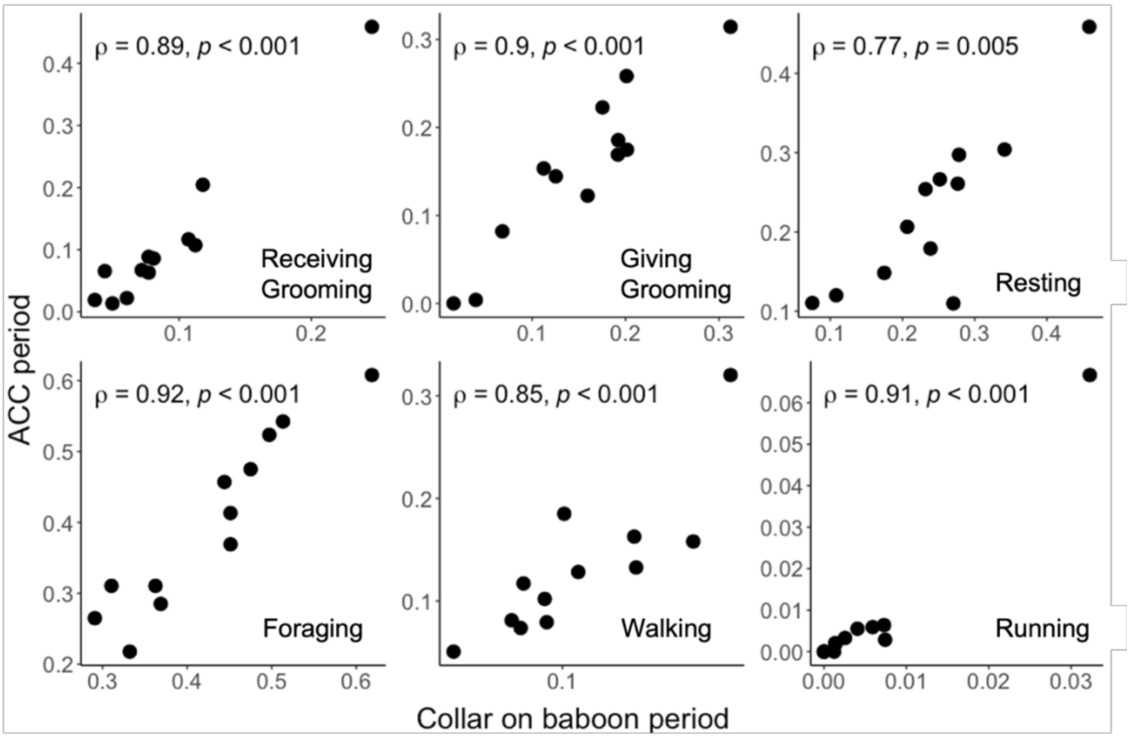


Figure II - S2: Correlation between the proportion of time engaged in each of the six state behaviours (receiving grooming, giving grooming, resting, foraging, walking and running) as calculated based on focal data (receiving and giving grooming based on continuous focal data; other behaviours based on scan data) adjusted for '*ACC period*' (time when accelerometer was collecting data; adjusted for each baboon; Table S II - 2) and '*Collar on baboon period*' (time while the collars were on the baboons, but not necessarily recording data, from 17/07/18 to 16/10/2018 for all baboons).

S2.1: Random Forest Model

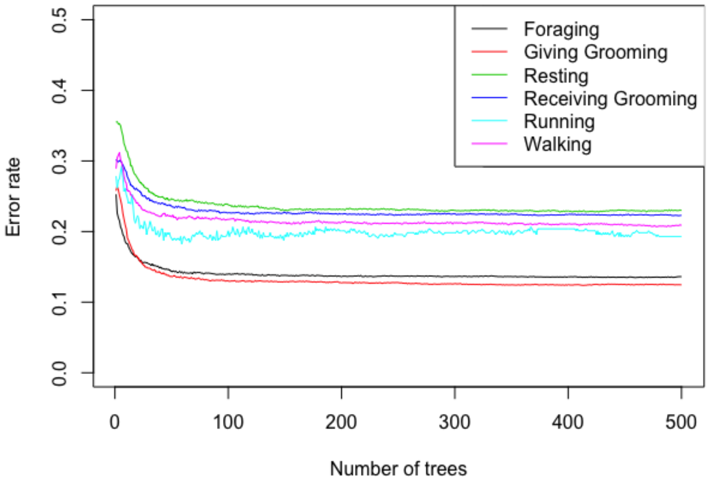


Figure II - S3: Error rate in the random forest model over the course of 500 iterations

Table II - S7: Medians, 1st and 3rd quartiles for each behaviour for five most important predictor variables in the pooled random forest model (in order of mean Gini index decrease). Behaviours that have no overlap of their 1st and 3rd quartiles with other behaviours are highlighted in dark grey, behaviours with a median that does not fall within the 1st and 3rd quartile are highlighted in light grey (following Fehlmann et al., 2017a). Interquartile ranges (IQ range) are shown with the behaviour with the largest range in bold.

		Resting	Receiving Grooming	Giving Grooming	Foraging	Walking	Running
VeDBAs	**Median**	0.03117395	0.0273643	0.045784	0.1334592	0.1983822	0.84934645
	1st quartile	0.02527744	0.02390728	0.03630547	0.0993058	0.1681141	0.62106768
	3rd quartile	0.05726455	0.03292845	0.05947971	0.17063955	0.24433327	1.0909455
	IQ range	0.03198711	0.00902118	0.02317425	0.07133375	0.07621917	**0.46987783**
stZ	**Median**	0.7062611	0.69053565	0.90576995	0.9121527	0.9189798	0.909785
	1st quartile	0.5977237	0.45470143	0.81592418	0.82100605	0.8675428	0.8516742
	3rd quartile	0.79547445	0.86418657	0.95606305	0.96300845	0.9572467	0.9630255
	IQ range	0.19775075	**0.40948514**	0.14013888	0.1420024	0.0897039	0.1113513
PSD2X	**Median**	0.000053	0.000045	0.000116	0.001209	0.00297	0.035104
	1st quartile	0.000034	0.000031	0.000066	0.000551	0.001726	0.018063
	3rd quartile	0.000112	0.000072	0.000202	0.002349	0.00516	0.068167
	IQ range	0.000078	0.000041	0.000136	0.001799	0.003434	**0.050104**
Pitch	**Median**	-0.640105	-0.2923079	-0.2440047	-0.0987443	-0.289488	-0.1792924
	1st quartile	-0.8103014	-0.653717	-0.461763	-0.3407599	-0.3785077	-0.2689091
	3rd quartile	-0.4937689	0.1031102	-0.1178439	0.1189534	-0.1954575	-0.0709256
	IQ range	0.31653253	**0.7568272**	0.34391908	0.4597133	0.1830502	0.19798343
stX	**Median**	-0.5972797	-0.288163	-0.2415906	-0.0989283	-0.2854616	-0.1783334
	1st quartile	-0.724495	-0.6081413	-0.4455271	-0.3350376	-0.3695343	-0.2656798
	3rd quartile	-0.4739479	0.10292763	-0.1175713	0.1184391	-0.1942154	-0.0708662
	IQ range	0.25054705	**0.71106889**	0.32795583	0.4534767	0.1753189	0.19481366

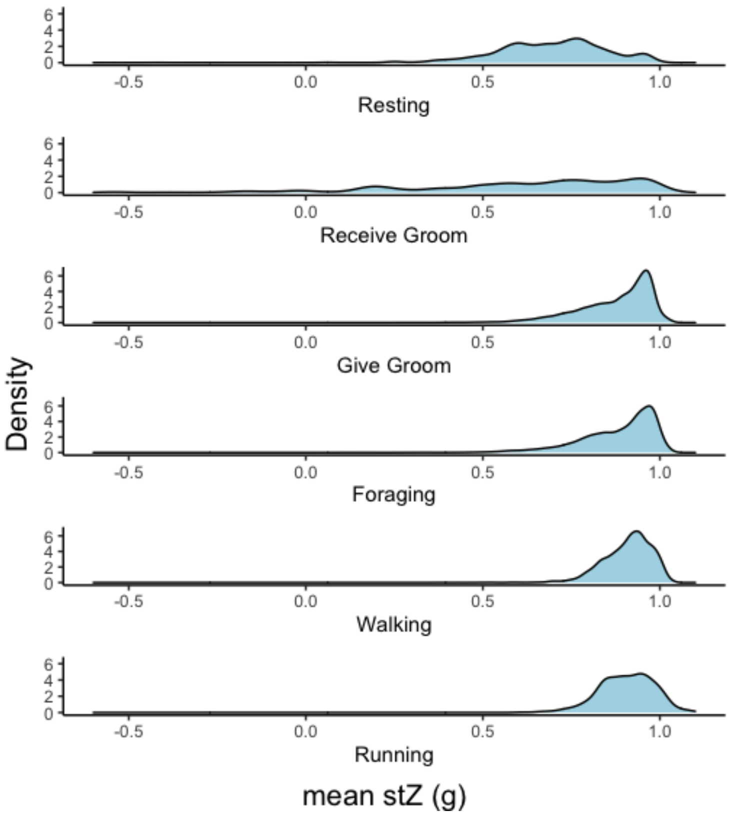


Figure II - S4: Density histogram plots of mean stZ (heave; 2nd most important variable in pooled data random forest models) associated with the six state behaviours.

S2.2: Activity budgets

Non-classified behaviours

Of the non-classified behaviours, the large majority had low VeDBA (<0.05 *g*) (n= 266,772, 84.2%) and unusual static acceleration channels (no overlap with any other behaviours, suggesting that the collar position was being flipped). This could be caused by grooming interactions during which individuals would sometimes turn the collar of a conspecific while manipulating the fur (pers. obs.). Some non-classified behaviours had higher VeDBAs (>0.05 *g*) (n=49,880, 15.8%). It is possible that these occurred during high-speed travel/jumps or fights where the collar temporarily swung into a different position on the neck or that they reflect behaviours not included in the ethogram which would have produced an acceleration profile that was sufficiently distinct to not fall into any of the six behavioural categories (e.g., mating/ mounting). The median number of excluded datapoints per day on which non-classified behaviours were recorded (n=82 days), was 2 min (Fig. II – S5).

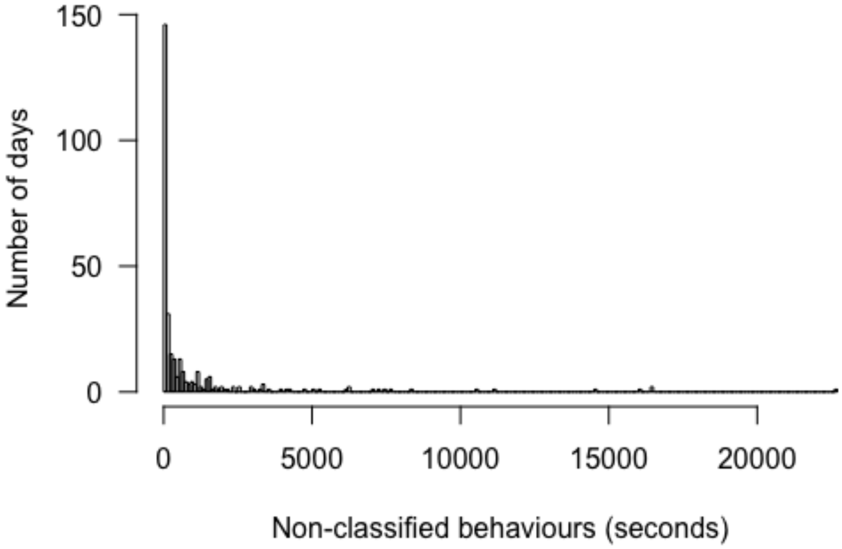


Figure II - S5: Number of seconds of non-classified behaviours per baboon per day for 11 baboons across 82 days (out of 680 days). N=1 baboon had no non-classified behaviours. Bins are set at 300 seconds (5 minutes).

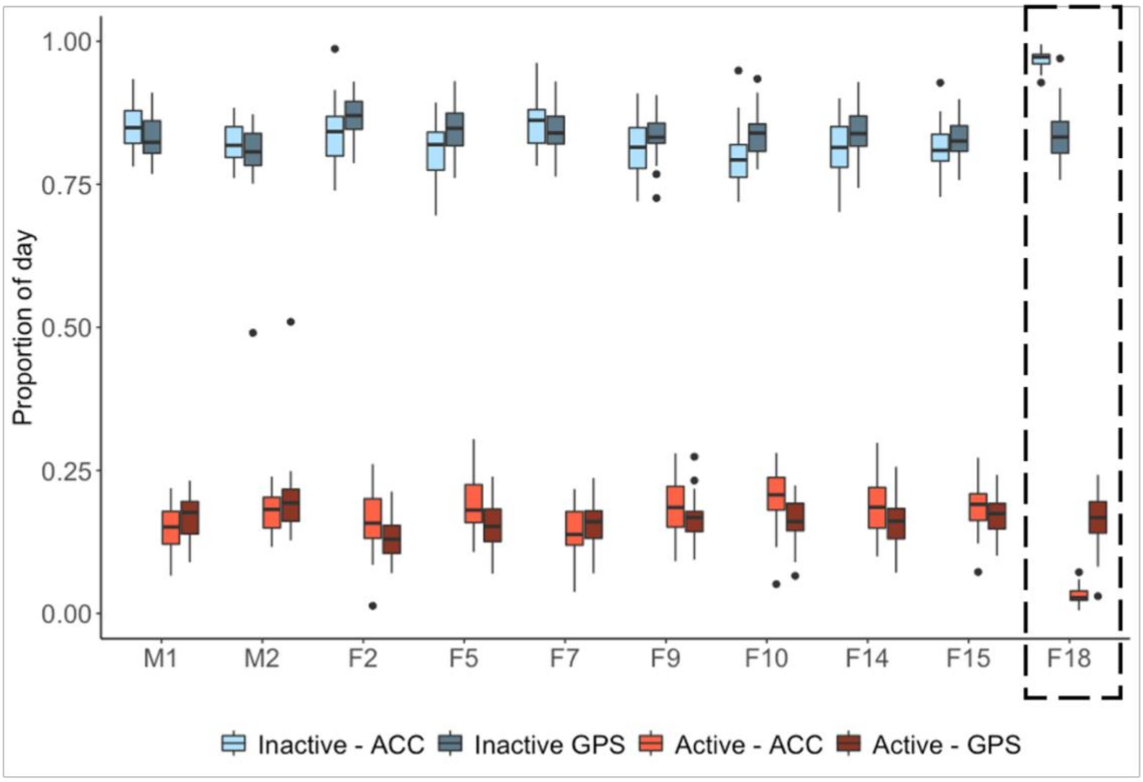


Figure II - S6: Comparison of GPS and accelerometer-identified periods of activity for n=11 baboons (number of baboons in the troop for which both GPS and accelerometer data were available). GPS-identified daily proportion of activity (24 hours) based on average speed, where moving at above 0.5 m/s was considered active, anything below was considered inactive. Accelerometer identified daily proportion of activity (24 hours) based on rates of travelling and running, plotted per individual. If F18 did indeed spend significantly higher proportions of time inactive (as ACC activity budgets suggested) compared to the other baboons, this should be reflected in her GPS-identified activity too. Based on the discrepancy between GPS-activity and ACC-activity for F18, this was ruled out and F18 was removed from further analyses and retrospectively removed from random forest model calculations.

Night vs. Day: Resting vs. Receiving grooming

Based on the results of the accelerometer identified activity budgets, which suggested receiving grooming may be confused for resting, particularly during the night, I calculated whether VeDBAs (the most important predictor variable; Fig. II - 1b) associated with resting overlapped more with receiving grooming during the night (defined as the time between 19:00 to 07:00 local time), relative to the overlap in VeDBAs during the day.

During the night, resting (median [1st and 3rd quartile]: 0.026 *g* [0.023 *g* – 0.031 *g*]) had much more overlap (48.8% of interquartile range of resting) with receiving grooming (median [1st and 3rd quartile]: 0.024 *g* [0.022 *g* - 0.027 *g*]). The overlap between resting (median [1st and 3rd quartile]: 0.035 *g* [0.026 *g* – 0.061 *g*) and receiving grooming (median [1st and 3rd quartile]: 0.026 *g* [0.024 *g* - 0.03*g*]) during the day was much less (9.7% of interquartile range of resting) (Fig. II - S7).

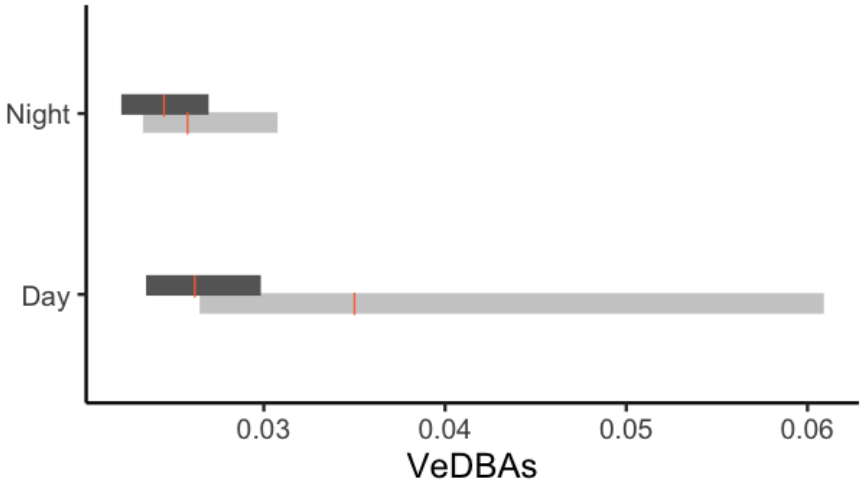


Figure II - S7: VeDBAs associated with receiving grooming (dark grey bars) and resting (light grey bars) during night (19:00 – 07:00) compared to day hours (07:00 – 19:00). Bars show interquartile ranges (1st and 3rd quartile) and orange stripe inside bars denotes the median value. Calculations based on all data from n=12 baboons.

S2.2: Individual vs. Pooled Random Forest Models

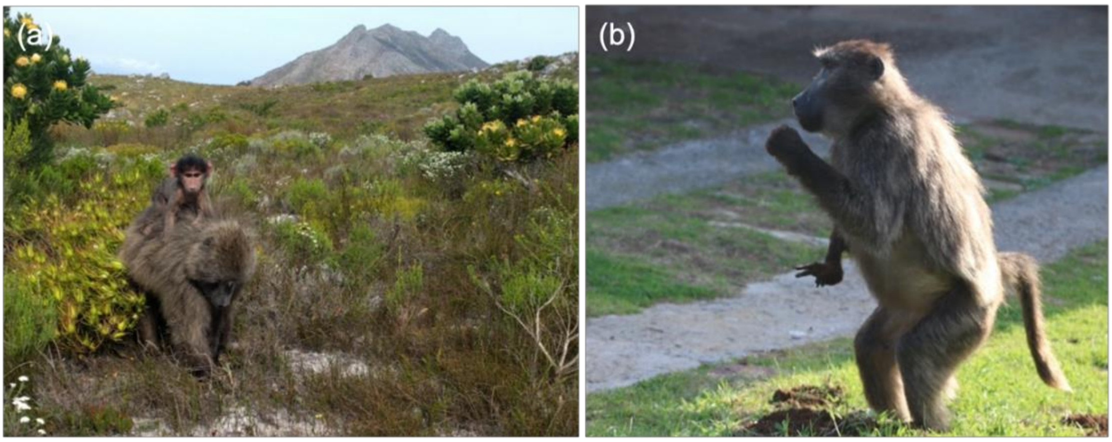


Figure II - S8: **(a)** Female (F13) with infant riding on back. **(b)** Female (F2) with a permanent injury on right hand which caused her to walk tripedally. Photo credit: **(a)** Charlotte Christensen; **(b)** Charlotte Solman.

Table II - S8: Comparison of precision, recall and MCC from individual versus pooled data random forest models. Test outputs from Wilcoxon signed-rank test (standardised *Z*-statistic and *p*-value) are shown. See Table II – 4 for mean precision and recall for individual versus pooled random forest models. Significant effects in bold. Note that for receiving grooming and running n=11 (no individual data for n=1 baboon to build the individual random forest models). All other behaviours are based on n=12 comparisons.

	Resting	Receiving Grooming	Giving Grooming	Foraging	Walking	Running
Precision	***Z= -3.10*** ***p*< 0.001**	***Z= -2.58*** ***p*= 0.005**	***Z*= -2.70** ***p*= 0.003**	***Z*= -2.25** ***p*= 0.012**	*Z*= -0.45 *p*= 0.327	*Z*= -0.70 *p*= 0.760
Recall	*Z*= -0.30 *p*= 0.38	***Z*= -1.61** ***p*= 0.037**	*Z*= -0.41 *p*= 0.339	*Z*= -0.52 *p*= 0.301	*Z*= 0.31 *p*= 0.62	***Z*= -2.09** ***p*= 0.037**
MCC	*Z*= -1.42 *p*= 0.077	***Z*= -2.08** ***p*= 0.020**	***Z*= -2.14** ***p*= 0.016**	*Z*= -1.42 *p*= 0.077	*Z*= -0.62 *p*= 0.266	*Z*= -0.94 *p*= 0.175

Comparing individual vs. pooled data random forest models

When comparing individual and pooled data random forest models, the absolute difference in giving grooming during observation hours was mean±SD 27±20 minutes and in receiving grooming was mean±SD 31±20 minutes (Table II - S9). When considering the entire data set (24-hour/day data) absolute difference in giving grooming was mean±SD 73±80 minutes and in receiving grooming activity budgets was mean±SD 130±106 minutes (Table II - S10).

The variation was larger between individuals for individual data models compared to pooled data models, particularly for resting and receiving grooming (Fig. II - 3), with a difference of 11 hours (per 24 hours) in the average amount of time receiving grooming between the two extremes (Table II - S10). A similar pattern was found for resting (12 hours between extremes; Table II - S12). In contrast, the pooled data models produced smaller ranges in estimates (Fig. II - 3), with a difference of ± 5 hours between two extremes for receiving grooming and resting across 24 hours (Table II – S10 & Table II - S12).

Table II - S9: Daily time (hrs; mean±SD) giving grooming and receiving grooming during observation hours (between 07:00 and 17:00) as estimated by pooled (n=12) and individual (n=1) random forest models for each baboon, using full days over the course of the collar data collection period (different lengths for each individual, see Table II - S2). ‘Difference’ column shows the discrepancy between the predictions of the two models, taking the pooled random forest models as the baseline (orange indicates the pooled random forest model estimated less time engaged in the behaviour, blue indicates that the pooled random forest model estimated more time engaged in the behaviour).

	Receiving Grooming			**Giving Grooming**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	1.6±0.6	0.03±0.2	🟦 1.3	1.5±0.4	0.9±0.3	🟦 0.6
M2	1.5±0.5	1.6±0.5	🟧 0.1	1±0.2	1.2±0.4	🟧 0.2
F2	1.7±0.6	0.9±0.5	🟦 0.8	2.3±0.5	1.8±0.6	🟦 0.5
F4	1.9±0.6	2.5±0.8	🟧 0.6	1.6±0.4	1.4±0.4	🟧 0.2
F5	1.1±0.4	0.5±0.3	🟦 0.6	2.6±0.6	3.4±0.7	🟦 0.8
F6	1.1±0.4	1.6±0.5	🟧 0.5	2.5±0.8	2.9±0.7	🟧 0.4
F7	1.1±0.5	NA	NA	1.3±0.4	1±0.6	🟦 0.3
F9	1.8±0.6	2±0.6	🟧 0.2	2.3±0.4	2.5±0.5	🟧 0.2
F10	1.6±0.5	2±0.6	🟧 0.4	2.1±0.5	2.1±0.4	0
F14	1.1±0.4	1.4±0.6	🟧 0.3	1.6±0.6	1.9±0.7	🟧 0.3
F15	2.2±0.6	2.5±0.7	🟧 0.3	2±0.4	2.5±0.4	🟧 0.6
F19	1.3±0.4	0.8±0.4	🟦 0.5	1.6±0.4	0.4±0.1	🟦 1.2

Table II - S10: Daily time (hrs; mean±SD) giving grooming and receiving grooming as estimated by pooled (n=12) and individual (n=1) random forest models per day (24 hours; mean ± SD) over the course of the collar data collection period (different lengths for each individual, see Table II - S2). 'Difference' column shows the discrepancy between the predictions of the two models, taking the pooled random forest models as the baseline (orange indicates the pooled random forest models estimated less time engaged in the behaviour, blue indicates that the pooled random forest models estimated more time engaged in the behaviour).

☾/☼	**Receiving Grooming**			**Giving Grooming**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	6.8±1.4	0.9±0.5	5.9	5±0.9	4.4±1.3	0.6
M2	7.6±1.1	7.1±1.8	0.5	3.3±1	4.3±1.1	1.0
F2	6.9±1.1	3.3±1.6	3.6	6.5±1.4	5.7±1.5	0.8
F4	8.1±1.3	10.3±1.4	2.2	4.1±1.1	3.6±1.1	0.5
F5	6.5±1	2.4±0.7	4.1	5.3±1.2	10±1.6	4.7
F6	6±0.9	6.1±1.3	0.1	6.5±1.8	8.6±1.7	2.1
F7	5.6±2	NA	NA	3.3±1	3.3±1.5	0.0
F9	8.6±1.4	9.5±1.5	0.9	4.8±1.1	4.8±1.0	0.0
F10	8.8±1.2	10.3±1.1	1.5	4.5±1.1	4.1±0.8	0.4
F14	5.6±1.3	6.5±1.3	0.9	3.6±1.2	5±1.6	1.4
F15	10.5±1.2	11.9±1.2	1.4	3.7±0.8	4.3±0.7	0.6
F19	6.1±0.9	3.3±1.2	2.8	3.6±0.8	1.1±0.4	2.5

Table II - S11: Daily time (hrs; mean±SD) resting, foraging, walking and running during observation hours (between 07:00 and 17:00) as estimated by pooled (n=12) and individual (n=1) random forest models for each baboon, using full days over the course of the collar data collection period (different lengths for each individual, see Table II - S2). 'Difference' column shows the discrepancy between the predictions of the two models, taking pooled random forest models as the baseline (orange indicates the pooled random forest models estimated less time engaged in the behaviour, blue indicates that pooled random forest models estimated more time engaged in the behaviour).

	Resting			**Foraging**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	2.6±0.7	4.2±0.8	1.6	3±0.7	3.3±0.7	0.3
M2	3.4±0.4	3.8±0.4	0.4	2.3±0.4	1.4±0.3	0.9
F2	1.3±0.4	3.1±0.6	1.8	3.2±0.7	2.9±0.6	0.3
F4	1.6±0.5	1.4±0.3	0.2	3.1±0.8	2.8±0.6	0.3
F5	1.3±0.4	1±0.4	0.3	3.3±0.7	3.5±0.8	0.2
F6	1.5±0.5	1±0.4	0.5	3.2±0.7	2.9±0.7	0.3
F7	2.6±0.6	3.6±1.1	1	3.6±0.9	3.9±0.8	0.3
F9	1.4±0.3	2.3±0.4	0.9	2.8±0.5	1.4±0.5	1.4
F10	0.8±0.3	0.6±0.2	0.2	3.7±0.7	3.8±0.7	0.1
F14	2.5±0.6	2.2±0.5	0.3	3.2±0.6	2.7±0.6	0.5
F15	1±0.3	0.2±0.1	0.8	3.1±0.6	3.2±0.6	0.1
F19	3.1±0.4	4.1±1	1	2.8±0.7	3.3±0.8	0.5

	Walking			**Running**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	1.2±0.3	1.1±0.3	0.1	0.2±0	0.1±0	0.1
M2	1.3±0.2	1.7±0.3	0.4	0.3±0.1	0.2±0.1	0.1
F2	1.3+0.3	1.2±0.3	0.1	0.2±0	0.1±0	0.1
F4	1.7±0.4	1.8±0.4	0.1	<0.1±0	<0.1±0	0
F5	1.6±0.4	1.6±0.4	0	0.1±0	NA	NA
F6	1.6±0.4	1.5±0.4	0.1	0.1±0	0.1±0	0
F7	1.1±0.3	1.1±0.3	0	0.2±0.1	0.2±0	0
F9	1.5±0.4	1.7±0.4	0.2	0.2±0.1	0.2±0	0
F10	1.7±0.4	1.5±0.4	0.2	0.1±0	0.1±0	0
F14	1.5±0.4	1.6±0.4	0.1	0.1±0	0.1±0	0
F15	1.5±0.4	1.5±0.4	0	0.2±0	0.2±0	0
F19	1.2±0.4	1.3±0.4	0.1	0.1±0	0.1±0	0

Table II - S12: Daily time (hrs; mean±SD) spent resting, foraging, walking and running as estimated by the pooled (n=12) and individual (n=1) random forest models per day (24 hours; mean ± SD) over the course of the collar data collection period (different lengths for each individual, see Table II - S2). 'Difference' column shows the discrepancy between the predictions of the two models, taking pooled random forest models as the baseline (orange indicates the pooled random forest model estimated less time engaged in the behaviour, blue indicates that the pooled random forest model estimated more time engaged in the behaviour).

	Resting			**Foraging**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	5.4±1	11.5±1.5	🟧 6.1	4.6±0.8	5.2±1	🟧 0.6
M2	7±1	7.5±1.4	🟧 0.5	3.5±0.4	2±0.4	🟦 1.5
F2	3.7±1.2	8.9±1.6	🟧 5.2	4.7±0.8	4±0.9	🟦 0.7
F4	4.5±1.4	3.3±0.8	🟦 1.2	4.5±0.9	3.8±0.8	🟦 0.7
F5	5±1	4.2±1.3	🟦 0.8	4.6±0.8	4.9±0.8	🟧 0.3
F6	4.4±1.2	2.6±0.8	🟦 1.8	4.5±0.8	4.2±0.7	🟦 0.3
F7	6.7±1.8	11.3±3	🟧 4.6	5.4±1.1	6.2±0.9	🟧 0.8
F9	4±1.1	5±1.3	🟧 1	4.1±0.6	1.9±0.5	🟦 2.2
F10	2.9±0.9	1.9±0.7	🟦 1	5±0.7	5.1±0.7	🟧 0.1
F14	8±2	6.4±1.7	🟦 1.6	4.4±0.6	3.6±0.6	🟦 0.8
F15	2.9±1	0.7±0.4	🟦 2.2	4.4±0.7	4.5±0.6	🟧 0.1
F19	8.3±1.6	12.5±1.8	🟧 4.2	4±0.7	4.9±0.9	🟧 0.9

	Walking			**Running**		
	Pooled	**Individual**	**Difference**	**Pooled**	**Individual**	**Difference**
M1	1.9±0.4	1.9±0.4	0	0.2±0	0.2±0	0
M2	2±0.3	2.6±0.4	🟧 0.6	0.4±0.1	0.3±0.1	🟦 0.1
F2	2.1±0.5	1.9±0.5	🟦 0.2	0.3±0.1	0.2±0	🟦 0.1
F4	2.6±0.6	2.7±0.6	🟧 0.1	0.1±0	0.1±0	0
F5	2.5±0.5	2.5±0.6	0	0.2±0	NA	NA
F6	2.4±0.5	2.3±0.5	🟦 0.1	0.2±0.1	0.2±0	0
F7	1.6±0.4	1.7±0.4	🟧 0.1	0.3±0.1	0.3±0	0
F9	2.2±0.5	2.5±0.6	🟧 0.3	0.4±0.1	0.3±0.1	🟦 0.1
F10	2.5±0.5	2.3±0.5	🟦 0.2	0.2±0	0.2±0	0
F14	2.2±0.5	2.4±0.5	🟧 0.2	0.2±0	0.2±0	0
F15	2.2±0.6	2.2±0.5	0	0.3±0.1	0.3±0.1	0
F19	1.9±0.5	2±0.5	🟧 0.1	0.2±0	0.2±0	0

S2.3: Focal vs. Pooled Random Forest Model

Table II - S13: Rates (mean±SD) based on accelerometer data during observation hours and rates calculated based on focal data for n=12 baboons (expressed as %). Note that receiving grooming and giving grooming are calculated using continuous focal data, while other behaviours are calculated from instantaneous focal data (see *Methods* for details). To make the sum of focal rates 100%, normalised focal rates (normaliser = rate*1/sum of rates) are also presented.

	Resting	**Receiving Grooming**	**Giving Grooming**	**Foraging**	**Walking**	**Running**
ACC Rates	19±9	15±4	19±5	31±4	14±2	1.5±1
Focal Rates	25±10	9±6	15±9	43±9	10±3	<1±<1
Norm. Focal Rates	24±10	9±5	14±8	41±8	10±2	<1±<1

Chapter 3: Different correlates of faecal and urinary glucocorticoid concentrations in wild chacma baboons (*Papio ursinus*)

Charlotte Christensen[1], Anna M. Bracken[1], M. Justin O'Riain[2], Michael Heistermann[3], Andrew J. King[1], Ines Fürtbauer[1]

Affiliations:

[1]Biosciences, School of Biosciences, Geography and Physics, Faculty of Science and Engineering, Swansea University, SA2 8PP Swansea, United Kingdom

[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch, 7701, South Africa

[3]Endocrinology Laboratory, German Primate Centre, 37077, Göttingen, Germany

Statement of contributions:

CC and IF designed the study. CC and AB conducted the fieldwork and collected behavioural observations and the faecal and urine samples. JOR provided logistical support in the field. CC compiled the data and conducted the statistical analysis with advice from IF. CC processed and extracted faecal samples supervised by IF, MH analysed faecal samples for glucocorticoid metabolites and IF analysed the urine samples for glucocorticoid metabolites. CC wrote the chapter with critical review, edits, and discussion from IF and final edits from AJK.

PC: Charlotte Solman

Chapter 3: Correlates of faecal and urinary glucocorticoid concentrations in chacma baboons

Parts of this work were used in the following publication:

"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*)", 2022. Charlotte Christensen, Anna M. Bracken, M. Justin O'Riain, Michael Heistermann, Andrew J. King, Ines Fürtbauer *General and Comparative Endocrinology*, 318, 113985.

Chapter 3: Correlates of faecal and urinary glucocorticoid concentrations in chacma baboons

Abstract

Glucocorticoids (GCs), a class of steroid hormones released through the activation of the hypothalamus-pituitary-adrenal (HPA)-axis, perform many vital functions essential for survival, including orchestrating the organism's response to stressors by modulating physiological and behavioural responses. Monitoring changes in GCs is a widely used research tool to investigate the physiological stress responses of wild animals. Identifying the general drivers of variation in GCs is crucial prior to investigating the various effects of acute, unpredictable events, such as daily stressors and (social) buffers that drive GC fluctuations. Here, I assess the main predictors of faecal GC-metabolites (fGCs) and urinary GC-metabolites (uGCs) in n=17 Cape chacma baboons (*Papio ursinus*), including long-term factors, i.e., dominance rank, month of year, and female reproductive state (cycling, pregnancy, lactation) and short-term factors, i.e., time of day and daily weather conditions. I found a significant effect of month of the year with high fGCs in winter and a gradual decrease into summer, which was predominantly driven by day length. Conversely, I found no seasonal effect on uGCs but 'rain days' were associated with higher uGCs. Pregnant females had significantly higher fGCs compared to cycling and lactating females, whereas uGCs were comparable across all three reproductive states. A circadian effect was observed in uGCs but not in fGCs. I found no effect of dominance rank on either fGCs or uGCs. Overall, the results suggest environmentally imposed time-constraints (short and/or rainy days) present a challenge, i.e., a reduced time-window in which energetic and social requirements must be met. Moreover, results lend empirical support to the different drivers of variation in fGCs and uGCs. While fGCs reflect cumulative HPA-axis activity, making them suitable for detecting long-term endocrine responses, uGCs undergo more fluctuation and reveal physiological responses to short-term stressors. In sum, this chapter lays out the main predictors of fGCs and uGC and highlights the temporal nature (cumulative vs. acute) of the stressors that can be captured using these non-invasive sampling techniques. This will need to be accounted for in future analyses in the context of the modulating effects of grooming on GCs.

Chapter 3: Correlates of faecal and urinary glucocorticoid concentrations in chacma baboons

Introduction

To survive an organism needs to maintain stability in body temperature, pH and glucose levels, and oxygen tension throughout its life (McEwen and Wingfield, 2003). Homeostasis is the stability of these systems in the body and is maintained through various physiological mediators, including hormones (Romero, 2002; Romero et al., 2009). During different life history stages or when changes in the physical or social environment perturb these vital processes (i.e., "stressors" as defined by Nelson, 2005) physiological mediators operate to reinstate and maintain this internal balance within the optimal ranges for bodily functions (McEwen and Wingfield, 2003). "Predictive homeostasis" (*sensu* Romero et al., 2009) describes the physiological response which operates to maintain homeostasis during predictable changes in an organism's life (e.g., circadian rhythms, seasons, life-history events), whereas "reactive homeostasis" denotes the increase in physiological responses when unpredictable or acute stressors occur (e.g., predation threat, severe weather events) (Romero et al., 2009). One of the primary physiological mediators in maintaining homeostasis are glucocorticoids (GCs) (Romero, 2002; Sapolsky et al., 2000). Along with a suite of other hormones, these steroid hormones are released from the adrenal cortex into the bloodstream, when the hypothalamic-pituitary-adrenal (HPA)-axis is activated in response to stressors (Sapolsky et al., 2000). GCs promote the mobilisation of energy needed to respond to the stressor and suspend processes that are not essential for immediate survival such as tissue repair, reproduction, or growth (Sapolsky et al., 2000), allowing the organism to cope and return to homeostasis (Romero and Wingfield, 2015). The prolonged or chronic activation of the HPA-axis (persisting for days or weeks) can have negative consequences as the physiological mediator itself (e.g., GCs) begins to disrupt normal bodily functions, including e.g., immune suppression, loss of muscle mass, reduced cognitive function, and impotence (Kirby et al., 2009; Korte et al., 2005; Sapolsky, 2002; Spencer et al., 2010). In these pathological cases, the organism moves from what is considered the adaptive "predictive" and "reactive" homeostasis range (the normal reactive scope) into "homeostatic overload" (Romero et al., 2009).

Researchers have been linking variation in GCs to stressors in wild animals since the 1970s (Romero, 2002). However, studies linking increased GCs to negative fitness outcomes (the “Cort-Fitness Hypothesis”) in the wild are inconclusive, finding either positive, negative, or no correlation (Bonier et al., 2009). Therefore, recent reviews highlight the importance of moving away from the view that GCs are detrimental “stress hormones” and moving toward the view that GCs serve an adaptive function first and foremost and are critical for coping with environmental challenges (Beehner and Bergman, 2017; Boonstra, 2013; MacDougall-Shackleton et al., 2019). As the HPA-axis can be activated by several stressors simultaneously, and is further influenced by individual characteristics, e.g., genetics, age, sex, reproductive state, life-history stage (Anestis, 2010; Creel et al., 2013), circulating GCs can be the additive and interactive result of multiple stressors (McEwen and Wingfield, 2003). As such, disentangling effects of interest can be challenging. Consideration of the exogenous (e.g., environmental and stable social factors) and endogenous (e.g., reproductive state and circadian rhythms) effects operating at any given time is needed to interpret variation in GCs. Below I discuss some of the main stressors considered in the study of stress physiology in wild animals.

Climatic conditions can exert both direct (e.g., physical weather conditions) and indirect (e.g., resource availability) pressures which vary across seasons and impact HPA-axis activity (de Bruijn and Romero, 2018). Rainfall and temperature are frequently considered in the context of physiological responses to seasonal changes in vertebrates (de Bruijn and Romero, 2018). Moreover, variation in day length, particularly at high latitudes where day length varies drastically throughout the year (Wielgolaski and Inouye, 2003) can be an important parameter in this context (Borniger et al., 2017). Direct impacts of temperature relate to thermoregulation costs, with low temperatures being linked to ‘cold stress’ across several taxonomic orders (primates: Beehner and McCann, 2008; Weingrill et al., 2004, galliformes: Shipley et al., 2019, passerines: Cīrule et al., 2017, ungulates: Huber et al., 2003, carnivores: Naidenko et al., 2011, rodents: Sheriff et al., 2012) and high temperatures being linked to ‘heat stress’ (primates: Carnegie et al., 2011; Gesquiere et al., 2008; Wessling et al., 2018, passerines: Fairhurst et al., 2012, ungulates: Millspaugh et al., 2001, lagomorphs: Wilkening et al., 2015). Heavy precipitation (e.g., during storms) can also lead to increased GCs (ungulates: Huber et al., 2003; Meza-Herrera et al., 2007, passerines: Astheimer et al., 1995, petrels: Smith et al., 1994), which may be linked to the increased metabolic cost or a fight-and-flight response to cope with the inclement weather (de Bruijn and Romero, 2013). The length of time an animal is exposed to light (photoperiod), which in a natural environment would be dictated by day length, can also have direct impacts on HPA-axis activity (Borniger et al., 2017). Increased photoperiod is linked to increased GCs in captive animals (Audet et al., 1986; Genin and Perret, 2000) and in humans (Vondrašová et al., 1997). In the wild, increased day length is likely an anticipatory cue for upcoming environmental challenges or of life-history events necessitating preparatory action (Borniger et al., 2017; Genin and Perret, 2000).

While extreme weather is usually directly linked to increases in GCs (see above), weather can also have indirect effects on GCs (de Bruijn and Romero, 2018) by influencing food abundance (Chung et al., 2013; Fay et al., 2000; Hay, 1990). In locations where rainfall is closely correlated with food availability, rain has been linked to lower GCs in e.g., primates (Gesquiere et al., 2011b; Pride, 2005), elephants (Foley et al., 2001) and ungulates (Pereira et al., 2006). In contrast, drought induced food scarcity may require increased time allocated to finding (Gesquiere et al., 2008; Iwamoto and Dunbar, 1983; Sapolsky, 1986) and/or to processing food (Alberts et al., 2005; van Doorn et al., 2010) and has been linked to increased GCs in primates (Gesquiere et al., 2008; Sapolsky, 1986), elephants (Foley et al., 2001) and passerines (Schoech et al., 2009). Day lenghth can constitute an indirect stressor for diurnal species by reducing the time window (i.e., daylight hours) during which animals can be active and meet energetic requirements (Gaynor et al., 2004; Hill et al., 2003). Unlike the direct effect of photoperiod on GCs, the indirect relationship between day length and GCs is negative, with longer days being associated with lower GCs (Weingrill et al., 2004).

In many animals, different reproductive stages are associated with changes in GCs, with increases often reflecting the energetic (Crespi et al., 2013; Romero, 2002) and social (Creel et al., 2013) challenges linked to reproductive function and behaviour. Moreover, for female mammals, reproductive state also affects GCs through endogenous changes (von der Ohe and Servheen, 2002).

Pregnancy is associated with an increase in GCs in several mammalian orders (lagomorphs: Scarlata et al., 2011, rodents: Dantzer et al., 2010, carnivores: Dloniak, French, & Holekamp, 2006, primates: Weingrill et al., 2004) and is essential for foetal development (Edwards and Boonstra, 2018). This increase in circulating GCs during gestation appears to be caused by either an increase in maternal or foetal GC production or by a decrease in maternal corticosteroid-binding globulin (CBG) production (reviewed in Edwards and Boonstra, 2018). Additionally, pregnancy can be associated with exogeneous stressors arising from reproductive conflict with same-sex conspecifics (Young et al. 2006) or from food scarcity during the energetically costly stages of gestation (Wasser et al., 2017) leading to further increased GCs.

After parturition, GC levels generally decrease but can still remain relatively elevated compared to cycling or non-reproductive females (Reeder and Kramer, 2005). This might be due to the energetic cost related to lactation (Barrett et al., 2006; Coehlo, 1986; Gittleman and Oftedal, 1987; Gittleman and Thompson, 1988), particularly when food availability is low (Emery Thompson et al., 2010; Foerster et al., 2012). Moreover, lactating females provide care for dependent offspring who are susceptible to predation (Linnell et al., 1995), leading to higher maternal GCs under increased predation pressure (Monclús et al., 2011; Sheriff et al., 2010). Conspecifics can also pose a threat to offspring, particularly in mammals where infanticide occurs (Agrell et al., 1998; Palombit et al., 1997), which can translate to increased GCs when infanticide risk is high (Engh et al., 2006b; Weingrill et al., 2004).

Finally, while cycling females usually have lower baseline GCs compared to pregnant females (Gesquiere et al., 2008; Setchell et al., 2008) and sometimes also compared to lactating females (Hoffman et al., 2011; Hunt et al., 2006; Weingrill et al., 2004), they do experience exogeneous stressors related to their reproductive state. Same-sex (Stockley & Bro-Jørgensen 2011) and opposite-sex conspecifics (Smuts and Smuts, 1993) can present a physical threat. Monopolisation of mating opportunities via male harassment and forced copulations when females are sexually receptive (Van Schaik et al., 2004) can result in injury or death (Smuts and Smuts, 1993) and have been linked to increased GCs in cycling females (Muller et al., 2007; Rodrigues et al., 2015). Moreover, female-female competition over breeding opportunities (Clutton-Brock and Huchard, 2013) can lead to increased aggression towards sexually receptive females (Huchard and Cowlishaw, 2011). While not in this context, increased rates of aggression between conspecifics have been linked to increased GCs (Wittig et al., 2015).

In group-living animals, the social environment forms a source of exogenous stressors (Creel et al., 2013). Stable social groups often form dominance hierarchies (Abbott et al., 2003; Creel, 2005; Lahti, 1998) which typically entail the lower ranking individuals having restricted access to resources, frequent exposure to physical and social stressors, and less opportunity for support compared to higher ranking individuals (Murray et al., 2007; Snyder-Mackler et al., 2016; Vogel, 2005). In this scenario, GCs would be predicted to be negatively correlated with dominance rank (i.e., the 'stress of subordination hypothesis': Creel, 2001; Mooring et al., 2006) and has been noted in primates (Manogue et al., 1975; Virgin Jr and Sapolsky, 1997), rodents (Blumstein et al., 2016) and elephants (Foley et al., 2001). However, in many group-living animals, attaining and maintaining dominance status is costly, resulting in higher GCs (i.e., the 'stress of domination hypothesis': Creel, 2001; Mooring et al., 2006), as shown in carnivores (Carlson et al., 2004; Sands and Creel, 2004), ungulates (Mooring et al., 2006) and primates (Gesquiere et al., 2011a). Finally, rather than being species-specific, the costs and benefits, and hence the physiological stress-levels, associated with hierarchical positioning can be context dependent (Goymann and Wingfield, 2004). For example, in primates, periods of rank-instability can flip the relationship between GCs and rank (Cavigelli and Caruso, 2015) with high-ranking individuals having lower GCs during stable periods and higher GCs during unstable periods (Bergman et al., 2005; Setchell et al., 2010). Moreover, in primates, the "traditional assumption" for low social status only holds true when low-ranking individuals receive less social support (e.g., coalition support, grooming) and are exposed to higher rates of aggression compared to higher-ranking individuals (reviewed by Abbott et al., 2003).

The ability to quantify GCs non-invasively in wild animals from urine and faecal samples has made it possible to monitor hormone levels without disrupting the study animals (Palme, 2019; Sheriff et al., 2011). However, obtaining hormone measurements from waste products introduces methodological considerations, both in terms of establishing the time-lag between the endocrine response and hormone excretion as well as choosing the sample type that is best suited to address the research question (Touma and Palme, 2005). GC production is inherently dynamic with temporal profiles that show peaks and troughs (Sapolsky et al., 2000). Whereas blood and saliva are a near-instantaneous representation of this physiological stress response, linking faecal GC metabolite and urinary GC metabolite measurements (hereafter referred to as fGCs and uGCs respectively) to behavioural and environmental data requires taking into account a time-lag (Heistermann, 2010; Touma and Palme, 2005).

The temporal nature of the stressor may also determine whether faecal or urine samples are the appropriate sample type to measure HPA-axis activity. fGCs capture the cumulative secretion of GCs over longer time periods (e.g., many hours/days) (Behringer and Deschner, 2017), making them a good measure of long-term stressors (Touma and Palme, 2005; Wielebnowski and Watters, 2007), as has been demonstrated by empirical studies linking fGCs to environmental factors (Gesquiere et al., 2008), reproductive state (Weingrill et al., 2004) and dominance rank (Bergman et al., 2005). Conversely, while urine is also a cumulative measure, it represents shorter time-windows (GC secretion over a few hours) (Behringer and Deschner, 2017), and is therefore more likely to capture the effect of stressors such as intra- and inter- group aggression (Smith and French, 1997a; Wittig et al., 2015; Wittig et al., 2016) or the effect of being handled in captivity (Smith and French, 1997a). uGCs also capture circadian patterns, i.e., the “cortisol awakening response” (Fries et al., 2009) which manifests itself in higher GCs upon waking with a gradual decrease throughout the day. This diurnal pattern has been documented in uGCs across several orders (primates: Czekala, Lance, & Sutherland-Smith, 1994; Muller & Lipson, 2003, ungulates: Hay, Meunier-Salaün, Brulaud, Monnier, & Mormède, 2000, elephants: Brown, Kersey, Freeman, & Wagener, 2010). Therefore, to measure the effect of long-term stressors without the ‘noise’ of circadian patterns in uGCs, the time at which the urine sample is collected needs to either be kept consistent (e.g., captive studies: Hay et al., 2000; Owen et al., 2005; Smith and French, 1997b; Ziegler et al., 1995) or accounted for in statistical analyses (e.g., studies on wild animals: Emery Thompson et al., 2010; Muller and Wrangham, 2004; Tkaczynski et al., 2020; Wessling et al., 2018). fGCs tend to not be affected by circadian rhythms, particularly in large-bodied animals (reviewed by: Behringer and Deschner, 2017; Heistermann, 2010).

Simultaneous measurements of uGCs and fGCs have been conducted in laboratory settings to determine excretion routes and time lags in a range of species (Fanson et al., 2013; Hirschenhauser et al., 2012; Medger et al., 2018; Medger et al., 2020; Palme et al., 1996; Schatz and Palme, 2001; Scheun et al., 2018; Teskey-Gerstl et al., 2000), including primates (Bahr et al., 2000; Chen et al., 2017; Freeman et al., 2018; Paramastri et al., 2007; Wasser et al., 2000). However, a direct comparison of the predictors of fGCs and uGCs in a wild population has not yet been conducted.

In this chapter, I assess the effects of (i) environmental seasonality (i.e., periodic and regular changes in climatic patterns such as temperature, precipitation and day length over the course of a year; Williams et al., 2017), (ii) female reproductive state and (iii) dominance rank on both fGCs and uGCs in a troop of wild chacma baboons on the Cape Peninsula, Western Cape, South Africa. As our study was conducted in the wild, sample collection occurred ad libitum throughout the day rather than at a set time, which introduces the effect of circadian rhythms on uGCs (see above). This could mask the effect of long-term stressors (see discussion in Muehlenbein et al., 2004), such as the ones tested in this chapter. However, as I control for sample collection time in the statistical models, it is possible that uGCs may capture long-term stressors (see e.g., Muller et al., 2021; Touitou et al., 2021).

(i) On the Western Cape, winter is characterised by high primary production, while summer is marked by lower food abundance (Hill, 1999; Hill et al., 2003; van Doorn et al., 2010). However, winter is also associated with lower temperatures, higher rainfall, and shorter days, imposing both thermoregulatory costs as well as compressed time budgets within which energetic requirements must be met (Barrett et al., 2006; Hill et al., 2003). In line with previous work on chacma baboons in this region, which found "harsher" winter months to be associated with higher fGCs than the summer months (Chowdhury et al., 2021; Weingrill et al., 2004), I predict a gradual decrease in fGCs from winter into summer months (i.e., from July to November in our study). uGCs have not been linked to environmental factors in baboons, but evidence from other primates suggests that seasonal food scarcity (Emery Thompson et al., 2010; Muller and Wrangham, 2004) and temperature extremes (Touitou et al., 2021; Wessling et al., 2018) can be associated with increased uGCs, suggesting that seasonal challenges reflected fGCs, may be reflected in uGCs in as well.

(ii) While environmental seasonality is evident, chacma baboons on the Western Cape are non-seasonal breeders (Clarke et al., 2012), allowing to investigate the effect of reproductive state and seasonal factors simultaneously. Higher fGCs have been associated with pregnancy across primates (Bardi et al., 2003; Cavigelli, 1999; Gesquiere et al., 2008), and wild chacma baboons specifically (Weingrill et al., 2004), thus I predict higher fGCs in pregnant compared to cycling females. While generally a return to baseline GCs is expected postpartum (Beehner et al., 2006b; Gesquiere et al., 2008), fGCs can remain elevated during lactation when the risk of infanticide is high (Weingrill et al., 2004). As the study period was marked by dominance rank instability (*sensu* Bergman et al., 2005), resulting in injury and death of infants, I predict fGCs in lactating females to be comparable to pregnant females due to this psychological stressor. Reproductive state and uGCs have not been linked in wild baboons, but work on captive female baboons showed that late stages of pregnancy are associated with elevated uGCs (French et al., 2004).

(iii) Recent work investigating the physiological correlates of dominance rank in female baboons, found that low-ranking females had higher fGCs than high-ranking females (Levy et al., 2020). However, this effect was only detectable over a long period (18 years), suggesting the effect of female rank is likely masked by variation in GCs driven by other factors in less longitudinal datasets (Levy et al., 2020), as corroborated by many studies finding no rank effect on fGCs in female baboons (Beehner et al., 2005; Engh et al., 2006b; Weingrill et al., 2004). Moreover, females inherit their rank which does not necessitate physical contest and is less likely to impact fGCs (Levy et al., 2020), in contrast to males who compete for dominance rank which impacts GCs (Bergman et al., 2005; Gesquiere et al., 2011a; Sapolsky, 1992). Considering that the study was conducted over a relatively short time-window and the adult composition in our study troop was mostly female (n=19 females, n=2 males), representing the majority of the collected samples (n=15 females), I test for the effect of rank across sexes and predict that any effect of rank will not be detectable in fGCs. For the reasons outlined above, I also do not predict dominance rank to be reflected in uGCs. While low-ranking individuals are more likely to be subjected to aggressive interactions (Barrett et al., 2002) which can be reflected in uGCs (e.g., Wittig et al., 2015), this analysis focusses on rank as a long-term stressor, rather than investigating the effects of rates of received aggression (e.g., Muller and Wrangham, 2004)

Methods

Study site and troop

The study was conducted on a troop of wild chacma baboons consisting of approximately 50 individuals (n=21 adults) in Da Gama Park, Western Cape, South Africa (-34.15562°N, 18.39858°E) between July and November 2018. Faecal and urine samples were collected from n=17 adult baboons of known identity (n= 15 females, n=2 males). A trapping event took place between 25/07/18 - 02/08/18 during which the baboons were fitted with tracking collars as part of a larger project, allowing for a biological validation of our faecal GC assay following a known stressor (e.g., Hämäläinen et al., 2014; Palme, 2005; Suedkamp Wells et al., 2003; Wasserman et al., 2013). Baboons were captured using baited cage-traps (fruit, vegetables, and corn) in collaboration with Human Wildlife Solutions (HWS; https://hwsolutions.co.za), following established protocols. Permission to conduct this work was granted by Swansea University's Ethics Committee (IP-1314-5) and local authorities (Cape Nature, permit number: CN44-59-6527) and SANparks, permit number: CRC/2018-2019/008 – 2018/V1). CITES approved export of samples (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: 0004549-2, -34.1480°N, 18.3190°E).

Faecal sample collection and processing

N=602 faecal samples were collected (mean±SD samples per individual: 35±11; n=17) opportunistically throughout the day. Faecal samples were stored in 40ml screw-top plastic pots. To achieve even distribution of hormones, large faecal samples were homogenised before being sub-sampled (Palme, 2005). The containers were labelled in the field (date, time, individual ID, sub-sample or whole-sample, and potential contamination with urine). Samples were kept on cool blocks in a cool bag throughout the day and were frozen at -20°C at the research house until further processing at the University of Cape Town (UCT).

Faecal samples were freeze-dried at -45°C for a minimum of 24 hours in either a New Brunswick (New Brunswick Scientific Co., Inc., New Jersey USA) or Scanvac CoolSafe (LaboGene ApS) freeze-dryer to remove the moisture at UCT. Samples were stored at -20°C until 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=602) was extracted with 80% methanol (Palme et al., 2013). Faecal suspensions were vortexed (1500 rpm, 10 min) in a TT-2500-VM Multi-Tube Vortex Mixer (Hercuvan Lab Systems SDN. BHD.) and centrifuged (3000 rpm, 10 min) in a VWR Mega Start 1.6 centrifuge (VWR), before decanting 1.5 ml into Eppendorf tubes and storing them at -20°C. Prior to hormone analysis, 0.25 ml of the faecal extract were transferred to microcentrifuge tubes and evaporated at -38°C under a stream of nitrogen. The dry tubes were sent to the endocrinology laboratory of the German Primate Centre, Göttingen, Germany for hormone analysis.

Urine sample collection and processing

N=385 urine samples (not diluted with rainwater) were collected (mean±SD samples per individual: 23±4; n=17) opportunistically throughout the day. Depending on the substrate, urine samples were either collected by synthetic swab Salivettes (Starstedt Salivette Cortisol code blue, order number 51.1534.500; n=193 (see Danish et al., 2015 for details) or by pipette, directly transferred into a 2ml Eppendorf tubes (n=192). Specific gravity was measured to correct for urine dilution (see below) (White et al., 2010), using a manual handheld refractometer. After return from the field, urine samples collected by Salivette were centrifuged (3000 RPM, 5 min) and transferred to 2ml safe-lock Eppendorf tubes. All urine samples were stored -20°C at the research house within a maximum of 12 hours of collection and were shipped to Swansea University on dry ice at the end of the field season. Samples were finally stored frozen at -20°C until analysis.

Hormone analyses

Faecal samples

Faecal extracts were analysed for immunoreactive 11β-hydroxyetiocholanolone, a major faecal metabolite of cortisol in primates (Heistermann et al., 2006), including *Macaca assamensis* (Fürtbauer et al., 2014), *Alouatta seniculus* and *Ateles hybridus* (Rimbach et al., 2013), *Pongo abelii* (Nugraha et al., 2017) and *Pan troglodytes*, (Reimers et al., 2007). Samples were diluted 1:50 – 1:300 with assay buffer prior to analysis. Sensitivity of the assay at 90% binding was 0.6 pg/well. Inter-assay coefficients of variation (n=19 plates) were 8.7% (high) and 11.0% (low). All faecal hormone data are expressed as ng/g faecal dry weight.

Urine samples

Urinary cortisol concentrations (uGCs) were quantified using commercial enzyme-linked immunosorbent assay kits (ELISA; IBL, Hamburg, Germany; Cat.-no.: RE52241). The majority of samples were measured undiluted (n=343 samples) and samples with concentrations above the highest standard curve value (>200 ng/ml) were diluted with Standard 0 (1:2-1:10; n= 42 samples). 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). uGC was corrected for specific gravity (SG), i.e., the density of urine relative to the density of distilled water, using the following formula: uGC SG = uGC ng/ml*(SGpop-1)/(SG-1), where SGPop is the mean SG value for the population (1.020) (see e.g., Fürtbauer et al., 2020; Miller et al., 2004). SG corrected uGC values are reported and expressed in ng/ml.

Assessment of female reproductive state

Female reproductive state assessment in our troop has been described previously (Fürtbauer et al., 2020). In brief, n=3 females transitioned from pregnancy to lactation and n=1 was lactating with a black infant throughout the study period. For the remaining n=11 females for whom the reproductive states were uncertain, faecal samples (n=336, mean±SD=30.5±10.6 samples per female) were analysed for progesterone metabolites. The monoclonal antibody (Quidel clone no. 425) cross-reacts with numerous progesterone metabolites, allowing to assess luteal function and pregnancy in various species (Graham et al., 2001), including baboons (Wasser et al., 1988). This analysis showed that n=4 females were acyclic (with brown infants of unknown age), n=1 female was pregnant throughout the study period, and n=6 females were cycling of which n=2 females conceived during the study.

Assessment of dominance rank

Calculation of female dominance rank has been described previously (Fürtbauer et al., 2020). In brief, rank was calculated based on the outcome of dyadic agonistic interactions (displacements, chases, aggressive displays, n=634). Analyses were run using the R packages ‘AniDom’ (Farine and Sánchez-Tójar, 2017) and ‘Compete’ (Curley, 2019) in R Studio (version 1.2.5033). The hierarchy was determined to be very steep (using the randomized Elo-rating method), repeatable (using the ‘estimate_uncertainty_by_repeatibility’ function in AniDom: score of 0.98) and highly linear (using triangle transitivity to assess ‘orderliness’; McDonald and Shizuka, 2013). Ranks were standardized between 0 and 1 (with 0 being the lowest and 1 the highest). In baboon troops, all adult males outrank all adult females (Engh et al., 2009; Silk et al., 2004). For the two males, rank was calculated based on chases and displacements (n=23) of which M1 won 73%. Moreover, M1 associated with the highest-ranking female whose infant received protection from M1 (suggesting his paternity) (Seyfarth, 1978). In this analysis, M1 and M2 were assigned the same standardised rank as F1 and F2 respectively to allow for sex and dominance rank to be included in the same model without causing covariation issues.

Statistical analysis

All analyses were run in R Studio (version 1.2.5033) using the R package ‘lmerTest’ (Kuznetsova et al., 2017). Linear mixed effect models (LMMs) were used to investigate the effect of various predictors on fGCs and uGCs. In all models, fGCs and uGCs were log-transformed to meet normality criteria. To assess whether normality assumptions were met, quantiles from the data were plotted against quantiles of a theoretical normal distribution (R function 'qqnorm') and visually assessed. To establish whether the full model provided a significantly better fit to the null model (which included only the random effects), likelihood ratio tests were used (R function 'anova'). To obtain the conditional and marginal r-squared values, which denote the variance explained by the full model (with random effects) and the variance explained by the fixed effects in the model respectively, the function 'r2_nakagawa' (R package 'performance') was used (Nakagawa and Schielzeth, 2013). Due to some of the samples being collected during the trapping period (see '*Biological validation*' below), introducing an unnatural stressor which may interfere with detecting the effect of the natural baseline predictors tested in this chapter, all analyses (LMM2 – LMM6) were also run with a reduced dataset not including fGCs from the trapping period (+2 days) and uGCs on the day of trapping, respectively. These models obtained comparable results (Table III - S16-20).

While some models (fGCs: LMM4a, LMM2b, LMM2a; uGCs: LMM5a, LMM5b) were run with the same dataset (hereby potentially increasing the Type I error rate; Frane, 2015), multiple testing-adjustments are performed when *different* hypotheses are tested simultaneously (Frane, 2015; Menyhart et al., 2021). Here, the monthly (LMM4a; LMM5a) and seasonal (LMM2b) models are 'coarser' versions of the same hypothesis (i.e., GCs vary due to environmental seasonality), with LMM2a and LMM5b testing whether daily weather parameters (which vary across months/seasons) affect GCs. Hence, LMM2a and LMM5b should be seen as the final models, obtained via the planned investigation of coarser patterns first (LMM4a, LMM2b, LMM5a), rather than a simultaneous investigation of separate hypotheses.

Biological validation

To biologically validate the immunoreactive 11β-hydroxyetiocholanolone assay, I tested for the predicted increase in fGCs in response to trapping (see '*Study site and troop*') (Boonstra et al., 2001; Charpentier et al., 2018; Hämäläinen et al., 2014; Wasserman et al., 2013). First, I used a Wilcoxon signed-rank test on samples collected from n=8 captured individuals to test for an increase in fGCs between "day zero" (day of capture) and "day two" (2 days after capture). The 2-day time lag was based on steroid hormone infusion experiments in captive baboons, where a time lag of hormone excretion was recorded between 24 and 48 hrs with peaks at either 26 or 36.4 hrs (Wasser et al., 2000; Wasser et al., 1994). For one individual for which three samples were collected on “day two”, the average value was used. Second, because the period of trapping likely constituted a stressor for the entire troop (all individuals observed capture of other individuals over the course of the trapping period), I predicted higher fGCs during the trapping period compared to pre- and post-trapping periods. To test this, I used a linear mixed effect model (LMM1), including fGCs data on n= 123 faecal samples from n=17 baboons. Trapping context was included as categorical fixed effect (pre-trapping: the 9-day period before trapping, n=23 samples; trapping: the 9-day trapping period, n=47; post-trapping: the 9-day period after trapping, n=53) to account for the 24-48 hr time lag-time of hormone excretion (see above), the three periods were shifted by +2 days. Based on the results of LMM3 (see *Results*) demonstrating a strong effect of pregnancy on fGCs, I included “pregnant” versus “not pregnant” (including lactating, cycling females, and males) as a categorical fixed effect. Baboon ID and Date were included as random effects. There were insufficient samples to test for the effect of trapping on uGCs.

Predictors of fGCs

The first general predictor model (n=603 samples, n=17 individuals; LMM2a) included: month (July, August, September, October, November), AM/PM (before/after 12PM; to account for potential effects of circadian cortisol rhythms: Coe and Levine, 1995; Fries et al., 2009), sex (male/female; to control for sex-differences in baseline GCs: Touma and Palme, 2005) and urine contamination as categorical fixed effects and standardized dominance rank as a continuous fixed effect. Baboon ID and Date were included as random effects to control for individual differences in fGCs and uneven sampling across time (Schielzeth and Forstmeier, 2009). Weather conditions (rainfall, temperature) differed between months (Fig. III – 2b-d), which motivated the testing of environmental factors at a monthly scale, rather than classifying them into overarching seasons. However, to facilitate discussion and comparison with other studies in this climatic region (Barrett et al., 2006; Fürtbauer et al., 2020; van Doorn et al., 2010; Weingrill et al., 2004), I also ran the same model but with months collapsed into seasons (following Fürtbauer et al., 2020): Winter (July-August), Spring (September-October), Summer (November)

(LMM2b; Table III – S2). Given that contamination with urine could lead to an overestimation of fGCs (Bahr et al., 2000), I included ‘urine contamination’ (n=55 samples) as fixed effect (see LMM2c, Table III – S4) for the same model not including urine contamination, which obtained comparable results).

To test for the effects of female reproductive state, I ran a model (LMM3) including data for females only (n=505 samples, n=15 individuals). I included the same predictors as in LMM2a (dominance rank, month, AM/PM, urine contamination) and added reproductive state (cycling, pregnant, lactating) as an additional categorical fixed effect. Baboon ID and Date were included as random effects.

To establish biologically relevant categorical levels of reproductive state, I tested whether there were statistical differences in uGCs and fGCs between early (±first 3 months) and late (±last 3 months) stages of pregnancy (Weingrill et al., 2004) and between early lactation (infants with black coat between 0-6 months) and late lactation (infants with brown coats between 6-12 months) (Altmann et al., 1977). Late gestation is associated with increased levels of plasma GCs in many mammals (Keller-Wood and Wood, 2001), and is reflected in fGCs (Cavigelli, 1999; Nguyen et al., 2008) and uGCs (Smith and French, 1997b; Ziegler et al., 1995) in non-human primates. Here, the difference between early and late pregnancy was not statistically significant in fGCs or uGCs (fGCs: Table III – S5, uGCs: Table III – S13) and thus “pregnancy” was considered as one category. No statistical difference was found between uGCs or fGCs for females in early or late lactation (fGCs: Table III – S6; uGCs: Table III – S14) and thus “lactation” was considered as one category.

Finally, as this chapter is an exploratory investigation of predictors of variation in fGCs and uGCs, “lactation” may require a different definition based on whether the underlying stressor is hypothesised to be energetic (e.g., Emery Thompson et al., 2010; Foerster et al., 2012) or psychosocial (e.g., Engh et al., 2006b; 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). If increased GCs are linked to the risk of infanticide, the definition should be based on whether the female is still caring for offspring vulnerable to infanticide (social definition). In this study n=2 females were cycling but also had brown infants that were targeted/injured by the beta male (pers. obs.), thereby falling into either the hormonal or social definition depending on which definition is used. Here, I present results using the hormonal definition (for results using the social definition see *Appendix*: fGCs: Table III - S7; uGCs: Table III – S15, findings are comparable)

Due to the results obtained from LMM2a suggesting a gradual decrease in fGCs (Fig. III - 2a) which matched the increase in day length (Fig. III - 2b), I ran another linear mixed model (LMM4a) investigating the effect of more detailed weather parameters on fGCs with the same samples as LMM2a (n=602 samples, n=17 individuals). Specifically, the effect of rain, minimum temperature (°C) and day length (minutes between sunrise and sunset, obtained from www.timeanddate.com) from 2 days prior to sample collection (see '*Biological validation*' and previous studies using the same time-lag in baboons (Bergman et al., 2005; MacLarnon et al., 2015) were included as fixed effects. Minimum temperature was used given that 'cold stress' is more likely than 'heat stress' in this climate (Chowdhury et al., 2021; Weingrill et al., 2004). Rain day was entered as a categorical variable (yes/no), defined as whether it rained during the hours the baboons were not at the sleep site (between 07:00 and 19:00). Based on the results from LMM3, a 2-level factor "pregnant" and "not pregnant" (including lactating and cycling females, and males) was included as a fixed effect. Baboon ID and Date were included as random effects. Considering that climatic factors are expected to co-vary to some extent, I tested for collinearity between predictor variables using Variance Inflation Factors (VIFs) using the R package 'usdm'. No issues of collinearity were found between the three weather parameters: minimum temperature, day length and rain day (maximum VIF = 1.5). Excluding factors with VIF > 3 is considered a stringent approach to rule out collinearity (Zuur et al., 2010).

Predictors of uGCs

The first general predictor model of uGCs (n=385 samples, n=17 individuals; LMM5a, Table III - S10) tested for the effect of sex (male/female), month (July, August, September, October, November) and sample collection method (pipette versus Salivette; as this can affect hormone measurements: Fürtbauer et al., 2020) as categorical fixed effects. Sample collection time (to account for effects of circadian cortisol rhythms in uGCs: Czekala et al., 1994; Muller and Lipson, 2003) and standardized dominance rank were included as continuous fixed effects. Baboon ID and Date were included as random effects.

Secondly, I ran a model (n=385 samples, n=17 individuals; LMM5b, Table III – S12) to test for the effects of daily weather conditions, including minimum daily temperature (°C), total day length (minutes between sunrise and sunset) on the day of sample collection as continuous fixed effects and whether it rained during the daytime (yes/no) as a categorical fixed effect, controlling for sample collection time and method (based on LMM5a) and including Baboon ID and Date as random effects. Based on the outputs of LMM5a and LMM5b, I obtained the final model LMM5c presented here (Table III - 5), keeping the following fixed effect: rain day (yes/no), sample collection time, collection method, dominance rank and sex. Baboon ID and Date were included as random effects.

To test for the effect of reproductive state on uGCs, I ran a model including female samples only (n= 338 samples, n=15 individuals; LMM6). I included dominance rank, collection method, time of collection, and reproductive state (cycling, pregnant, lactating) as fixed effects. I used the hormonal definition (for results using the social definition see Table III - S15; findings are comparable). Baboon ID and Date were included as random effects.

Results

Biological validation

fGCs were significantly higher on “day 2” (mean±SD = 1054±588 ng/g) following trapping (“day zero”; mean±SD = 714±282 ng/g; Wilcoxon signed rank test: Z = -2.41, *p* =0.015, n=8; Fig. III - 1a). During the 27-day period (comprising 9 days pre-trapping, 9 days trapping and 9 days post-trapping), fGCs ranged from 102.1 to 2400 ng/g and fGCs were significantly higher during the 9-day trapping period compared to the post-trapping period, but not the pre-trapping period (Fig. III - 1b; Table III - 1).

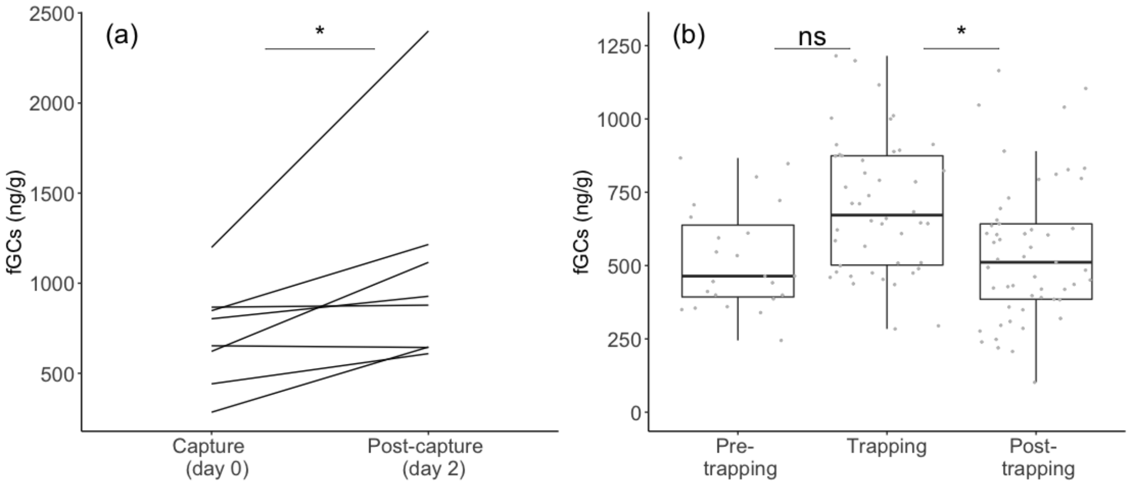


Figure III – 1: Effect of trapping on baboon fGCs (a) Paired comparison of fGCs in n=8 individuals between capture day and 2 days post-capture. **(b)** Effect of trapping period on troop fGCs (n=17 individuals). Note that one outlier is not shown (trapping period; 2400 ng/g; pregnant female (see **(a)**). Significant differences between trapping periods are denoted by: *= *p*<0.01, ns = not significant (*p*>0.05).

Table III – 1: Effect of trapping on baboon fGCs Effects of trapping period (pre, during, post) and reproductive state (pregnant vs. not pregnant) on fGCs (ng/g) for n=17 wild chacma baboons (LMM1). Baboon ID was included as a random effect. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Trapping (pre)*	-0.202	0.122	-1.66	0.11
Trapping (post)*	-0.259	0.107	-2.409	**0.027**
Reproductive state (Pregnant)	0.48	0.147	3.263	**0.004**

**Reference category: Trapping*

Predictors of variation in fGCs

fGCs ranged from 79.7 to 2400.0 ng/g (n= 603 samples). The main model (LMM2a) was significantly different from the null model ($\chi2 = 60.43$, $p < 0.001$). Baboon ID (random effect) was highly significant, indicating consistent individual differences in fGCs ($p<0.001$). Dominance rank and sex had no significant effect on fGCs (Table III - 2). Month had significant overall effect on fGCs ($\chi2 = 52.63$, $p < 0.001$), with a decrease from July to November (Table III - 2; Fig. III - 2a and see Table III – S3a-d in *Appendix* for models with the other months as reference). When grouping months by seasons, fGCs were significantly higher in winter compared to spring and summer, and fGCs were significantly higher in spring than summer (Table III – S2: LMM2b).

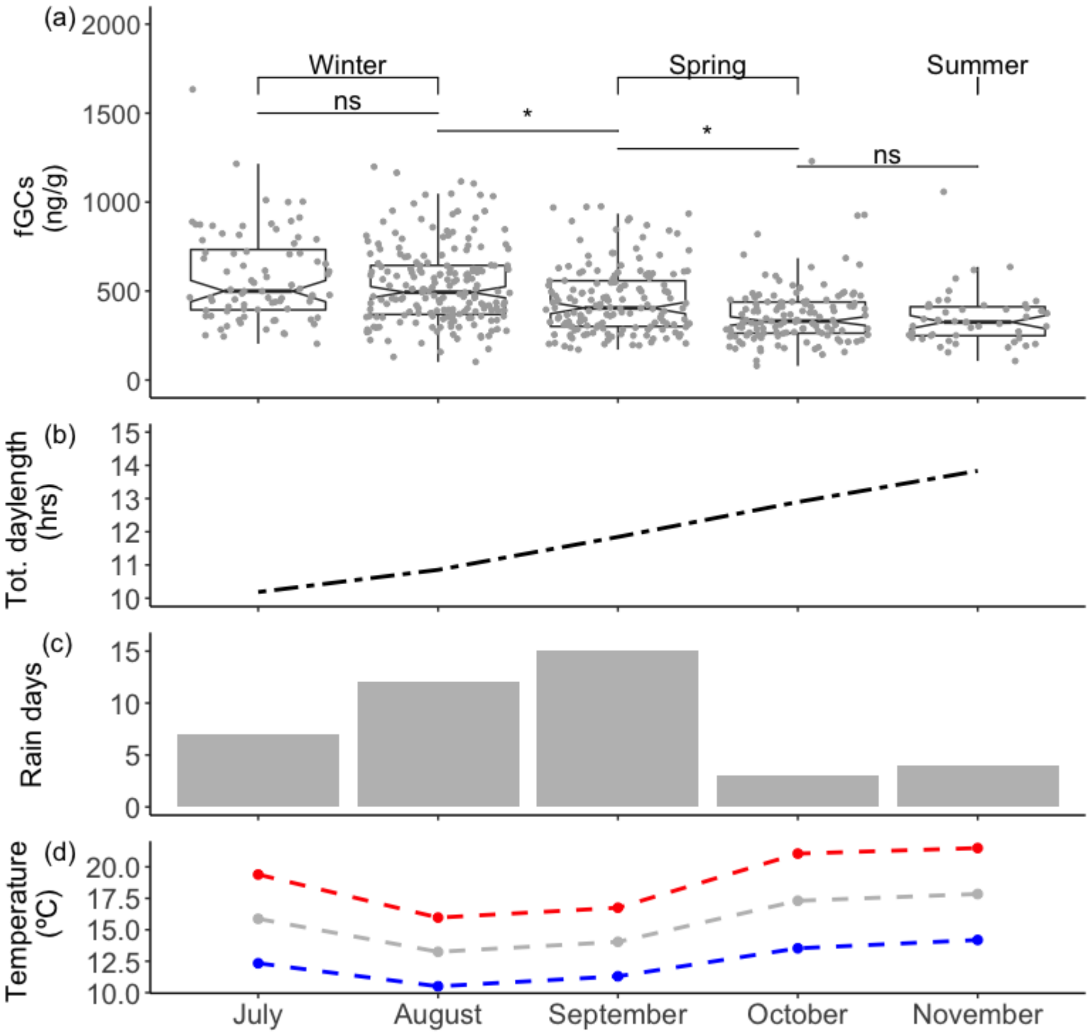


Figure III – 2: Monthly variation in fGCs and weather (a) Effect of month on fGCs in wild chacma baboons (n=17 individuals, n=602 samples). Note that non-transformed data are shown. The boxes show the interquartile range of fGC concentrations (i.e., between the 1st and 3rd quartile), the lines denote the median fGC concentration, with the notches showing the 95% confidence interval around the median. The upper and lower whiskers denote the maximum and minimum value respectively. Significant differences between months are denoted by: * = $p<0.01$, ns = $p>0.05$. Grey dots represent real data (note that one data point is not shown from August, fGC measure from a pregnant female: 2400 ng/g). **(b-d)**: Variation in environmental factors, including **(b)** mean monthly day length (hours), **(c)** number of rain days, **(d)** minimum (blue), mean (grey), and maximum (red) monthly temperatures (°C) across the study months.

Table III – 2: Main fGCs model Effects of sex, dominance rank, month, time of day (AM/PM) and urine contamination (yes/no) on fGCs (ng/g) for n=603 samples from n=17 wild chacma baboons (LMM2a). Baboon ID and Date were included as random effects. Significant effects are in bold. The fixed effects in LMM2a explain 14.9% of the variance in fGCs, the full LMM2a (with random terms) explains 54.4% of the variance

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	0.128	0.18	0.712	0.482
Dominance rank	0.025	0.196	0.132	0.897
Month (August)*	-0.058	0.068	-0.853	0.396
Month (September)*	-0.247	0.07	-3.51	**<0.001**
Month (October)*	-0.419	0.07	-5.941	**<0.001**
Month (November)*	-0.469	0.085	-5.551	**<0.001**
AM/PM (PM)	0.04	0.031	1.314	0.189
Urine contamination (Y)	0.121	0.049	2.487	**0.013**

**Reference category: July*

fGCs were significantly higher in pregnant females compared to cycling and lactating females (Table III - 3, Fig. III - 3; LMM3: full versus null model: $\chi2 = 158.95$, $p < 0.001$). No significant differences in fGCs were found between cycling and lactating females (estimate±se = 0.08±0.1, t-value=0.89, *p*=0.383; Fig. III - 3).

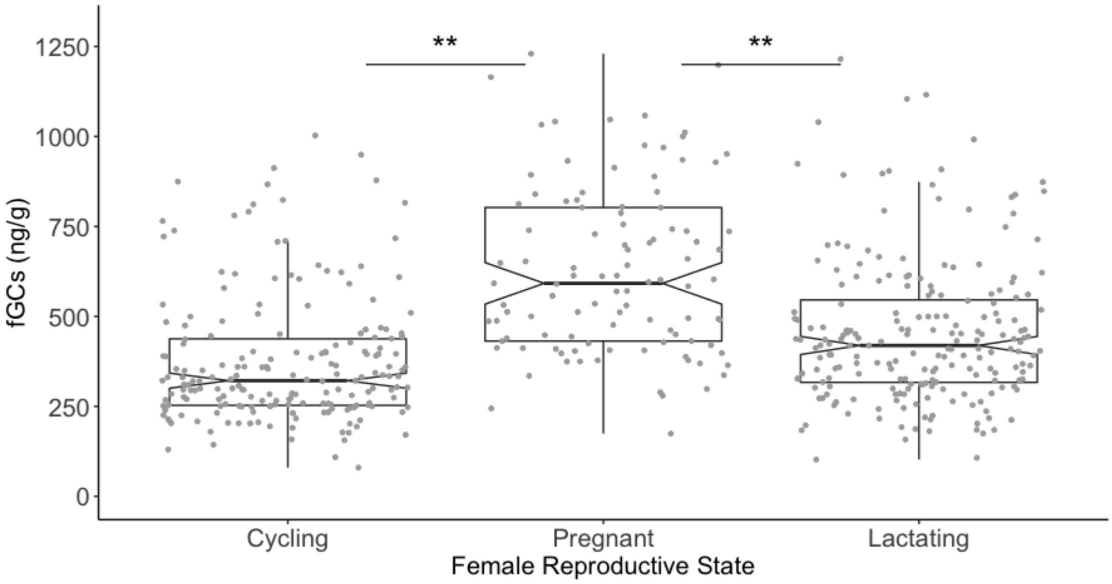


Figure III – 3: Effect of female reproductive state on fGCs fGCs (ng/g) for n=15 wild female chacma baboons. Significant differences between months are denoted by: ** = *p*<0.001. Grey dots represent real data (two data point are not shown from one lactating female (1633.6 ng/g) and one pregnant females (2400 ng/g)). The boxes show the range of fGC concentrations between the 1st and 3rd quartile, the line denotes the median fGC concentration, with the notches showing the 95% confidence interval around the median. The upper and lower whiskers denote the maximum and minimum value respectively.

Table III – 3: Female reproductive state fGCs model Effects of dominance rank, month, reproductive state, time of day (AM/PM) and urine contamination (yes/no) on fGCs (ng/g) for n=506 samples from n=15 female chacma baboons (LMM3). Baboon ID and Date were included as random effects. Significant effects are in bold. The fixed effects in LMM3 explain 29% of the variance in fGCs, the full LMM3 (with random terms) explains 44.8% of the variance.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Dominance rank	0.123	0.153	0.807	0.436
Month (August)*	-0.133	0.072	-1.842	0.069
Month (September)*	-0.324	0.074	-4.364	**<0.001**
Month (October)*	-0.494	0.075	-6.549	**<0.001**
Month (November)*	-0.576	0.091	-6.305	**<0.001**
Reproductive state (Lactating)*	-0.467	0.074	-6.293	**<0.001**
Reproductive state (Cycling)*	-0.395	0.081	-4.848	**<0.001**
AM/PM (PM)	0.054	0.033	1.632	0.106
Urine contamination (Y)	0.119	0.049	2.429	**0.015**

**Reference category: July*
***Reference category: Pregnant*

LMM4a was significantly different from the null model ($\chi2$ = 107.33, *p*<0.001). fGCs were significantly positively correlated with day length (Table III - 4). Minimum temperature and rain days did not predict fGCs (Table III - 4).

Despite the low VIF (see *Methods*), there was a significant correlation between minimum temperature and day length (Pearson correlation r = 0.52, *p*<0.001), which motivated the testing of the model with either "day length" (LMM4b; Table III – S8) or "minimum temperature" (LMM4c; Table III – S9). LMM4c showed that low temperatures were associated with higher fGCs, however comparing these models showed that the model with day length was a significantly better fit ($\chi2$ = 48.464, *p*<0.001).

Table III – 4: Weather fGCs model Effects of rain day (yes/no), minimum temperature and day length on fGCs (ng/g) for n=603 samples from n=17 chacma baboons (LMM4a). Urine contamination (yes/no) and reproductive state (pregnant vs. non-pregnant) were controlled for based on LMM2a and LMM3. Baboon ID and Date were included as random effects. Significant effects are in bold. The fixed effects in LMM4a explain 25.7% of the variance in fGC, the full LMM4a (with random terms) explains 55.2% of the variance.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Rain day (Y)	-0.027	0.047	-0.561	0.577
Minimum Temperature (°C)	0.009	0.011	0.835	0.406
Day length (hrs)	-0.168	0.021	-8.128	**<0.001**
Reproductive state (Pregnant)	0.406	0.061	6.663	**<0.001**
Urine contamination (Y)	0.124	0.05	2.64	**0.009**

Predictors of variation in uGCs

uGCs ranged from 2.58 to 1007.36 ng/ml (n= 385 samples). The main model (LMM5c) was significantly different from the null model ($\chi2$ = 68.685, *p*<0.001). Time of collection had a significant effect on uGCs (with higher uGCs recorded at earlier times; Table III - 5, Fig. III - 4). uGCs were significantly lower in samples collected with Salivettes compared to pipettes (Table III - 5) and uGCs were significantly higher on rain days (Table III - 5). Sex and rank did not predict uGCs (LMM5c, Table III - 5). Female reproductive state did not predict uGCs (LMM6, Table III - 6).

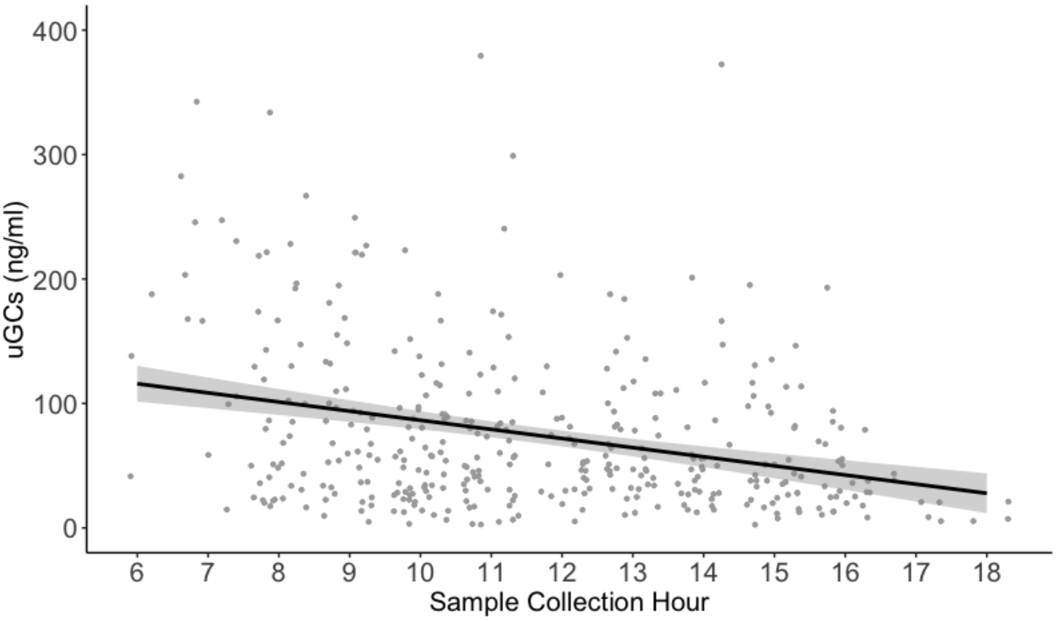


Figure III – 4: Effect of sample collection time on uGCs uGCs (ng/ml) in wild chacma baboons (n=17). Note that four data points are not shown (>500 ng/ml; collected before 8:00). Dots present real datapoints, the black line is the linear regression line (uGC ~ Time) with 95% confidence intervals in grey.

Table III – 5: Main uGCs model Effects of sex, dominance rank, rain day (yes/no), collection time and method on uGCs (ng/ml) for n=385 samples from n=17 chacma baboons (LMM5c). Baboon ID and Date included as random effects. Significant effects are in bold. The fixed effects in LMM5c explain 14.5% of the variance, the full model (with random terms) explains 43.9% of the variation.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	-0.22	0.439	-0.502	0.624
Dominance rank	0.416	0.412	1.011	0.329
Rain day (Y)	0.232	0.106	2.196	**0.032**
Collection time (hour)	-0.126	0.015	-8.3	**<0.001**
Collection method (Salivette)	-0.219	0.081	-2.7	**0.007**

Table III – 6: Female reproductive state uGCs model Effects of dominance rank, rain day (yes/no), reproductive state, collection time and method on uGCs (ng/ml) for n=15 female chacma baboons (LMM6), n=338 samples. Baboon ID and Date included as random terms.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Dominance rank	0.467	0.466	1.002	0.341
Rain day (Y)	0.249	0.112	2.221	**0.031**
Reproductive state (Cycling)*	-0.0632	0.217	-0.292	0.771
Reproductive state (Lactating)*	-0.147	0.208	-0.705	0.483
Collection time (hour)	-0.115	0.016	-7.044	**<0.001**
Collection method (Salivette)	-0.223	0.085	-2.607	**0.01**

**Reference category: Pregnant*

Discussion

This chapter set out to determine the main predictors of fGCs and uGCs in a troop of wild chacma baboons. HPA-axis activity can be stimulated simultaneously by a range of stressors and identifying key drivers can be challenging (Romero, 2002). Here, I consider factors known to impact GCs that relate to the physical and social environment, and to endogenous physiological changes associated with female reproductive state. Month was an important predictor of fGCs, with fGCs gradually decreasing from winter to summer months (July-November). Further investigation into environmental parameters revealed that day length was the most important driver of this variation in fGCs. uGCs, in contrast, did not show seasonal variation but were higher on rainy days. Pregnant females had higher fGCs than lactating and cycling females, whereas uGCs did not differ significantly between reproductive stages. As expected, the circadian pattern in cortisol (peak in the morning followed by a gradual decrease throughout the day; ‘cortisol awakening response’; Fries et al., 2009) was reflected in uGCs but not in fGCs. I did not find an effect of dominance rank on either fGCs or uGCs. Overall, these findings are in line with previous work on female chacma baboons on the Western Cape, where day length and reproductive state were also the most important predictors of fGCs (Weingrill et al., 2004). I discuss each finding in detail below.

Seasonal changes in GCs are found across vertebrate species (Romero, 2002), either through environmental conditions imposing direct stressors (e.g., thermoregulatory) or indirect stressors through their effect on food availability (de Bruijn and Romero, 2018).

The former case, where GCs have been directly linked to weather conditions, is usually described for animals that experience extreme low (Astheimer et al., 1995; Beehner and McCann, 2008; Huber et al., 2003) or high (Gesquiere et al., 2008; Wessling et al., 2018; Wilkening et al., 2015) temperatures and rainfall (for additional references see *Introduction*). In less extreme environments, a direct link between temperature and/or rainfall and GCs is usually absent (Crockford et al., 2008; Girard-Buttoz et al., 2009). Alternatively, HPA-axis activity can be influenced indirectly by environmental factors which drive resource availability (de Bruijn and Romero, 2018). Periods marked by low food availability may require increased efforts to meet energetic demands (Gesquiere et al., 2008) or metabolic adjustments to cope with reduced food intake (Lewanzik et al., 2012), reflected in increased GCs. For animals living at high latitudes, seasonal changes in day length can pose an environmental stressor by limiting the time window within which they can be active (Gaynor et al., 2004; Hill et al., 2003; Weingrill et al., 2004).

As predicted, fGCs decreased gradually from winter to summer months and this was likely driven by increases in day length. Winter on the Western Cape is typically characterised by wet and cold conditions (Hill et al., 2003) which can impose thermoregulatory costs and increase fGCs (e.g., in Geladas: Beehner and McCann, 2008). However, during this study period, spring (September) was marked by the highest rainfall (60.8 mm; 15 rain days) and had minimum temperatures (7.9°C) similar to those recorded in the prior winter months (July: 9°C; August: 7.8°C; Fig. III – 2d). Nevertheless, baboons had lower fGCs in September compared to July and August, suggesting the drivers were unlikely to be rain or temperature. Instead, the gradual decrease in fGCs between July and November was associated with increasing day length, which is in line with previous work on baboons in the Western Cape (De Hoop), where day length (and minimum temperature) predicted fGCs (Weingrill et al., 2004). In the De Hoop analysis, minimum temperature and day length were highly correlated, preventing the authors from disentangling the effects. While the present study does not entirely rule out the effect of temperature, the low collinearity (VIF < 1.5) between temperature and day length allowed the inclusion of both terms in the model, revealing the importance of day length over temperature. It is possible that thermo-regulatory costs are less important in our troop. Although both studies took part on the Western Cape, temperature extremes differ between the sites. The minimum temperature reported for the De Hoop field site (3°C) is considerably lower than the one recorded at our field site during the study period (7.8 °C). Moreover, the use of urban sleep sites (see below) may buffer against the effect of cold nights in the winter, perhaps reducing the direct thermo-regulatory effects on fGCs in our troop.

While seasonal changes in fGCs could be linked to changes in food availability, this seems unlikely in the present study. The seasonal variation in food availability on the Western Cape (Hill et al., 2003) is not as extreme as documented for baboons living in desert (Hamilton, 1985) or savannah habitats (Altmann, 1998), where increased fGCs during drought are likely linked to food deprivation (Gesquiere et al., 2008). Work on our troop during the same study period showed that uCP levels (a non-invasive marker of energy balance in primates; Deschner et al., 2008; Thompson and Knott, 2008) were lowest during spring compared to winter and summer (which were comparable), suggesting spring to be more energetically challenging (Fürtbauer et al., 2020). Unlike fGCs, uGCs did not show any seasonal pattern (Table III – S10-11), nor was there an effect of minimum temperature or day length on uGCs (Table III – S12). While these weather parameters can present physiological challenges, temperature and day length do not tend to fluctuate drastically on an hourly basis, which is the time frame that would be reflected in uGCs (Behringer and Deschner, 2017). Conversely, rain showers can occur abruptly, and days with rain did have a weak effect on uGCs with higher uGCs on rainy days (Table III – 5). This could indicate a thermo-regulatory cost of rainfall, as has been suggested for other primates (Foerster et al., 2012).

Alternatively, the negative relationship between fGCs and day length, as well as uGCs and rain days, may point towards an indirect environmental stressor, i.e., time constraints on activity budgets (*sensu* Dunbar et al., 2009). For diurnal primates, seasonal variation in day length has implications for the amount of time that can be devoted to four essential activities: feeding, moving, resting and grooming (Agetsuma and Nakagawa, 1998; Lawes and Piper, 1992; Lewis et al., 2004; van Doorn et al., 2010), which are mutually exclusive and hence require trade-offs (Dunbar et al., 2009). For Cape chacma baboons, who experience four hours of difference in day length between summer and winter (Hill et al., 2003), winter imposes a temporal bottleneck. This was proposed by Weingrill et al. (2004) as an explanation for the heightened levels of fGCs during winter, as baboons spent less time resting on average in winter months compared to summer months. The surplus time in the summer devoted to resting may have facilitated coping with unpredictable stressors (heat, aggressive conspecifics) leading to lower fGCs (Weingrill et al., 2004). Another environmental factor that can constrain time budgets is rain. Similar to how high temperatures can force animals to seek shade at the expense of feeding (Hill, 2006; McFarland et al., 2014), rain may prompt animals to reduce activity (Hanya et al., 2018) and seek shelter (Kennedy, 1970; Proops et al., 2019). In Barbary macaques, rain disrupts usual activity patterns, with increased resting (due to seeking shelter) and decreased time moving or engaging in social behaviour (including grooming) (Majolo et al., 2013). In the present study, uGCs were higher on days where it rained. On these days, rainfall ranged from 0.2 to 14.4 mm (mean±SD 2.69±3.31) per day, which, compared to the aforementioned studies (e.g., max. 117mm/day: Majolo et al., 2013; max. 266/day: Hanya et al., 2018), is not a large amount of rain. However, it may be important to take shelter during rainy days, particularly in the winter, to avoid compounding thermo-regulatory costs (Beehner and McCann, 2008).

The finding of increased fGCs during short days, and increased uGCs during rainy days merits further investigation into activity budgets on these days, to test whether there is a behavioural link between environmentally imposed time constraints and GCs. While grooming is considered a “lower biological priority” which can be reduced when foraging efforts need to be increased (Hill et al., 2003), primates do rely on maintaining social bonds with group-members from which they reap fitness benefits for both themselves and their offspring (Palombit et al., 1997; Silk et al., 2003a; Silk et al., 2010b). Devoting time to grooming is pivotal in maintaining these social bonds (Dunbar, 1991; Lehmann et al., 2007). Moreover, in terms of physiological consequences, grooming has been demonstrated to have alleviating effects on HPA-axis activity, reflected in lower GCs (Engh et al., 2006a; Fürtbauer et al., 2014; Shutt et al., 2007; Wittig et al., 2008; Wittig et al., 2016). Previous work on the Western Cape found that resting and grooming were a negative function of the other activities (Hill et al., 2003), suggesting that time spent on both activities are determined by how much time is left after foraging demands are met (Dunbar, 1992). Contrary to the findings from Weingrill et al. (2004), another study on the Cape found that grooming but not resting increased during longer days (van Doorn et al., 2010), suggesting that the “excess” time on long days may be devoted to grooming over resting.

An additional explanation for heightened fGCs during winter months could be seasonal differences in anthropogenic contact. On the Cape Peninsula, baboons living in proximity to humans select sleep sites nearer to urban settlements (Hoffman and O'Riain, 2012). The Da Gama troop frequently used sleep sites in the urban area: >60% over the course of the 5-month study period and >85% during winter months July and August (source: publicly available HWS monthly reports; pers. obs.). Time in town is often associated with raiding bins and residential properties (Fehlmann et al., 2017b; pers. obs.), which causes conflict with humans (Hoffman and O’Riain, 2011), posing a potential stressor. Moreover, over the last two decades, baboon rangers have formed part of a comprehensive effort to reduce human-baboon overlap by actively herding baboons away from urban areas (Kansky and Gaynor, 2000; van Doorn, 2009) using noise and pain-aversion techniques (Fehlmann et al., 2017b; van Doorn and O'Riain, 2020). Considering that raiding tends to increase during winter (van Doorn et al., 2010) and, as a result, herding efforts may become intensified, heightened HPA-axis activity during this already “harsher” period may become further exacerbated. Additionally, access to human-derived food can have profound impacts on activity budgets (Fehlmann et al., 2020), which may indirectly affect GCs. On the one hand, having access to human food sources can reduce foraging time, freeing up time for resting or socialising, as has been noted for other baboon populations with access to crops and food from refuse pits (Altmann and Muruthi, 1988; Strum, 2010). On the other hand, foraging on clumped human food sources can increase within-group aggression (Barbary macaques; El Alami et al., 2012; Ram et al., 2003) and reduce social interactions such as grooming (bonnet macaques *Macaca radiata* (Balasubramaniam et al., 2020; Marty et al., 2019). Recent work on the Cape found that chacma baboons spent less time socialising and had higher levels of fGCs when ranging in anthropogenic habitats (Chowdhury et al., 2020), suggesting that urban space use alters both behaviour and physiology. This recent study did however not take into account seasonal effects (e.g., day length) which have been previously found (Weingrill et al., 2004) and presently confirmed to be an important predictor of fGCs and which co-vary with urban space use (i.e., anthropogenic space use increases during winter months; see above). Future studies are needed to better understand the potential direct and indirect effects of both management and spending time in urban space on fGCs and uGCs, while taking into account other important predictors.

For females, reproductive state is an important driver of GCs, both through endogenous and exogeneous stressors (von der Ohe and Servheen, 2002). Previous work in human and non-human primates has demonstrated that pregnancy is associated with high levels of GCs (Cavigelli, 1999; French et al., 2004; Gesquiere et al., 2008; McLean and Smith, 1999; Smith and French, 1997b; Ziegler et al., 1995). This can be ascribed to the interaction between elevated levels of oestrogen during pregnancy and the HPA-axis (Coe et al., 1986; Pepe et al., 1982), as well as to the release of CRH corticotropin-releasing hormone (CRH) which can further increase HPA-axis activity (McLean and Smith, 1999). Post-partum GCs are expected to return to pre-pregnancy levels as both oestrogen and CRH levels drop (McLean and Smith, 1999). In line with this, I found pregnant females to have significantly higher levels of fGCs compared to the cycling and lactating females. uGCs did not show significant differences between reproductive stages. While uGCs have been shown to be elevated before giving birth and decrease post-partum in captive settings in female baboons (French et al., 2004), these measurements were taken at a consistent time of the day, limiting the effect of circadian HPA-axis activity rhythm on uGCs (see *Introduction*). Moreover, while the difference between late and early pregnancy uGCs did not reach statistical significance in our dataset, visual inspection of the data does show an increase in uGCs in late pregnancy (Fig. III - S1). This is in line with both human and non-human primate studies which show that uGCs start to markedly increase in the late gestation phases (Jung et al., 2011; Smith and French, 1997b).

In the wild, risks associated with lactation can be reflected in high GCs (e.g., predation pressure: Monclús et al., 2011; infanticide: Engh et al., 2006b). Wild female chacma baboons were found to have similar levels of fGCs during lactation and pregnancy (Weingrill et al., 2004), which was ascribed to the psychosocial stressor posed by infanticide, a relatively common phenomenon in chacma baboons (Palombit et al., 1997). In this study, fGCs in lactating females were comparable to those of cycling females, which was contrary to my predictions, as I expected the persistent infanticide threat in our study troop to be reflected in GCs. It is possible that while infanticide threat was present, it did not translate into markedly higher fGCs in lactating females relative to pregnant females. For instance, lactating chacma baboons in Botswana, whose infants were at risk of attack by males had increased fGCs when a new immigrant male arrived, compared to pregnant and cycling females. However, overall, pregnant females still had highest fGCs compared to the other reproductive states (Engh et al., 2006b). As such, it is possible that lactating females did experience elevated GCs in our study troop but not to such an extent that their fGCs were as high as those measured in pregnant females. On the Cape Peninsula, turnover of alpha males is particularly high, possibly due to the removal of “problematic” males who are frequently involved in conflict with humans (Beamish, 2009). This may contribute to high rates of infanticides on the Cape (Beamish, 2009; Kansky and Gaynor, 2000). It is therefore noteworthy that in a population and a troop where infanticide was certainly a risk, this was not reflected in fGCs of lactating females.

Other aspects of the social environment related to living in hierarchical groups can also impact GCs (reviewed in Creel et al., 2013). Dominance relationships are reflected in GC-profiles across different taxa, with evidence for both “stress of subordination” (Blumstein et al., 2016; Foley et al., 2001) and “stress of dominance” (Carlson et al., 2004; Mooring et al., 2006). Across primate systems, there is no consistent pattern for whether low or high rank translates into higher or lower GCs (Abbott et al., 2003). Rather, rank-related differences are context dependent (Abbott et al., 2003; Cavigelli and Caruso, 2015). Low-ranking individuals display higher GCs when exposed to stressors related to social subordination, such as increased aggression or decreased access to resources (Abbott et al., 2003; Virgin Jr and Sapolsky, 1997). Conversely, high-ranking individuals show increased GCs when challenges occur that threaten the maintenance of their rank (Bergman et al., 2005; Setchell et al., 2010). In female chacma baboons, rank has generally not been found to be reflected in fGCs (Beehner et al., 2005; Engh et al., 2006b; Weingrill et al., 2004). While low-ranking females receive higher rates of aggression than high-ranking females (Barrett et al., 2002), the predictable nature of the stressor may reduce its impact (Weiss, 1970; Wingfield and Ramenofsky, 1999) and even low-ranking females form social bonds through which they can receive support, potentially buffering the physiological cost of being subordinate (Barrett and Henzi, 2002; Silk et al., 2010b). Nonetheless, a recently published long-term study did find higher rank to be associated with lower fGCs, suggesting rank-effects on GCs are present but only detectable over long periods of time in females (Levy et al., 2020). In line with shorter-term studies (Beehner et al., 2005; Engh et al., 2006b; Weingrill et al., 2004), I found no effect of rank on fGCs or uGCs in our study.

Non-human primates have been extensively studied both in captivity and in the wild as a model system for stress-physiology (Beehner and Bergman, 2017; Behringer and Deschner, 2017). While studies linking GCs to fitness in primates are scarce (Beehner and Bergman, 2017), a recent review on the link between GCs and fitness across taxa showed that overall reproductive success was negatively correlated with baseline GCs and that higher GCs were negatively associated with survival in long-lived species (Schoenle et al., 2020). Indeed, recent work on baboons showed that GCs were negatively associated with survival, with females with cumulative fGCs scores in the top 90% living almost 5 years shorter than females with fGCs in the bottom 10% (Campos et al., 2021). In this chapter, I have discussed the physiological stress response from the point of view that GCs indicate metabolic activity which is within the normal reactive scope (predictive and reactive homeostasis) and is adaptive given the exogeneous and endogenous stressors the individual is exposed to (Beehner and Bergman, 2017; Romero et al., 2009). However, high levels of GCs can be indicative of homeostatic overload (Romero et al., 2009) and many primates that live in complex societies experience psychosocial stressors (Sapolsky, 2021), which may result in GC-levels with deleterious consequences for health (Campos et al., 2021; Sapolsky, 2005). To untangle the importance of social interactions in modulating HPA-axis activity, a challenge exists in identifying the multiple drivers of GCs, including the basic predictors considered in this chapter.

Conclusions

This chapter highlights some of the key drivers of fGCs and uGCs in Cape chacma baboons. The variation in GCs driven by these factors is presumably part of the predictive homeostasis response expected for chacma baboons given the predictable seasonal and life-history challenges they experience. Future analyses will have to take into account these basic predictors before investigating effects of more acute psychological stressors (which may push physiological responses into reactive homeostasis or homeostatic overload ranges: Romero et al., 2009). While rank and sex did not significantly predict fGCs nor uGCs, it is evident from our model that other individual differences produce variation in fGCs and uGCs. One source of individual variation which has important fitness consequences is an individual's social bonds (Silk et al., 2010b), which are maintained through grooming (Dunbar, 1991; Lehmann et al., 2007). Primates devote a considerable amount of their activity budget to grooming (Dunbar, 1991), with demonstrated positive links to GCs (Engh et al., 2006a; Fürtbauer et al., 2014; Wittig et al., 2008). This motivates the investigation of grooming budgets in our study troop (Chapter 4), to determine its role in modulating GCs (Chapter 5). Finally, it is worthwhile noting that fGCs and uGCs are not predicted by the same factors. Long-term stressors (i.e., reproductive state and changes in day length) were reflected in fGCs. Conversely, uGCs reflected short-term stressors such as rainy days and captured diurnal fluctuations in cortisol levels (i.e., the cortisol awakening response). This confirms that the longer delay between hormone secretion and excretion in large-bodied primates (Heistermann, 2010) make fGCs a more robust measure of long-term stressors as it reflects cumulative hormone secretion over many hours/days (Behringer and Deschner, 2017; Touma and Palme, 2005). On the other hand, uGCs capture fluctuations in GC production across the day (lag-time of a few hours), making them less suitable for capturing the effect of long-term stressors which do not fluctuate on an hourly basis and more suitable for acute stressors. This distinction introduces methodological considerations for the testing of stressors and buffers of different temporal natures.

Appendix

Table III – S1: Overview of supplementary material for Chapter 3

Content	Tables & Figures
S1: Results	
S1.1: fGCs additional analyses	
S1.1.1: Main models	
Season model (LMM2b)	Table III – S2
LMM2a with monthly categories swapped	Table III – S3a-d
LMM2a without urine contaminated faecal samples (LMM2c)	Table III – S4
S1.1.2: Female reproductive state models	
Early vs. late pregnancy model	Table III – S5
Early vs. late lactation model	Table III – S6
‘Social’ lactation definition model	Table III – S7
S1.1.3: Weather models	
Day length only model (LMM4b)	Table III – S8
Minimum temperature only model (LMM4c)	Table III – S9
S1.2: uGCs additional analyses	
S1.2.1: Main models	
Monthly model (LMM5a)	Table III – S10
Season model	Table III – S11
Weather model (LMM5b)	Table III- S12
S1.2.2: Female reproductive state models	
Early vs. late pregnancy model	Table III – S13
Early vs. late lactation model	Table III – S14
‘Social’ lactation definition models (LMM6)	Table III – S15
S1.3: Reduced data set (no trapping samples) models	
LMM2a	Table III - S16
LMM3	Table III - S17
LMM4a	Table III – S18
LMM5c	Table III – S19
LMM6	Table III – S20

S1.1: fGCs additional analyses

S1.1.1: Main models

Table III – S2: Effects of sex, dominance rank, season, time of day (AM/PM) and urine contamination (yes/no) on fGCs (ng/g) for n=603 samples from n=17 wild chacma baboons (LMM2b). Baboon ID and Date were included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	0.127	0.18	0.707	0.485
Dominance rank	0.027	0.196	0.136	0.893
Season (Spring)*	-0.293	0.046	-6.304	**<0.001**
Season (Summer)*	-0.429	0.075	-5.755	**<0.001**
AM/PM (PM)	0.044	0.031	1.415	0.158
Urine contamination (Y)	0.127	0.049	2.605	**0.009**

**Reference category: Winter*

Table III – S3a: Main fGCs model (LMM2a) with August as 'Month' reference category.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	0.128	0.18	0.712	0.482
Dominance rank	0.025	0.196	0.129	0.899
Month (July)*	0.058	0.068	0.853	0.396
Month (September)*	-0.188	0.059	-3.218	**0.002**
Month (October)*	-0.361	0.059	-6.093	**<0.001**
Month (November)*	-0.411	0.076	-5.419	**<0.001**
AM/PM (PM)	0.04	0.031	1.321	0.187
Urine contamination (Y)	0.121	0.049	2.482	**0.013**

**Reference category: August*

Table III – S3b: Main fGCs model (LMM2a) with September as 'Month' reference category.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	0.128	0.18	0.712	0.482
Dominance rank	0.025	0.196	0.129	0.899
Month (July)*	0.247	0.07	3.505	**<0.001**
Month (August)*	0.188	0.059	3.218	**0.002**
Month (October)*	-0.173	0.061	-2.812	**0.006**
Month (November)*	-0.223	0.078	-2.867	**0.005**
AM/PM (PM)	0.04	0.031	1.321	0.187
Urine contamination (Y)	0.121	0.049	2.482	**0.013**

**Reference category: September*

Table III – S3c: Main fGCs model (LMM2a) with October as 'Month' reference category.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	0.128	0.18	0.712	0.482
Dominance rank	0.025	0.196	0.129	0.899
Month (July)*	0.419	0.07	5.947	**<0.001**
Month (August)*	0.361	0.059	6.093	**<0.001**
Month (September)*	0.173	0.061	2.812	**0.006**
Month (November)*	-0.05	0.078	-0.644	0.521
AM/PM (PM)	0.04	0.031	1.321	0.187
Urine contamination (Y)	0.121	0.049	2.482	**0.013**

**Reference category: October*

Table III – S3d: Main fGCs model (LMM2a) with November as reference category for month.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	0.128	0.18	0.712	0.482
Dominance rank	0.025	0.196	0.129	0.899
Month (July)*	0.469	0.084	5.555	**<0.001**
Month (August)*	0.411	0.076	5.419	**<0.001**
Month (September)*	0.223	0.078	2.867	**<0.001**
Month (October)*	0.05	0.078	0.644	0.521
AM/PM (AM)	0.04	0.031	1.321	0.187
Urine contamination (Y)	0.121	0.049	2.482	**0.013**

**Reference category: November*

Table III - S4: Effects of sex, dominance rank, month and time of day (AM/PM) on fGCs (ng/g) for n=548 samples from n=17 wild chacma baboons (LMM2c). Baboon ID and Date were included as random effects. Significant effects are in bold. This model excludes urine contaminated faecal samples.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	0.116	0.177	0.651	0.520
Dominance rank	0.048	0.193	0.248	0.807
Month (August)*	-0.04	0.068	-0.593	0.554
Month (September)*	-0.232	0.07	-3.304	**0.001**
Month (October)*	-0.404	0.07	-5.791	**<0.001**
Month (November)*	-0.462	0.084	-5.505	**<0.001**
AM/PM (PM)	0.032	0.032	0.999	0.318

**Reference category: July*

S1.1.2: Female reproductive state models

Table III – S5: Effect of late vs. early pregnancy on fGCs for n=104 samples from n=6 baboons (n=3 early pregnancy, n=3 late pregnancy). Month and urine contamination (yes/no) were controlled for based on LMM2a. Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Pregnancy (late)	0.164	0.202	0.809	0.465
Month (August)*	-0.09	0.129	-0.693	0.49
Month (September)*	-0.248	0.128	-1.939	0.055
Month (October)*	-0.382	0.134	-2.846	**0.005**
Month (November)*	-0.463	0.157	-2.952	**0.004**
Urine contamination (Y)	0.199	0.101	1.964	0.052

**Reference category: July*

Table III – S6: Effect of early vs. late lactation on fGCs for n=209 samples from n=8 lactating females (n=4 early lactation, n=4 late lactation). Month and urine contamination (yes/no) were controlled for based on LMM2a. Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Lactating (late)	-0.001	0.175	-0.007	0.994
Month (August)*	-0.195	0.099	-1.975	0.051
Month (September)*	-0.274	0.102	-2.696	**0.008**
Month (October)*	0.451	0.103	-4.365	**<0.001**
Month (November)*	-0.746	0.126	-5.93	**<0.001**
Urine contamination (Y)	0.0448	0.066	0.675	0.501

**Reference category: July*

Table III – S7: Effects of dominance rank, month, reproductive state, time of day (AM/PM) and urine contamination on fGCs (ng/g) for n=506 samples from n=15 female chacma baboons (LMM3a). Lactating females are defined as females with dependent infants (i.e., 'social definition') (n=10 females with infants, n=3 cycling females). Baboon ID and Date were included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Dominance rank	0.142	0.181	0.784	0.447
Month (August)*	-0.134	0.072	-1.859	0.066
Month (September)*	-0.321	0.074	-4.328	**<0.001**
Month (October)*	-0.487	0.075	-6.468	**<0.001**
Month (November)*	-0.569	0.091	-6.24	**<0.001**
Reproductive State (Infant)**	-0.441	0.088	-5.038	**<0.001**
Reproductive State (Cycling)**	-0.427	0.080	-5.317	**<0.001**
AM/PM (PM)	0.052	0.033	1.605	0.109
Urine contamination (Y)	0.121	0.049	2.474	**0.014**

**Reference category = July*
***Reference category = Pregnant*

S1.1.3: Weather models

Table III – S8: Effects of rain day (yes/no) and day length on fGCs (ng/g) for n=603 samples from n=17 chacma baboons (LMM4b). Urine contamination (yes/no) and reproductive state (pregnant vs. non-pregnant) were controlled for based on LMM2a and LMM3. Baboon ID and Date included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Rain day (Y)	-0.034	0.047	-0.734	0.465
Day length (hrs)	-0.159	0.017	-9.139	**<0.001**
Reproductive state (Pregnant)	0.406	0.061	6.668	**<0.001**
Urine contamination (Y)	0.122	0.047	2.6	**0.010**

Table III – S9: Effects of minimum temperature and rain day (yes/no) on fGCs (ng/g) for n=603 samples from n=17 chacma baboons (LMM4c). Urine contamination (yes/no) and reproductive state (pregnant vs. non-pregnant) were controlled for based on LMM2a and LMM3. Baboon ID and Date included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Rain day (Y)	-0.035	0.062	-0.562	0.576
Minimum Temperature (°C)	-0.042	0.012	-3.37	**0.001**
Reproductive state (Pregnant)	0.405	0.062	6.618	**<0.001**
Urine contamination (Y)	0.115	0.047	2.422	**0.016**

S1.2: uGCs additional analyses

S1.2.1: Main models

Table III – S10: Effect of sex, dominance rank, month, collection time and method on uGCs (ng/ml) for n=385 samples from n=17 baboons (LMM5a). Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	-0.223	0.44	-0.507	0.62
Dominance rank	0.444	0.413	1.076	0.3
Month (August)*	0.285	0.197	1.45	0.151
Month (September)*	0.234	0.196	1.193	0.237
Month (October)*	0.092	0.203	0.455	0.65
Month (November)*	0.15	0.253	0.591	0.556
Collection time (hour)	-0.123	0.015	-8.083	**<0.001**
Collection method (Salivette)	-0.232	0.085	-2.742	**0.006**

**Reference category: July*

Table III – S11: Effects of sex, dominance rank, season, collection time and method on uGCs (ng/ml) for n=385 samples from n=17 baboons. Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	-0.228	0.44	-0.517	0.613
Dominance rank	0.427	0.413	1.033	0.319
Season (Spring)*	-0.053	0.104	-0.509	0.612
Season (Summer)*	-0.076	0.2	-0.38	0.705
Collection time (hour)	-0.123	0.015	-8.007	**<0.001**
Collection method (Salivette)	-0.228	0.085	-2.694	**0.007**

**Reference category: Winter*

Table III – S12: Effect of minimum temperature, day length, rain day (yes/no), collection time and method on uGCs (ng/ml) for n=385 samples for n=17 baboons (LMM5b). Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Minimum Temperature (°C)	0.0171	0.027	0.623	0.536
Daylength (hrs)	-0.049	0.06	-0.754	0.453
Rain day (Y)	0.234	0.107	2.18	**0.036**
Collection time (hour)	-0.125	0.015	-8.26	**<0.001**
Collection method (Salivette)	-0.225	0.084	-2.685	**0.008**

S1.2.2: Female reproductive state models

Table III – S13: Effect of late vs. early pregnancy for n=83 samples from n=6 females (n=3 early pregnancy and n=3 late pregnancy) on uGCs (ng/ml). Controlling for rain day (yes/no) and collection time and method based on LMM5c. Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Pregnancy (late)	1.248	0.571	2.184	0.091
Rain day (Y)	0.292	0.276	1.061	0.295
Collection time (hour)	-0.09	0.038	-2.372	**0.021**
Collection method (Salivette)	-0.682	0.203	-3.356	**0.001**

Table III – S14: Effect of early vs. late lactation in hormonally confirmed lactating females on uGCs (ng/ml) for n=151 samples from n=7 females (n=3 early lactation, n=4 late lactation). Controlling for rain day (yes/no) and collection time and method based on LMM5c. Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Lactation (late)	-0.115	0.275	-0.419	0.692
Rain day (Y)	0.321	0.154	2.084	**0.042**
Collection time (hour)	-0.144	0.022	-6.414	**<0.001**
Collection method (Salivette)	-0.009	0.116	-0.075	0.94

Table III – S15: Effects of dominance rank, reproductive state (based on 'social definition' of lactating), rain day (yes/no), collection time and method on uGCs (ng/ml) for n=338 samples from n=15 female chacma baboons (LMM6a). Baboon ID and Date included as random effects. Significant effects in bold.

Predictor variable	Estimate	SE	T	*p*
Dominance rank	0.33	0.442	0.747	0.48
Reproductive state (Cycling)*	-0.191	0.279	-0.686	0.498
Reproductive state (Pregnant)*	-0.011	0.207	-0.056	0.956
Rain day (Y)	0.253	0.113	2.234	**0.030**
Collection time (hour)	-0.115	0.016	-7.014	**<0.001**
Collection method (Salivette)	-0.215	0.086	-2.503	**0.013**

Reference category: Lactating (infant)

S1.3: Reduced data set (no trapping samples) models

Table III – S16: LMM2a without trapping samples in July/August. Effects of sex, dominance rank, month, time of day (AM/PM) and urine contamination (yes/no) on fGCs (ng/g) for n=550 samples from n=17 wild chacma baboons Baboon ID and Date were included as random effects. Significant effects are in bold.

Predictor variable	Estimate	SE	T	*p*
Sex (male)	0.13	0.181	0.715	0.48
Dominance rank	0.047	0.199	0.237	0.815
Month (August)*	-0.027	0.071	-0.377	0.707
Month (September)*	-0.167	0.072	-2.336	**0.021**
Month (October)*	-0.342	0.072	-4.772	**<0.001**
Month (November)*	-0.434	0.087	-5.004	**<0.001**
AM/PM (PM)	0.037	0.031	1.183	0.237
Urine contamination (Y)	0.097	0.049	1.966	**0.049**

**Reference category: July*

Table III – S17: LMM3 without trapping samples in July/August. Effects of dominance rank, month, reproductive state, time of day (AM/PM) and urine contamination (yes/no) on fGCs (ng/g) for n=463 samples from n=15 female chacma baboons. Baboon ID and Date were included as random effects. Significant effects are in bold.

Predictor variable	Estimate	SE	T	*p*
Dominance rank	0.125	0.153	0.815	0.432
Reproductive state (Cycling)*	-0.451	0.076	-5.976	<0.001
Reproductive state (Lactating)*	-0.322	0.084	-3.828	<0.001
Month (August)**	-0.113	0.076	-1.490	0.139
Month (September)**	-0.259	0.076	-3.408	**<0.001**
Month (October)**	-0.431	0.077	-5.597	**<0.001**
Month (November)**	-0.561	0.094	-5.974	**<0.001**
AM/PM (PM)	0.049	0.033	1.467	0.143
Urine contamination (Y)	0.092	0.05	1.853	0.065

**Reference category: Pregnant*
***Reference category: July*

Table III – S18: LMM4a without trapping samples. Effects of rain day (yes/no), minimum temperature and day length on fGCs (ng/g), controlling for urine contamination (yes/no) and reproductive state (pregnant vs. not pregnant) for n=550 samples from n=17 chacma baboons. Baboon ID and Date were included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Rain day (Y)	-0.045	0.033	-1.37	0.171
Minimum Temperature (°C)	0.013	0.008	1.714	0.087
Day length (hrs)	-0.173	0.016	10.918	**<0.001**
Reproductive state (Pregnant)	0.354	0.066	5.362	**<0.001**
Urine contamination (Y)	0.089	0.049	1.807	0.071

Table III – S19: LMM5c without trapping samples. Effects of sex, dominance rank, rain day (yes/no), collection time and method on uGCs (ng/ml) for n=380 samples from n=17 chacma baboons. Baboon ID and Date included as random effects. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Sex (male)	-0.231	0.436	-0.531	0.604
Dominance rank	0.397	0.409	0.971	0.348
Rain day (Y)	0.229	0.106	2.166	**0.034**
Collection time (hour)	-0.124	0.0151	-8.247	**<0.001**
Collection method (Salivette)	-0.207	0.081	-2.560	**0.011**

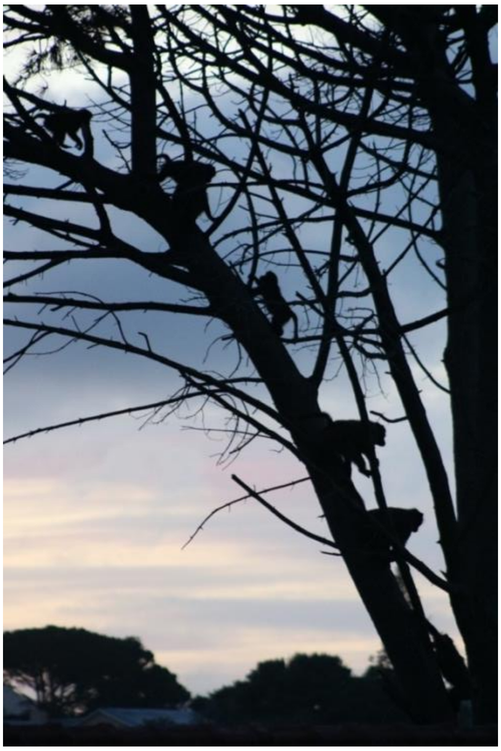
Table III – S20: LMM6 without trapping samples. Effects of dominance rank, reproductive state, rain day (yes/no), collection time and method on uGCs (ng/ml) for n=334 samples from n=15 female chacma baboons (LMM6). Baboon ID and Date included as random terms. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Dominance rank	0.448	0.464	0.965	0.359
Reproductive state (Cycling)*	-0.043	0.216	-0.198	0.843
Reproductive state (Lactating)*	-0.145	0.207	-0.702	0.485
Rain day (Y)	0.208	0.116	1.794	0.078
Collection time (hour)	-0.114	0.016	-6.995	**<0.001**
Collection method (Salivette)	-0.203	0.085	-2.388	**0.018**

**Reference category: Pregnant*

Chapter 4: Environmentally imposed time constraints affect grooming activity in a non-equatorial primate *Papio ursinus*

Charlotte Christensen[1], Anna M. Bracken[1], M. Justin O'Riain[2], Andrew J. King[1], Ines Fürtbauer[1]



Affiliations:
[1]Biosciences, School of Biosciences, Geography and Physics, Faculty of Science and Engineering, Swansea University, SA2 8PP Swansea, United Kingdom
[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch, 7701, South Africa

Statement of contributions:

CC and IF designed the study. CC and AB conducted the fieldwork and built the collars. JOR provided logistical support in the field. CC compiled the data and conducted the statistical analysis with advice from IF. CC wrote the chapter with critical review, edits, and discussion from IF and final edits from AJK.

PC: Charlotte Solman

Chapter 4: Environmental constraints on grooming activity in chacma baboons

Abstract

Environmental factors can impose time constraints on animals' behavioural budgets, including their social time. While investing in socio-positive interactions has important fitness implications, time needs to be allocated to other essential activities as well within a given time-window (e.g., daytime in diurnal animals). Animal populations living at high latitudes, marked by seasonal differences in day length and rainfall, provide an opportunity to test how social animals respond to environmentally imposed temporal bottlenecks. Using 24-hour data on accelerometer-identified behaviours, I address this question in a non-equatorial primate that experiences marked seasonal changes in day length and rainfall – the Cape chacma baboon. Shorter days were associated with less giving grooming overall, driven by shorter and fewer bouts. Similarly, days with more hours with rainfall were associated with less time giving grooming. After rainy days, dusk was associated with an increase in giving grooming, potentially indicating compensation for 'lost' social time during the day. In contrast, reduced giving grooming on short days was not compensated outside the daylight window. Rather, there was a trade-off between foraging and grooming: more foraging occurred during dusk on shorter days, while giving grooming during twilight increased as days got longer, suggesting that while both behaviours are constrained by day length, 'catching up' on foraging takes priority on short days. Together, these results indicate that environmental factors affect both (1) the total time invested in grooming (driven by changes in both bout length and frequency) and (2) the temporal pattern of social activity outside the daylight window. These findings further suggest potential behavioural mediators of the relationships between environmental factors (day length and rain) and faecal and urinary glucocorticoid metabolites identified in Chapter 3.

Introduction

To survive, animals need to invest time in various fitness-relevant activities which are mutually exclusive (Dunbar, 1992; Dunbar et al., 2009; Pollard and Blumstein, 2008). For many social animals, a significant part of this activity budget is devoted to social time (Dunbar, 1992). Allo-grooming (the grooming of a conspecific, hereafter "grooming") is an activity which many social animals devote time to, e.g., primates (Dunbar, 1991; Henzi and Barrett, 1999), carnivores (Kern and Radford, 2018; Matoba et al., 2013), bats (Carter and Leffer, 2015), birds (Morales Picard et al., 2020; Radford and Du Plessis, 2006) and equids (Cameron et al., 2009; Kimura, 1998). Although grooming is thought to have evolved primarily for its hygienic function (Dunbar, 1991; McFarland, 2018), it plays a pivotal role in forming and maintaining social bonds (Braun and Bugnyar, 2012; Carter and Leffer, 2015; Silk et al., 2010a) which, in turn, are linked to ultimate fitness benefits such as longer life-spans (Archie et al., 2014; Barocas et al., 2011; Silk et al., 2010b; but see: Thompson and Cords, 2018) and increased infant survival (Cameron et al., 2009; Silk et al., 2003a). Grooming also functions as a tradeable commodity (Barrett et al., 1999b; Schino and Aureli, 2007), given in exchange for coalition support (Borgeaud and Bshary, 2015), tolerance (Carne et al., 2011; Tiddi et al., 2011), protection (Palombit et al., 1997), infant handling (Gumert, 2007; Henzi and Barrett, 2002), or grooming itself (Barrett et al., 1999b). Finally, grooming also has physiological benefits and has been linked to reduced HPA-axis activity in several primate species (Engh et al., 2006a; Fürtbauer et al., 2014; Shutt et al., 2007; Wittig et al., 2008; Wittig et al., 2016; Wooddell et al., 2017). The fitness implications of sustained heightened HPA-axis activity, which prompts the release of glucocorticoids (GCs) (Sapolsky et al., 2000), are not straightforward in wild animals (Beehner and Bergman, 2017; Bonier et al., 2009). However, high GCs exposure has been linked to negative health consequences in human (see Shields and Slavich, 2017 for review) and non-human primates (Mendoza et al., 2000; Sapolsky, 2005) and recent work has shown that higher life-long cumulative GCs are associated with reduced lifespans in wild female baboons (Campos et al., 2021).

While grooming clearly serves several important functions (see above), it needs to contend with other fitness-relevant activities. When studying the activity budgets of social animals, the four main categories usually considered are: feeding, travelling, resting and social interactions (Dunbar et al., 2009; Pollard and Blumstein, 2008). The time invested in each activity will depend on i) the amount of time needed to adequately satisfy physiological requirements (e.g., feeding until nutritional needs are met), but also ii) how much time is available when certain activities take priority over others. As such, time is a ‘limited commodity’, with time invested in each activity depending on its importance to survival (Dunbar et al., 2009). The order of assumed priority is: feeding > moving > resting (enforced) > social activity > resting (free) (Dunbar et al., 2009), and changes in context can highlight the presence of this hierarchy. For instance, there is a positive relationship between food abundance and time devoted to grooming in savanna baboons *Papio cynocephalus* (Alberts et al., 2005; Bronikowski and Altmann, 1996; Saunders, 1988), vervet monkeys *Cercopethicus aethiops* (Lee, 1984), rhesus macaques *Macaca mulatta* (Seth and Seth, 1986), Japanese macaques *Macaca fuscata* (Agetsuma and Nakagawa, 1998) and François’ langurs *Trachypithecus francoisi* (Zhou et al., 2007), suggesting that if environmental conditions are favourable and nutritional requirements are met, time can be devoted to grooming rather than foraging. This is also supported by studies comparing grooming budgets in wild primates to captive primates (Franz, 1999) or primates with access to anthropogenic foods (Altmann and Muruthi, 1988; Brennan et al., 1985; Bronikowski and Altmann, 1996; Strum, 2010), where the latter engage in more grooming potentially due to the ‘freed up’ foraging time, as energetic requirements are met more quickly when food is easily obtained and/or high in calories (Strum, 2010). On the other hand, if energetic requirements increase (e.g., due to reproductive state), social activities can be sacrificed to meet foraging demands, as shown in female lactating gelada baboons (Dunbar and Dunbar, 1988).

Food availability affects time for social activity (see examples above), but other abiotic environmental factors can also impose temporal constraints. For instance, animals may interrupt activities to seek shelter from temperature extremes (Hill, 2006; Ostner, 2002; Wolf, 2000) or rain (Brindley et al., 1989; Hanya et al., 2018; Majolo et al., 2013; Thies et al., 2006). Additionally, for diurnal animals living at high latitudes, day length poses a time constraint (Dunbar and Shi, 2013; Gaynor et al., 2004; Hill et al., 2003). How these environmental factors impact on grooming behaviour has received relatively little attention. Rain was found to interrupt grooming activity in Barbary macaques *Macaca sylvanus* (Majolo et al., 2013) and shorter day length is associated with decreased grooming time in chacma baboons *Papio ursinus* (Chowdhury et al., 2021; Hill et al., 2003; van Doorn et al., 2010), black snub-nosed monkeys *Rhinopithecus bieti* (Xiang et al., 2010) and tufted capuchin monkeys *Cebus apella* (Di Bitetti, 1997). In response to high temperatures, baboons living at high latitudes increase grooming (Hill, 2006), while equatorial baboons spend more time resting (Stelzner, 1988). This could be due to the heat not being as intense at high latitudes, meaning that time spent shading can be used for a slightly more active behaviour, i.e., grooming (Hill, 2006). Taken together, animals living in highly seasonal habitats where factors, such a day length, rain and temperature impose constraints on what activities can take place, are thus likely to experience changes in their social time budgets.

The most straightforward way in which time constraints may influence activity budgets is through the reduction of time invested in a given activity. Dunbar et al. (2009) assume that as long as ‘free’ resting time (i.e., the surplus time that can be used for other activities and differentiates itself from ‘enforced’ resting time which is physiologically imposed) remains equal or above zero, an animal can survive. As such, sacrificing activities may be necessary as it keeps the animal from reaching this limit. As highlighted in the examples above, animals may sacrifice social time when energetic demands increase (Bronikowski and Altmann, 1996; Dunbar and Dunbar, 1988) or when environmental factors constrain (Hill et al., 2003; Xiang et al., 2010) or interrupt (Majolo et al., 2013) social time. However, there are other ways in which environmental factors might affect grooming, specifically *how* (quality) and *when* (timing) grooming takes place. These two aspects may be important for understanding the full cost of environmental time constraints on social time and are considered below.

First, rather than the absolute quantity (i.e., total grooming duration), the quality of social activities may be adjusted when time is constrained. For instance, baboons have been found to focus their grooming interactions on core social partners in response to shorter days (Ellwanger, 2020) or nutritional constraints (Saunders, 1988). However, quality can also be altered by changing the grooming activity itself, e.g., by engaging in shorter or less frequent grooming bouts. For instance, ten minutes of continuous grooming and ten separate grooming bouts of one minute, amount to the same total duration, but these differences in quality likely have implications for the value of grooming. Generally, the length of a grooming bout has been considered an indicator of its value (Fruteau et al., 2011; Manson et al., 2004). Indeed, grooming bouts become longer when the traded commodity becomes scarcer (Fruteau et al., 2009) and higher-ranking individuals receive grooming in longer bouts than low-ranking individuals (Boccia et al., 1982; Gumert and Ho, 2008). Bout length has also been proposed to be positively associated with higher "concentration" of the groomer during the interaction (Saunders, 1988). Grooming bout frequency could trade-off with bout length when time becomes constrained, as individuals must choose whether to engage in shorter bouts with more grooming partners or longer bouts with fewer individuals (Henzi et al., 1997). Grooming quality has been considered in the context of anthropogenic disturbances. For instance, in human-dominated landscapes, lion-tailed macaques (*Macaca silenus*) initiated grooming just as frequently, but bouts were of shorter length than when they were in forested areas of their home-range (Dhawale et al., 2020), and rhesus macaques had shorter grooming bouts when interacting with humans (Kaburu et al., 2019). Similarly, natural environmental changes could affect grooming activity. In a recent study, female chacma baboons were found to decrease the frequency of grooming interactions but maintain their length as days became shorter, suggesting that aspects of the quality were preserved despite time constraints (Ellwanger, 2020). Capuchin monkeys also had fewer, but longer grooming sessions during short winter days (Di Bitetti, 1997). Apart from these examples, there are few studies on changes in grooming quality (length and frequency) in response to environmental constraints, as these details are hard to obtain using direct observations. Nevertheless, these components could hypothetically affect the adaptive functions of grooming, both as a tradeable commodity and as a physiological buffer.

Second, grooming may be temporally shifted due to environmental imposed time constraints. Animals living in climates with marked seasonal changes have been found to shift their activities to different time periods, known as 'temporal niche switching' (Levy et al., 2019). In extreme cases, this can entail becoming active at night rather than day or vice versa (Curtis et al., 1999; Davimes et al., 2017; Levy et al., 2007). However, for many animals, these switches may be more subtle. For instance, on shorter days, animals may extend their 'active period' by becoming active earlier on in the day (i.e., dawn) (Pagon et al., 2013) or later into the day (i.e., dusk) (Mace, 1989). Collecting data on activity between sunset and sunrise in the wild is logistically difficult, but recent works using remote sensing have investigated night-time activity in wild primates (Ayers et al., 2020; Isbell et al., 2017). Moreover, captive primate studies using night-vision cameras have shown that night-time waking periods are used for various activities, including grooming (Muñoz-Delgado et al., 1995; Videan, 2006). A study using dual-axis accelerometers to investigate night-time activity in baboons at southerly latitudes found baboons to be more active at night when days were short (Ayers et al., 2020), and while it was hypothesised that nocturnal activity could be a strategic response to seasonal constraints, the nature of the activity was not known. Anecdotally, grooming is frequently observed at sleep sites at the start or end of the day in several primates (Anderson, 1998; Kinzey and Wright, 1982; Noser and Byrne, 2007; Schreier and Swedell, 2009), but whether grooming at the sleep site could be used to compensate for time constraints during the day, has not been investigated.

Baboons are known for their remarkable behavioural flexibility (Fischer et al., 2019), allowing them to cope with environmental changes by adapting their diet (Gesquiere et al., 2008; Hill and Dunbar, 2002; van Doorn et al., 2010), social associations (Bracken, in press; Bracken et al., 2021; King and Cowlishaw, 2009), and activity budgets (Bronikowski and Altmann, 1996; Fehlmann et al., 2017b). Here, I test two hypotheses regarding grooming activity in relation to environmentally imposed time constraints in chacma baboons living on the Cape Peninsula, South Africa, which is characterised by marked seasonal changes in day length and rainfall (Cowling et al., 1996). First, I consider the ‘reduction hypothesis’ and test whether grooming time is reduced during short, rainy days and if so, whether this is due to changes in bout frequency and/or bout length. Several studies on chacma baboons on the Western Cape report a decrease in grooming during winter months when day length is reduced (Chowdhury et al., 2021; Ellwanger, 2020; Hill et al., 2003; van Doorn et al., 2010). Other behaviours become reduced too during this seasonal bottleneck (Chowdhury et al., 2021; Hill et al., 2003; van Doorn et al., 2010). Despite the reduction in grooming time, recent work suggests that grooming bout length remains stable between seasons, suggesting this aspect is preserved despite the overall time invested in grooming and the frequency of grooming bouts declining (Ellwanger, 2020). Second, I consider the ‘temporal shift hypothesis’, and test, if indeed day-time grooming is reduced in response to these factors, whether this may be ‘compensated’ by grooming more outside the day light window, i.e., at dusk, dawn or night. Baboons at southerly latitudes were found to be more active at night when days were short (Ayers et al., 2020), but whether this included grooming activity is unknown. Here, I used continuous accelerometer-identified grooming data which allows to investigate total grooming duration and quality (bout length and frequency) and temporal distribution (grooming outside the day light window) in response to environmental predictors. Aside from grooming, other activities are likely also affected by environmentally imposed bottlenecks and temporal trade-offs between mutually exclusive activities are expected (Dunbar et al., 2009). Therefore, I test how environmental time constraints affect other core activities (i.e., resting, foraging, and travelling) and present/discuss these results where relevant for temporal constraints on grooming activity.

Methods

Study site and subjects

The study was conducted on a troop of wild chacma baboons consisting of approximately 50 individuals (n=21 adults) in Da Gama Park, Western Cape, South Africa (–34.15562°N, 18.39858°E) between July and November 2018. Due to the qualitative differences in grooming relationships between male and female baboons (females are the philopatric sex and maintain long-term bonds through grooming: Silk et al., 2006a; Silk et al., 2010a), which may, for instance, influence the relationship between giving and receiving grooming (Palombit et al., 1997) and the amount of time devoted to grooming (Saunders, 1988), this study focusses on n=10 collared females only.

Environmental factors

Day length data was obtained from www.timeanddate.com and ranged from 10.3 to 12.8 hours during the collar-period. 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: 0004549-2, -34.1480°N, 18.3190°E). Weather data has been described in detail in Chapter 3. In this Chapter, I use "number of rain hours in the day" as a predictor, rather than a categorical yes/no for "rain day" (see Chapter 3), as the aim here is to investigate temporal constraints imposed by environmental factors, and rain per hour is the most high-resolution data available, I used this measure for the analysis. A 'rain hour' is an hour in which rain was recorded, but it did not necessarily rain continuously for that hour (median and range rain per hour: 0.44 mm; 0.2-16.6 mm). During the collar-period, it rained on n=31 of n=82 day (median and range of rain hours per rain day: 2 hours; 1-7 hours). Urban sleep sites were used n=64 nights out of the n=82, n=3 nights were excluded from the analysis when the group was split between natural and urban sleep sites, and n=1 night (28-29 September 2018) was excluded as the sleep site was unknown.

Activity budgets

Daily activity budgets were calculated based on accelerometer-identified behaviours from collars: resting, receiving grooming, giving grooming, foraging/feeding and travelling (see Chapter 2 for details) for n=10 female baboons, which resulted in mean±SD = 57±18 days per female (Table IV - 1). I treated giving and receiving grooming separately rather than as a single ‘grooming’ category, to test if and how the two grooming roles varied independently in response to environmental factors.

Grooming bout qualities

To test whether the quality of grooming bouts, specifically bout length and frequency, changed in response to environmental predictors, continuous giving and receiving grooming bouts were extracted by identifying consecutive minutes of the same behaviour (R package 'plyr': Wickham, 2011). If the majority of the seconds within a minute was spent “giving grooming”, the minute would be classified as “giving grooming”. If the next minute was also spent “giving grooming”, this would be stitched to the first, and so forth until a minute was identified with a new behaviour at which point the bout was considered to have ended. For each phase (see ‘*Activity phases*’), I calculated the total number of bouts (frequency) and the average bout length.

Dominance rank and female reproductive state

Dominance rank calculations have been described previously in Chapter 3 for n=21 adult baboons and in (Bracken et al., 2021; Fürtbauer et al., 2020). Assessment of female reproductive state is also described in detail in Chapter 3 and in (Fürtbauer et al., 2020). Here, I used the ‘social definition’ for lactating, where females who were still caring for infants were classified as lactating despite having resumed cyclic ovarian activity (see

Chapter 3). Considering that these females groom their infant and other adults and that infants may make them more attractive grooming recipients (Frank and Silk, 2009; Henzi and Barrett, 2002), this definition seemed more appropriate for investigating grooming patterns than the 'hormonal definition' which is based on the absence of cyclic ovarian activity (i.e., lactational amenorrhea). By the above definition, of the n=10 females wearing tracking collars, n=1 female was cycling, n=1 was pregnant, and n=6 females were lactating throughout the collar period. N=1 cycling female conceived (cycling to pregnant), and n=1 female gave birth (pregnant to lactating) during the collar period (Table IV - 1).

Statistical analysis

All statistical analysis were performed in R Studio (version 1.4.1717). For the LMMs (R package 'lmerTest') (Kuznetsova et al., 2017), response variables were transformed to meet normal distribution where necessary (see Table IV - S2 for transformations). Normality assumptions were visually confirmed by plotting residuals in Q-Q plots. To establish whether full models provided a significantly better fit to the null models (which included only the random effects), likelihood ratio tests were used (R function 'anova'). Random slopes were fitted in preliminary analyses for each individual (Barr et al., 2013), however these resulted in non-convergence warnings and were therefore removed, while keeping random intercepts (Grueber et al., 2011). Inspection of the individual slopes in response to environmental predictors (not presented here) showed large variation around individual estimates and similar directions of individual slopes, both of which reduce the importance of fitting random slopes (Schielzeth and Forstmeier, 2009). To test for collinearity between predictor variables, Variance Inflation Factors (VIFs) were calculated (R package 'car'; all VIFs < 1.6) (Fox et al., 2012).

Reduction Hypothesis: Environmental predictors of grooming duration and quality of grooming bouts during the day

To test whether absolute time invested in grooming (and other activities) changed in response to environmental constraints ('reduction hypothesis'), I ran a model with time spent engaged in each activity (i.e., giving grooming (LMM1); receiving grooming

(LMM2); foraging (LMM5); travelling (LMM6)) per day as the response variable, testing effects of the following predictors: day length (hours between sunrise and sunset), number of day hours in which it rained, and minimum temperature (°C). While the aim was to test the effect of environmental time constraints, reproductive state (cycling, pregnant, lactating) and ordinal dominance rank were included in the model as these might influence grooming patterns (Barrett et al., 1999b; Frank and Silk, 2009; Rowell, 1968; Seyfarth, 1976; Silk et al., 1999) as well as other activities (Altmann and Muruthi, 1988; Barrett et al., 2006; Dunbar and Dunbar, 1988; Muruthi et al., 1991). Based on the finding that giving grooming was reduced during short days (Table IV - 2), I tested whether this was caused by a decrease in bout frequency (LMM3) and/or bout length (LMM4) (see '*Grooming bout qualities*' for details). I ran a model with mean grooming bout length and number of bouts per day as the response variables, with the same predictors as described above.

Temporal Shift Hypothesis: Environmental predictors of temporal patterns of grooming

Based on the results of the above models, confirming that environmental factors affect the amount of time invested in giving grooming and the quality of grooming interactions during the day ('reduction hypothesis'; Table IV - 2; Fig. IV - 1a-c), I test whether baboons shift grooming outside of the diurnal window in response to environmental time constraints ('temporal shift hypothesis').

In response to short days, baboons might increase giving grooming during dusk, dawn and night hours. Thus, I ran a model with time invested in giving grooming at dusk and dawn (LMM7) and night (LMM8), with day length as a predictor and controlling for the same factors as LMM 1-6. In response to rain hours during the day, baboons might compensate giving grooming at dusk. Thus, I ran a model with time invested in giving grooming at dusk (LMM9), with rain hours as a predictor, controlling for the same factors as LMM 1-6. The reason I used dusk rather than dusk *and* dawn for rain-driven shifts in grooming is because, presumably, rain hours during the day are sporadic, unpredictable time constraints for which baboons cannot compensate pre-emptively, whereas reduced day length is a gradual, predictable time constraint for which baboons could compensate prior to (dawn) and following (dusk) short days.

Foraging was also strongly affected by day length (Table IV - 3; Fig. IV - 1a). Therefore, I ran the same analysis for foraging during dusk and dawn (LMM10) and night (LMM11). These results revealed a potential trade-off between giving grooming and foraging time during dusk and dawn (Table IV - 4; Fig. IV - 2a), thus I tested whether they were in fact negatively correlated using Pearson's correlation test.

Activity phases

To calculate the activity outside the day-time window, the data was split into the following phases: (1) night, (2) twilight (dusk and dawn) and (3) only dusk. I treated twilight periods (which I refer to as dawn (AM twilight) and dusk (PM twilight) throughout) as separate periods to night because the remaining or precursory illumination from the sun would allow for some visibility, making dusk and dawn categorically different from night, with implications for activity (Dominy and Melin, 2020; *Appendix* Fig. IV - S1 for distribution of baboon activity across a 24-hour cycle). Night ranges from the end of astronomical twilight to the beginning of astronomical twilight the following day, dawn ranges from the start of astronomical twilight to the sunrise, day ranges from sunrise to the sunset, and dusk ranges from sunset to astronomical twilight (Dominy and Melin, 2020). Time invested in activities was calculated based on the relevant time points of that day, obtained from www.timeanddate.com. In all the models (LMM7-11), I also controlled for sleep site (urban vs. not urban), because urban space-use has been shown to alter activity patterns in Cape baboons (Fehlmann et al., 2020; Fehlmann et al., 2017b) and grooming activity in several non-human primates (Chowdhury et al., 2020; Kaburu et al., 2019; Scheun et al., 2019).

Results

Reduction Hypothesis: Reduce activity in response to environmental time constraints?

Grooming

All grooming models were significantly different from their null models (Table IV - S3). Longer days were associated with more giving grooming but not more receiving grooming (Table IV - 2; Fig. IV - 1a). More giving grooming on longer days was driven by more frequent and longer giving grooming bouts (Table IV - 2; Fig. IV - 1 b & c). Days with more rain hours were associated with less giving grooming (Table IV - 2; Fig. IV - 2b), which was driven by less frequent and shorter giving grooming bouts (Table IV - 2). Days with more rain hours were associated with more receiving grooming (Table IV - 2), but as this result was likely due to technical rather than biological reasons (see *Discussion*), this was not further explored.

Total giving grooming time did not differ between reproductive states (Table IV - 2; cycling vs. pregnant: estimate±se = 0.052±0.098, t-value=0.531, *p*=0.596) but lactating females gave grooming more frequently than pregnant and cycling females (Table IV - 2). There was no significant difference between cycling and pregnant females in giving grooming frequency (estimate±se = 2.313±2.038, t-value = 1.135, *p*=0.257) or bout length (estimate±se = -0.065±0.402, t-value = -0.161, *p*=0.872). No difference in time spent receiving grooming was found between lactating and other reproductive states (Table IV - 2). Pregnant females received more grooming than cycling females (estimate±se = -1-.541±2,354, t-value=-1.436, *p*=0.152), but this effect was driven by one female (F15), and when removed from the analysis, receiving grooming time did not differ between reproductive states.

Other activities

The main models were significantly different from their null models (Table IV - S3). Longer days were associated with significantly more foraging and walking, but less resting (Table IV - 2; Fig. IV - 1a). Days with more rain hours and higher minimum temperatures were associated with more resting (Table IV - 2).

Cycling females spent less time resting than lactating females (Table IV - 2) and pregnant females (estimate±se = -13.163±2.044, t-value=-6.439, *p*<0.001) and more time foraging than lactating females (Table IV - 2) and pregnant females (estimate±se = 0.935±0.108, t-value=8.700, *p*<0.001). Moreover, lactating females foraged more than pregnant females (Table IV - 2). There was no significant difference between reproductive states in time spent walking per day (Table IV - 2; pregnant vs. cycling; estimate±se = -0.100±0.068, t-value=-1.487, *p*=0.138).

Temporal Shift Hypothesis: Shift activity in response to environmental time constraints?

Longer days were associated with more giving grooming during dusk and dawn (Table IV - 4). More giving grooming occurred at dusk after days with more rain hours (Table IV - 4; Fig. IV - 2b). There was no significant effect of day length or rain hours on giving grooming at night. More foraging occurred at dusk (Fig. IV - 2a; Table IV - 4) and at night (Table IV - 4) when days were shorter. Foraging was significantly negatively correlated with giving grooming during dusk and dawn (Pearson correlation: R = -0.19, *p*<0.001).

Table IV – 1: Grooming descriptives Grooming (giving and receiving) duration, number of bouts and mean bout length (mean±SD) during the day for n=10 female chacma baboons.

			Giving Grooming			*Receiving Grooming*		
ID	**Reproductive state**	**Days of data**	**Hours/ day**	**Bouts/ day**	**Bout length/ day (min)**	**Hours/ day**	**Bouts/ day**	**Bout length/ day (min)**
F2	Lactating	48	2.3 ± 0.6	44 ± 10	3 ± 1	1.5 ± 0.6	30 ± 12	3 ± 1
F4	Lactating	79	1.7 ± 0.5	31 ± 11	3 ± 1	1.8 ± 0.5	37 ± 9	3 ± 1
F5	Lactating	63	2.7 ± 0.7	37 ± 9	4 ± 1	0.9 ± 0.4	16 ± 8	3 ± 1
F6	Lactating	62	2.5 ± 0.7	36 ± 10	4 ± 1	0.9 ± 0.4	18 ± 8	3 ± 1
F7	Cycling	65	1.4 ± 0.4	32 ± 11	2 ± 1	0.8 ± 0.5	15 ± 8	3 ± 1
F9	Pregnant	62	2.5 ± 0.5	45 ± 10	3 ± 1	1.5 ± 0.6	28 ± 10	3 ± 1
F10	Lactating	42	2.2 ± 0.5	33 ± 10	4 ± 1	1.3 ± 0.6	29 ± 10	3 ± 1
F14	Lactating	24	1.5 ± 0.5	27 ± 13	3 ± 1	0.9 ± 0.3	21 ± 6	2 ± 1
F15	Cycling	35	2.1 ± 0.5	40 ± 9	3 ± 1	1.9 ± 0.7	44 ± 12	3 ± 1
	Pregnant	46	2.4 ± 0.6	40 ± 13	3 ± 1	2.2 ± 0.7	41 ± 12	4 ± 1
F19	Pregnant	17	1.4 ± 0.3	29 ± 8	2 ± 1	1.3 ± 0.3	27 ± 6	2 ± 1
	Lactating	25	1.7 ± 0.4	43 ± 12	2 ± 0	1.1 ± 0.3	29 ± 9	3 ± 1

Table IV – 2: Predictors of grooming activity Predictors of giving and receiving grooming during the day (total time between sunrise and sunset) for n=10 female chacma baboons for a total of n= 569 days (n=82 unique dates) and of giving grooming bout length and frequency. Baboon ID and Date included as random intercepts. Significant effects are in bold.

Predictor Variable	**Estimate**	**SE**	**T**	***p***
Giving Grooming (LMM1)				
Intercept	-1.131	0.780	-1.450	0.150
Day length (hrs)	0.289	0.067	4.333	**<0.001**
Rain hours	-0.099	0.026	-3.885	**<0.001**
Minimum Temperature	-0.017	0.026	-0.681	0.492
Dominance Rank	0.522	0.543	0.961	0.364
Reproductive state (Cycling)*	-0.120	0.156	-0.770	0.442
Reproductive state (Pregnant)*	-0.172	0.123	-1.402	0.162
Receiving Grooming (LMM2)				
Intercept	75.572	19.344	3.907	**<0.001**
Day length (hrs)	-2.327	1.670	-1.394	0.166
Rain hours	1.356	0.644	2.105	**0.039**
Minimum Temperature	1.324	0.636	2.081	**0.041**
Dominance Rank	0.046	12.992	0.004	0.997
Reproductive state (Cycling)*	-6.297	3.759	-1.675	0.095
Reproductive state (Pregnant)*	4.244	2.955	1.436	0.152
Giving Grooming Bout length (LMM3)				
Intercept	6.504	2.555	2.546	**0.013**
Day length (hrs)	0.582	0.207	2.813	**0.006**
Rain hours	-0.153	0.074	-2.062	**0.043**
Minimum Temperature	0.006	0.075	0.084	0.933
Dominance Rank	2.513	2.105	1.194	0.270
Reproductive state (Cycling)*	0.886	0.639	1.388	0.167
Reproductive state (Pregnant)*	0.951	0.502	1.895	0.059
Giving Grooming Bout frequency (LMM4)				
Intercept	11.324	14.931	0.758	0.450
Day length (hrs)	3.104	1.254	2.474	**0.015**
Rain hours	-1.674	0.471	-3.553	**<0.001**
Minimum Temperature	-0.273	0.468	-0.584	0.561
Dominance Rank	-2.923	10.818	-0.270	0.795
Reproductive state (Cycling)*	-9.579	3.242	-2.955	**0.003**
Reproductive state (Pregnant)*	-11.892	2.550	-4.664	**<0.001**

**Reference category: "Lactating"*

Note that response variables for LMM2 and LMM3 are transformed (see Table IV - S2 for details), thus effect sizes should not be compared to untransformed effect sizes (LMM1 and LMM4).

Table IV – 3: Predictors of other activities Predictors of resting, foraging and walking during the day (total time between sunrise and sunset) for n=10 female chacma baboons for a total of n=569 days (n=82 unique dates). Baboon ID and Date included as random intercepts. Significant effects are in bold.

Predictor Variable	**Estimate**	**SE**	**T**	***p***
Resting (LMM5)				
Intercept	114.559	18.812	6.090	**<0.001**
Day length (hrs)	-3.181	1.393	-2.284	**0.025**
Rain day (Y)	2.253	0.534	4.219	**<0.001**
Minimum Temperature	1.237	0.528	2.341	**0.022**
Dominance Rank	-17.707	19.217	-0.921	0.384
Reproductive state (Cycling)*	-10.173	3.375	-3.015	**0.003**
Reproductive state (Pregnant)*	2.991	2.632	1.136	0.256
Foraging (LMM6)				
Intercept	-4.077	1.019	-4.003	**<0.001**
Day length (hrs)	0.775	0.096	8.108	**<0.001**
Rain day (Y)	-0.039	0.038	-1.029	0.307
Minimum Temperature	-0.069	0.037	-1.858	0.067
Dominance Rank	0.086	0.362	0.238	0.818
Reproductive state (Cycling)*	0.544	0.158	3.442	**0.001**
Reproductive state (Pregnant)*	-0.391	0.127	-3.079	**0.003**
Walking (LMM7)				
Intercept	0.321	0.776	0.413	0.680
Day length (hrs)	0.164	0.073	2.244	**0.027**
Rain day (Y)	-0.025	0.030	-0.850	0.398
Minimum Temperature	-0.030	0.029	-1.051	0.297
Dominance Rank	0.201	0.295	0.681	0.517
Reproductive state (Cycling)*	-0.068	0.105	-0.656	0.513
Reproductive state (Pregnant)*	0.032	0.083	0.384	0.702

**Reference category: "Lactating"*

Note that the response variable for LMM5 is transformed (see Table IV - S2 for details) and should not be compared to untransformed effect sizes (LMM6 and LMM7).

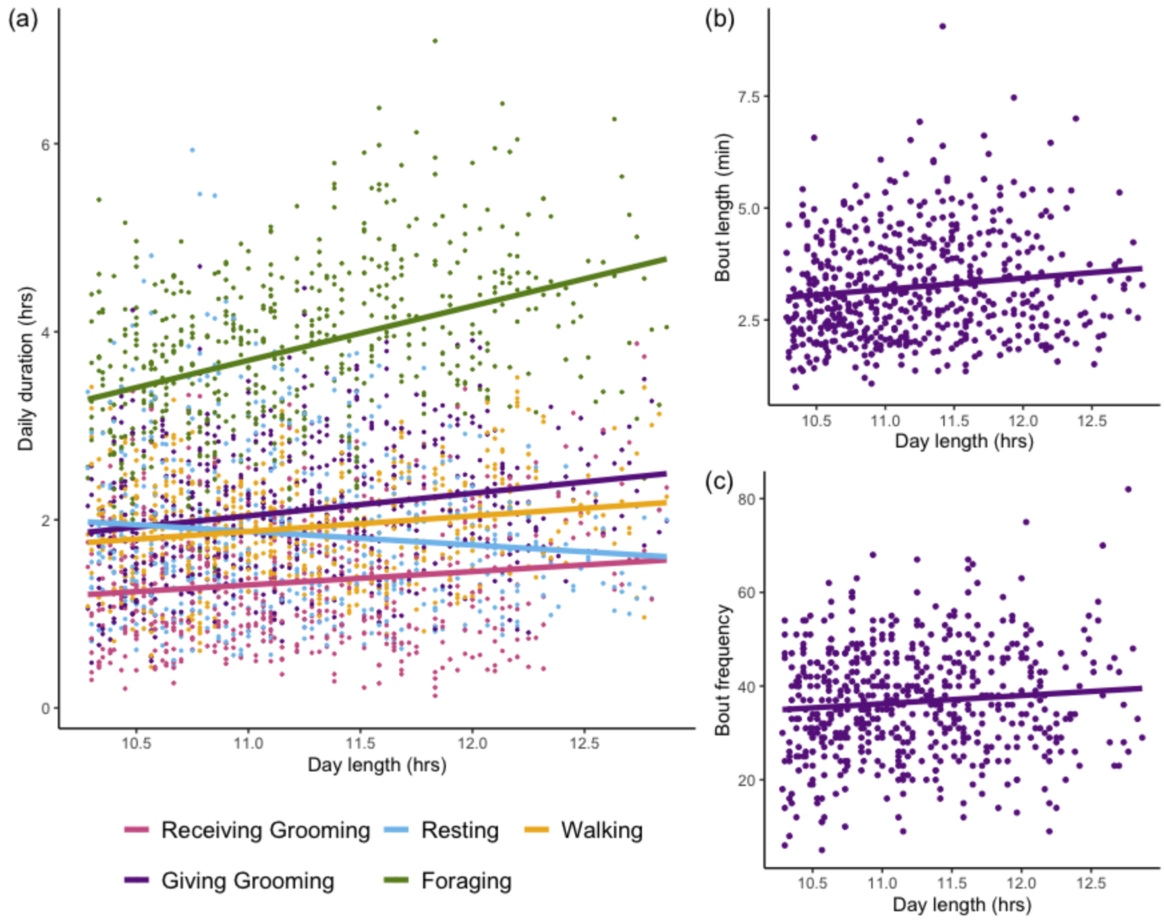


Figure IV – 1: Day length effects on baboon activity Effect of day length (hours) on daily activity for n=10 female chacma baboons. Points represent non-transformed data points with linear regression lines (Daily activity time ~ Day length). In function of increasing day length: **(a)** daily duration of activities, **(b)** giving grooming bout length and **(c)** and giving grooming bout frequency.

Table IV - 4: Predictors of dusk, dawn, and night activity Predictors of giving grooming and foraging time during dusk and dawn, and night hours across n=553 nights (n= 77 unique dates) for n=10 female chacma baboons. Baboon ID and Date included as random intercepts. Significant effects in bold.

Predictor Variable	**Estimate**	**SE**	**T**	***p***
Giving Grooming dusk & dawn (LMM8)				
Intercept	-0.351	7.631	-0.046	0.963
Day length (hrs)	2.111	0.600	3.517	**<0.001**
Dominance Rank	7.139	4.569	1.562	0.167
Reproductive state (Cycling)*	1.455	2.313	0.629	0.534
Reproductive state (Pregnant)*	-2.187	1.849	-1.183	0.242
Sleep site (Urban)	-0.084	0.943	-0.089	0.930
Giving Grooming dusk (LMM9)				
Intercept	1.234	7.991	0.154	0.876
Day length (hrs)	1.449	0.646	2.241	**0.027**
Rain hours	0.839	0.225	3.726	**<0.001**
Dominance Rank	5.474	3.786	1.446	0.188
Reproductive state (Cycling)*	3.155	1.877	1.681	0.100
Reproductive state (Pregnant)*	0.021	1.511	0.014	0.989
Sleep site (Urban)	-1.344	1.122	-1.198	0.235
Giving Grooming night (LMM10)				
Intercept	20.344	30.666	0.663	0.509
Day length (hrs)	3.185	2.476	1.286	0.201
Rain hours	1.612	0.907	1.777	0.080
Dominance Rank	31.789	14.037	2.265	0.057
Reproductive state (Cycling)*	1.767	6.476	0.273	0.786
Reproductive state (Pregnant)*	-6.832	5.176	-1.320	0.191
Sleep site (Urban)	7.678	4.439	1.730	0.088
Foraging dusk & dawn (LMM11)				
Intercept	49.730	6.448	7.713	**<0.001**
Day length (hrs)	-2.611	0.546	-4.778	**<0.001**
Dominance Rank	6.043	1.237	4.883	**<0.001**
Reproductive state (Cycling)*	1.782	0.837	2.130	0.059
Reproductive state (Pregnant)*	-0.846	0.797	-1.061	0.302
Sleep site (Urban)	1.418	0.977	1.452	0.151
Foraging night (LMM12)				
Intercept	8.852	0.742	11.928	**<0.001**
Day length (hrs)	-0.181	0.061	-2.959	**0.004**
Dominance Rank	0.492	0.211	2.329	**0.048**
Reproductive state (Cycling)*	0.420	0.119	3.527	**0.002**
Reproductive state (Pregnant)*	0.311	0.099	3.138	**0.003**
Sleep site (Urban)	-0.333	0.112	-2.975	**0.004**

**Reference category: "Lactating"*

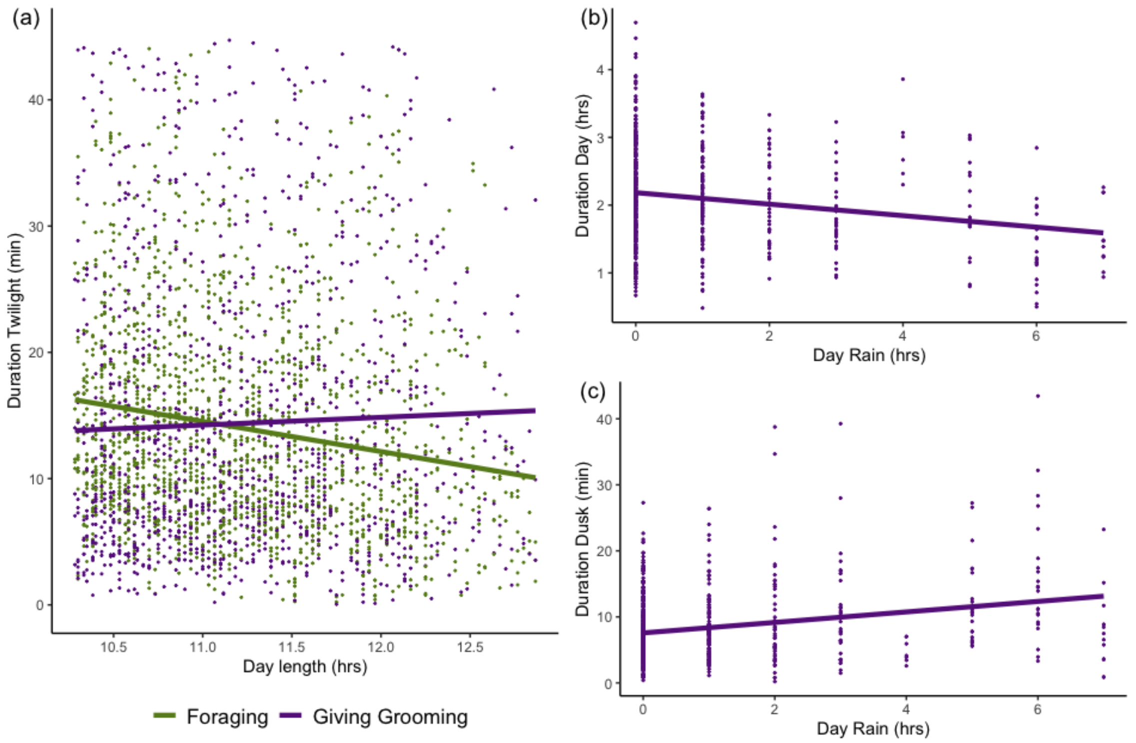


Figure IV - 2: Environmental effects on activity Effect of environmental time constraints on giving grooming and foraging for n=10 female chacma baboons. Points represent non-transformed data points with linear regression lines (Activity time ~ Day length or Rain hours per day): **(a)** giving grooming and foraging time during dawn and dusk in function of increasing day length; **(b)** giving grooming time during the day in function of hours with rain during the day; **(c)** giving grooming time during dusk in function of hours with rain during the preceding day.

Discussion

In this chapter, I tested if and how environmental factors shape activity, and grooming in particular, in wild female chacma baboons living in a highly seasonal habitat. In response to environmental time constraints, baboons might sacrifice grooming during the day ('reduction hypothesis') and/or compensate for 'lost' grooming time during the day by grooming outside of daylight hours (e.g., during dawn, dusk and night periods; 'temporal shift hypothesis'). In support of the 'reduction hypothesis', I found that baboons spent less time giving grooming on shorter days and on days with more rain hours (Fig. IV - 1a). This was explained by giving grooming bouts being both shorter (Table IV - 3; Fig. IV - 1b) and less frequent (Table IV - 3; Fig. IV - 1c). The 'temporal shift hypothesis' was partly supported. After days with more rain hours, baboons spent more time giving grooming at dusk (Table IV - 4; Fig. IV - 2b), suggesting they may be compensating after social time was reduced during the day. Conversely, baboons did not increase giving grooming during dawn and dusk in response to short days, but rather increased foraging (Fig. IV - 2a), suggesting that compensating for constrained foraging time takes priority over constrained social time when days are short. This was further confirmed by the significant negative correlation between foraging and giving grooming during dusk and dawn. Receiving grooming did not show comparable patterns to giving grooming, which could be due to biological and/or technical reasons which are discussed below. Taken together, these findings lend support to the two proposed ways in which grooming could be affected by environmental time constraints and by other activities which take biological priority (Dunbar et al., 2009), like foraging. I discuss my findings and the potential physiological consequences of these environmental temporal bottlenecks on grooming activity below.

At high latitudes, such as the Western Cape, animals need to contend with marked changes in day length within an annual cycle (Gaynor et al., 2004). In line with previous studies on baboons on the Western Cape reporting decreased grooming during winter (Chowdhury et al., 2021; Ellwanger, 2020; Hill et al., 2003; Lewis and O'Riain, 2017; van Doorn et al., 2010), I found that baboons spent less time giving grooming on shorter days (17 minutes less giving grooming for every hour decrease in day length, based on effect size in Table IV - 2). Regarding other activities, and similar to Van Doorn et al., 2010, winter was associated with less foraging and travelling, but more resting (although this increase was proportional, not absolute like in the present study). Differences in seasonal activity budgets between troops on the Western Cape could be due to differences in access to anthropogenic foods. Unlike troops that are exclusively wild foraging (Hill et al., 2003; Lewis and O'Riain, 2017), troops with access to anthropogenic foods (present study, Chowdhury et al., 2021; van Doorn et al., 2010) tend to have winter diets which are supplemented by high-calorie "sit-and-wait" foods (Chowdhury et al., 2021; van Doorn et al., 2010), which could result in less foraging and more resting time during winter (van Doorn et al., 2010). While access to anthropogenic foods has been linked to increased social time in other baboon populations (Altmann and Muruthi, 1988; Strum, 2010), it does not seem to offset the time constraint of short days in Western Cape troops who have access to human foods as winters are still associated with less time spent grooming (present study, Chowdhury et al., 2021; van Doorn et al., 2010). Decreases in social time when days are short have also been noted in other primates (Di Bitetti, 1997; Xiang et al., 2010) as well as other social animals, such as free-ranging horses (Kimura, 1998) and waterfowl (Beauchamp, 2012).

Along with shorter days, the winters on the Western Cape are also associated with higher rainfall (Cowling et al., 1996). Baboons spent less time giving grooming and more time resting on days with more rain hours (6 minutes less giving grooming for every hour in which it rained during the day based on effect size in Table IV - 2), presumably due to interrupting activities to shelter from rain (pers. obs., Fig. IV - S2b; noted in other primates: Bernstein and Mason, 1963; Hanya et al., 2018; Majolo et al., 2013). In theory, if sheltering together, this time could be used for grooming, as proximity could facilitate social contact and encourage 'tension reduction' through grooming (Judge et al., 2006); however, close proximity can also lead to decreased social contact to avoid conflict (Aureli et al., 1995; Judge and de Waal, 1993), which may explain the observed reduction in giving grooming here.

Given that grooming interactions can vary in quality (Fruteau et al., 2009; Saunders, 1988; Surbeck and Hohmann, 2015), I investigated variation in grooming bout length and frequency and found that shorter days were associated with both shorter and less frequent giving grooming bouts. Moreover, I found the same effect of rain hours on giving grooming, suggesting that these changes in grooming quality do not only occur gradually in response to day length, but can be short-term responses to sporadic environmental changes (e.g., "short-term optimization": Henzi et al., 2009). One interpretation could be that a reduction in giving grooming bout length reflects females reducing bout length gradually to the point where the number of bouts will eventually be capped (Henzi et al., 1997), and that, in this study, environmental time constraints drove females to both reduce grooming partners (reflected in fewer giving grooming bouts) and reduce the length of grooming bouts (reflected in shorter giving grooming bouts). This, in part, contrasts with findings by Ellwanger (2020), who found that while grooming frequency declined, the length of grooming bouts was preserved on shorter days. Having less frequent grooming bouts limited the number of grooming partners, but the maintenance of grooming bout length should allow for the reduced number of grooming relationships to remain reciprocal (Ellwanger, 2020). Indeed, a minimum time investment per grooming bout is expected for reciprocation to take place (Dunbar, 1992; Henzi et al., 1997; Manson et al., 2004). Although a direct comparison should not be made (here I investigate receiving and giving grooming separately, rather than as one grooming category), it is possible that using accelerometer-identified grooming revealed more subtle differences in average bout lengths across a day, which are harder to capture using focal data.

In response to environmental time constraints, activities may shift to different phases of the day-night cycle (Levy et al., 2019). Here, I found that on days with more hours of rain, baboons spent less time giving grooming during the day (Table IV - 2; Fig. IV - 2b) but spent more time giving grooming during dusk (Table IV - 4; Fig. IV - 2c). To my knowledge, this is the first evidence of social activity ‘lost’ during the day, being ‘compensated’ later in the day. Similar temporal patterns have however been noted for foraging. For instance, Przewalski horses (*Equus ferus przewalskii*) forage more at night if days are hot and disturbance of flying insects is high (Berger et al., 1999). Similarly, black grouse (*Tetrao tetrix*) forage later in the evening if experimentally induced human disturbance occurs during the day (Arlettaz et al., 2015). A similar ‘compensation’ for lost social time could have been expected in response to shorter day lengths (‘temporal shift hypothesis’) but was not found. Rather, baboons foraged more during dusk, dawn and night on shorter days (Table IV - 4; Fig. IV - 2a) and spent more time giving grooming during dusk and dawn on longer days (Table IV - 4; Fig. IV - 2a). This suggests that foraging during short days is given priority outside the daylight window as would be expected based on its biological priority (Dunbar, 1992), and as demonstrated by the negative correlation between grooming and foraging found in several primate studies (present study; Hill et al., 2003; Post, 1981; Saunders, 1988; Zhou et al., 2007).

As days get longer, and foraging becomes less constrained during the day, dawn and dusk can be used for social activity instead. Ayers et al. (2020) reported higher ‘general activity’ during the night when days were short in n=3 female chacma baboons studied in South Africa. While it was hypothesised that this time may be used strategically to compensate for the seasonal time constraint, the activity was ascribed to disturbed sleeping patterns rather than “true” activity taking place. However, the present study shows that grooming and foraging does take place during both twilight and night. While direct comparison is precluded, as dual-axis accelerometers used in Ayers et al. (2020) were not used to identify behaviours, it is possible that the nature of the activity may indeed differ due to characteristics of the field sites. In our study system, natural predators are absent (Beamish and O'Riain, 2014) and therefore being active at night may not carry the same risk as in troops where predation pressure is present (Ayers et al., 2020; Bidner et al., 2018). Moreover, our study troop used urban sleep sites almost 80% of the nights when collars were collecting data. Urban space use can alter behaviour substantially (Fehlmann et al., 2020) and with artificial illumination at night (Fig. IV - S2a) could allow for 'day-time typical' activity to take place (Russart and Nelson, 2018).

In contrast to the clear environmental effects on giving grooming, receiving grooming was unaffected. While unintuitive - for each giver there is a receiver - increased giving grooming in the absence of increased receiving grooming could occur if females expand their grooming network as day length increases (as has been noted: Ellwanger, 2020; Hill, 1999), by including individuals that are more likely to receive than to give grooming, i.e., juveniles and immature adults (Cheney, 1978; Johnson, 1984). Most studies on grooming focus on adults, but Hill (1999) showed that female baboons, when faced with ecological constraints (shorter days), sacrifice grooming relationships with immatures and juveniles in favour of adult females. Given that accelerometer-identified giving grooming does not discriminate between the age-class of the recipient, this could explain the observed seasonal effect on giving but not receiving grooming in the present study. Alternatively, this could be due to the confusion between receiving grooming and resting (see Chapter 2). Resting time was higher on long days (Table IV - 3; Fig. IV - 1a), which could result in the instances of 'false receiving grooming' (resting) also increasing, hereby diluting the estimated time of 'true receiving grooming' (which trends upwards, similar to giving grooming; see Fig. IV - 1a). Confusion seems likely when considering the grooming response to rain hours per day, where giving grooming decreased while receiving grooming increased (Table IV - 2). Rain is associated with lower VeDBAs (Morgan et al., in prep), which increases the likelihood of confusion between receiving grooming and resting (see Chapter 2). As such, inactivity during rain (as found here and in other primates: Hanya et al., 2018; Majolo et al., 2013), may be confused with receiving grooming. Finally, resting may look different during long, warm days compared to short, cold days (maximum temperature increased from 12.5°C to 25°C during the collar-period). Cold temperatures are associated with hunched body postures to retain heat (Stelzner and Hausfater, 1986), whereas hotter temperatures are associated with more spread-out postures (e.g., lying down with extended limbs) to allow heat to dissipate

(Dasilva, 1993; Lopes and Bicca-Marques, 2017), which may result in lower VeDBAs (Diosdado et al., 2015; Graf et al., 2015). Thus, there could be a seasonal effect on the confusion between receiving grooming and resting that could contribute to the absence of an effect of day length on receiving grooming.

Female reproductive state also has marked effects on grooming activity in primates (Baniel et al., 2016; Maestripieri, 1994; Mitchell and Tokunaga, 1976). Despite small and unbalanced sample sizes of female reproductive states (Table IV - 1), some effects were found. Lactating females tended to spend more time giving grooming (Table IV - 2) and groomed more frequently than cycling and pregnant females (Table IV - 3). This may be explained by the fact that lactating females groom their infants as well as other adult females (Nash, 1978), and both types of interactions would count towards the accelerometer-identified giving grooming times. In terms of the other behaviours, patterns also resemble previously described effects of reproductive state. Both pregnant and lactating females foraged less and rested more than cycling females (Table IV - 3), which points towards an energy-conserving strategy (Vasey, 2005), where the increased energetic demands of these reproductive states (Gittleman and Thompson, 1988) are offset by reduced energy expenditure rather than increased energy intake. This has been reported for captive pregnant baboons (Schlabritz-Loutsevitch et al., 2007) and for wild lactating baboons (Barrett et al., 2006), and could also be linked to increased vigilance while caring for vulnerable infants in the wild (Barrett et al., 2006).

Conclusions

Given the alleviating effect of grooming on HPA-axis activity (Shutt et al., 2007; Wittig et al., 2008; Wittig et al., 2016; Wooddell et al., 2017), the environmentally imposed time constraints on grooming time and quality could have implications for baboon physiological status. In Chapter 3, I show that shorter days are associated with increased fGCs, confirming previous findings (Chowdhury et al., 2021; Weingrill et al., 2004). In the present Chapter, I find evidence for reduced giving grooming when days are shorter, suggesting a link between reduced giving grooming and increased HPA-axis activity. That being said, foraging also decreased on shorter days, and while winter was not found to be more energetically challenging than summer in our study troop (Fürtbauer et al., 2020), it is also possible that reduced time foraging is linked to higher fGCs in winter. Furthermore, in Chapter 3, I show that rain days are associated with increased uGCs. Here, I find that giving grooming is reduced on days with more hours with rain. Similar to short days, this environmental constraint could pose a stressor by limiting the time for grooming. Moreover, if resting during rain-bouts is associated with close proximity, this crowding could increase physiological stress-levels as shown e.g., in captive baboons (Pearson et al., 2015). Chapter 4 will investigate direct links between grooming and uGCs and fGCs through matching grooming to GC measures directly.

Appendix

Table IV - S1: Overview of supplementary material for Chapter 4

Content	**Tables & Figures**
S1: Methods	
Data transformation	Table IV - S2
Activity across 24-hour cycle	Fig. IV – S1
S2: Results	
Null model comparisons	Table IV - S3
S3: Discussion	
Night and rain activity photos of baboons	Fig. IV – S2

Table IV - S2: Transformation of response variables in LMMs

Model	**Response variable transformation**
Giving Grooming (LMM1)	Raw data (hrs)
Receiving Grooming (LMM2)	Sqrt-transformed (seconds)
Giving Grooming Bout length (LMM3)	Sqrt-transformed (seconds)
Giving Grooming Bout frequency (LMM4)	Raw data (n)
Resting (LMM5)	Sqrt-transformed (seconds)
Foraging (LMM6)	Raw data (hrs)
Walking (LMM7)	Raw data (hrs)
Giving Grooming twilight (LMM8)	Sqrt-transformed (seconds)
Giving Grooming dusk (LMM9)	Sqrt-transformed (seconds)
Giving Grooming night (LMM10)	Sqrt-transformed (seconds)
Foraging twilight (LMM11)	Sqrt-transformed (seconds)
Foraging night (LMM12)	Log-transformed (seconds)
*Foraging*Grooming Pearson Correlation*	Both sqrt-transformed

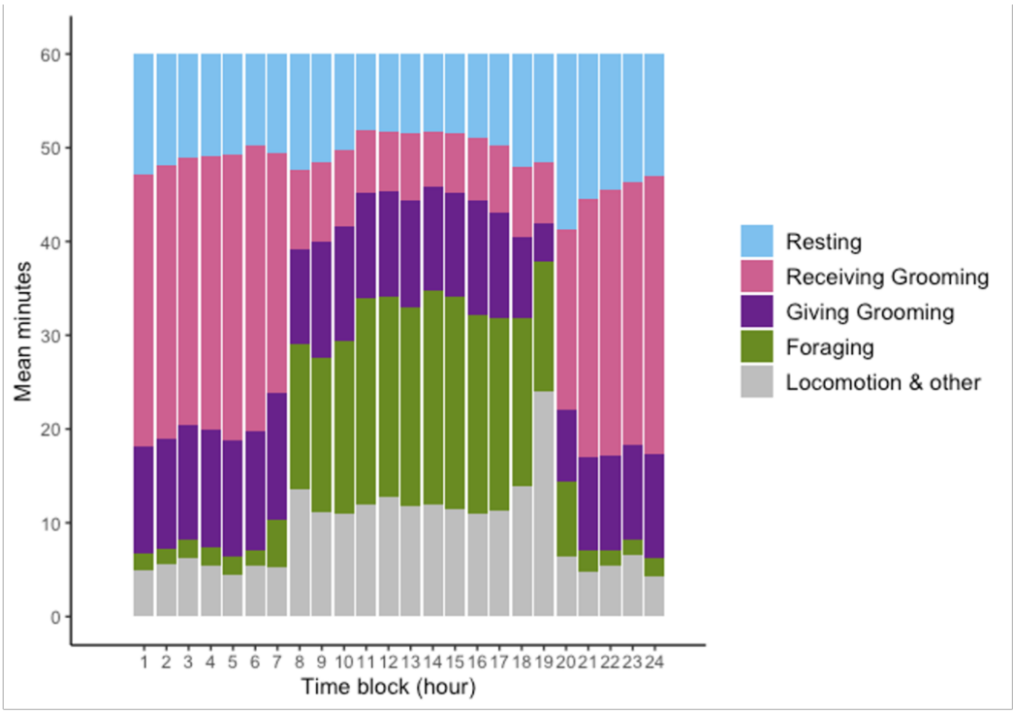


Figure IV - S1: Mean minutes per hour block across n=569 baboon days (n=82 unique dates) for n=10 female chacma baboons. Time block represents hour of the day on a 24-hour scale (1= 1:00 AM, 2 = 2:00 AM, etc.). During the collar-period sunrise ranged from 06:06 to 07:44 and sunset ranged from 18:01 to 18:58. 'Locomotion & other' includes walking, running and unclassified behaviours. Note that high 'Receiving Grooming' means during the night are expected due to confusion with resting (see Chapter 2).

Table IV - S3: Full model vs. null model comparisons. See *Methods* and Table IV - 2 & IV - 3 for full models. Null models contained only random intercepts. Models were compared using 'anova' R function. Significant terms in bold.

Model	**$\chi 2$**	***p***
Giving Grooming (LMM1)	33.292	**<0.001**
Receiving Grooming (LMM2)	29.844	**<0.001**
Giving Grooming Bout length (LMM3)	17.525	**0.007**
Giving Grooming Bout frequency (LMM4)	34.032	**<0.001**
Resting (LMM5)	60.729	**<0.001**
Foraging (LMM6)	114.430	**<0.001**
Walking (LMM7)	9.604	0.142
Giving Grooming twilight (LMM8)	18.925	**0.002**
Giving Grooming dusk (LMM9)	26.653	**<0.001**
Giving Grooming night (LMM10)	19.693	**0.003**
Foraging twilight (LMM11)	52.096	**<0.001**
Foraging night (LMM12)	28.767	**<0.001**

Figure IV - S2: (a) Baboons at dusk (18:38 SAST; local time) in the urban space near an urban sleep site. Sunset occurred at 18:01. Exposure was increased from the original picture to better see the baboons. **(b)** F9 sheltering from the rain underneath rocky outcrops with other baboons behind her (not visible). Photo credit: Charlotte Christensen

Chapter 5: Linking high-resolution grooming data to faecal and urinary glucocorticoids: a short-term cost for a long-term benefit?

Charlotte Christensen[1], Anna M. Bracken[1], M. Justin O'Riain[2], Michael Heistermann[3], Andrew J. King[1], Ines Fürtbauer[1]

PC: Charlotte Solman

Affiliations:
[1]Biosciences, School of Biosciences, Geography and Physics, Faculty of Science and Engineering, Swansea University, SA2 8PP Swansea, United Kingdom
[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch, 7701, South Africa
[3]Endocrinology Laboratory, German Primate Centre, 37077, Göttingen, Germany
Statement of contributions

Statement of contributions:
CC and IF designed the study. CC and AB built the collars, conducted the fieldwork and collected behavioural observations and the faecal and urine samples. JOR provided logistical support in the field. CC compiled the data and conducted the statistical analysis with advice from IF. CC processed and extracted faecal samples supervised by IF, MH analysed faecal samples for glucocorticoid metabolites and IF analysed the urine samples for glucocorticoid metabolites. CC wrote the chapter with critical review, edits, and discussion from IF and final edits from AJK.

Chapter 5: Linking grooming to glucocorticoid concentrations in chacma baboons

Abstract

Social bonds increase individual fitness in a range of social mammals. In primates, these social bonds are built, maintained, and repaired through grooming. Grooming has been linked to reduced HPA-axis activity, suggesting that a potential pathway by which social bonds increase fitness is via reducing the physiological wear-and-tear of chronically elevated HPA-axis activity. What proximate role physical touch (i.e., the act of grooming itself) plays in down-regulating HPA-axis activity is debated. While long-term measures of social (grooming) bonds have been found to be negatively correlated with HPA-axis activity, few studies have directly linked grooming to subsequent glucocorticoid measurements. This, however, could inform whether grooming directly influences HPA-axis activity. Here, I investigate the physiological consequences of giving and receiving grooming, using accelerometer-identified grooming (total duration, bout frequency, and mean bout length) from n=10 female chacma baboons combined with non-invasive faecal and urinary glucocorticoid measures (fGCs and uGCs) as markers of HPA-axis activity. Consistent with previous work, I found a negative (but non-significant) correlation between individual mean fGCs and mean grooming rates obtained from focal data (±2.5 months) and accelerometer data (±1.5 months). However, when matching grooming to each GC measurement, I found that more grooming, and in particular, giving grooming, was followed by higher fGCs and uGCs. This short-term upregulation of HPA-axis activity suggests a short-term, likely psychosocial, cost of grooming, which to date has only been documented on a behavioural level (e.g., increase in self-directed behaviours indicative of anxiety). This finding further suggests that, in the wild, grooming may not be as tension-reducing as studies in captivity suggest. Nevertheless, social bonds are serviced through grooming and the overall negative association between grooming and fGCs suggests that investing time in grooming ultimately leads to overall reduced HPA-axis activity, with implications for health and fitness.

Introduction

Social bonds positively impact fitness (Snyder-Mackler et al., 2020), and long-term studies on various social mammals have shown increased survival and reproductive success for individuals with strong social bonds (Archie et al., 2014; Barocas et al., 2011; Feldblum et al., 2021; Nuñez et al., 2015; Silk et al., 2003a; Silk et al., 2010b; Stanton and Mann, 2012). Social bonds can facilitate access to fitness-relevant resources such as huddles which provide thermoregulatory benefits (Campbell et al., 2018; McFarland et al., 2015), food through increased tolerance (King et al., 2011; Tiddi et al., 2012; Ventura et al., 2006) and protection against predators (Micheletta et al., 2012) or aggressive conspecifics (Nguyen et al., 2009; Palombit et al., 1997). Additionally, social bonds may confer fitness benefits through modulating HPA-axis activity (Hostinar et al., 2014). HPA-axis activity involves the release of steroid hormones called glucocorticoids (Sapolsky et al., 2000). Glucocorticoids serve important functions in maintaining homeostasis during environmental and life-history challenges (Romero et al., 2009; Sapolsky et al., 2000), but can be detrimental to health and survival in human and non-human primates with high cumulative exposure (Campos et al., 2021; Juster et al., 2010; Sapolsky, 2021). In primates, social bonds have been shown to reduce HPA-axis activity, potentially reducing these detrimental effects to health (Crockford et al., 2008; Wittig et al., 2008; Young et al., 2014).

Social bonds are maintained through allo-grooming (the social grooming of conspecific; hereafter grooming) (Cooper and Bernstein, 2000; Dunbar, 1991; Silk et al., 2006a). Different aspects of grooming may be important for modulating HPA-axis activity, with some studies highlighting the effect of focussed grooming networks (Crockford et al., 2008; Wittig et al., 2008), grooming clique size (Shutt et al., 2007), grooming balance (Yamanashi et al., 2018) and grooming partner identity (Fürtbauer et al., 2014), but also total time recorded grooming (Engh et al., 2006a; Shutt et al., 2007; Wooddell et al., 2017). While it is clear that social bonds have ultimate fitness benefits (see above) and that grooming is a fundamental part of maintaining these bonds (Silk et al., 2006b), it is less clear whether grooming serves a ‘means to an end’ (i.e., servicing social bonds), ultimately leading to lower overall HPA-axis activity or whether grooming has direct (short-term) consequences for HPA-axis activity. The former would suggest that the physiological benefits are an indirect consequence of grooming, where the forged social bonds provide support or access to resources (see examples above) or influence the perception of stressors (*sensu* 'social buffering': Crockford et al., 2017; Hostinar et al., 2014). The latter option (a direct link) would suggest that grooming in and of itself reduces HPA-axis activity, potentially through a neurochemical pathway mediated by social touch (Morrison, 2016; Walker and McGlone, 2013), which may help to reinforce grooming behaviour (Jablonski, 2021). For the purpose of investigating the direct consequences of grooming, and the potential role in HPA-axis activity modulation, it is necessary to distinguish between these short- and long-term benefits of grooming (Pérez and Veà, 1998; Russell and Phelps, 2013). In the long term, both receiving (Gust et al., 1993) and giving (Shutt et al., 2007) grooming is associated with lowered HPA-axis activity, but whether there is a direct short-term effect is not clear.

The short-term beneficial effects of receiving grooming, often described as ‘hedonic’ or ‘tension-reducing’, seem intuitive (Dunbar, 2010). In primates, recipients of grooming show decreased heart rate (Aureli et al., 1999; Boccia et al., 1989) and lower behavioural indices of stress, such as auto-grooming, yawning, body-shaking and scratching (Goosen, 1981; Schino et al., 1988; Ueno et al., 2015). Similarly, horses and cows also show reduced heart rates when being groomed by a conspecific (Sato, 1993) or a human mimicking conspecific grooming (Feh and de Mazières, 1993). Oxytocin and endorphins are two key neuropeptides that are released prior to or in response to being groomed and both have ‘rewarding’ effects which may play a role in creating the neurochemical environment in which social bonds can develop (reviewed in: Depue and Morrone-Strupinsky, 2005; Dunbar, 2010). Oxytocin down-regulates HPA-axis activity (Heinrichs et al., 2003; Szczepanska-Sadowska, 2008), and thus may be important in down-regulating HPA-axis activity in response to being groomed (Brent et al., 2014; Crockford et al., 2017). Although human studies have shown that physical contact can reduce cortisol levels (Ditzen et al., 2007; Grewen et al., 2005), there are, to my knowledge, no studies on non-human animals that directly link receiving grooming to reduced HPA-axis activity.

In contrast to receiving grooming, giving grooming can be seen as paying a short-term cost (*sensu* biological markets: Noë and Hammerstein, 1995; Russell and Phelps, 2013). However, some lines of evidence suggest that giving grooming may also be directly tension-reducing, as it can be followed by lower behavioural indices of stress in primates

(Aureli and Yates, 2010; Ueno et al., 2015) and birds (Radford, 2012), suggesting that giving grooming may be 'self-rewarding' (e.g., De Waal et al., 2008). In humans, being actively prosocial (e.g., helping others) is linked to stress buffering effects (Brown and Brown, 2017). For instance, people have lower salivary cortisol on days where they volunteer at hospitals, schools or other organisations compared to days they do not (Han et al., 2018). Again, oxytocin may play a modulating role here (see above), which in chimpanzees was found to be released regardless of whether grooming was given or received (Crockford et al., 2013). However, if giving grooming reduces HPA-axis activity directly, the pathway is likely not exactly the same as for receiving grooming. First, the 'hedonic' benefits are likely not equal when engaging in the 'labour' of giving grooming versus being the stationary recipient (Russell and Phelps, 2013). Second, the pathway may be psychosocial, with giving grooming serving as a mitigation strategy against potential aggression from nearby conspecifics, hereby reducing tension following giving grooming (Aureli and Yates, 2010).

It is important to acknowledge that a key factor in direct HPA-axis regulation may not be social touch alone (Crockford et al., 2017), but also whether the grooming partner is a close social bond. In chimpanzees, urinary oxytocin and glucocorticoid levels do not up- and down-regulate in the same way when grooming with non-bond partners compared to bond partners (Crockford et al., 2013; Wittig et al., 2016). However, grooming with a close social bond still downregulates HPA-axis activity more than merely being in their presence (Wittig et al., 2016). In humans, physical touch by strangers (e.g., massages) reduces cortisol (Field et al., 2005) or precursors thereof (adrenocorticotropin hormone ACTH; Morhenn et al., 2012) and in Japanese macaques behavioural indices of stress are reduced even if the donor is not a close social bond (Field et al., 2005; Ueno et al., 2015), suggesting that the physiological benefits of physical touch, at least for the recipient, may not always be limited to close social bonds. Giving grooming, on the other hand, was found only to have a tension-reducing effect when the grooming is given to an affiliated individual in Japanese macaques (Ueno et al., 2015). Taken together, both receiving and giving grooming could have short-term down-regulating effects on HPA-axis activity, but probably operate through different pathways.

Investigating potential direct effects of grooming on HPA activity would further our understanding of whether long-term benefits of social bonds are subserved by directly ‘rewarding’ aspects of grooming (see above), as has been suggested (Aureli and Yates, 2010; Russell and Phelps, 2013). However, to date, most studies on the physiological correlates of grooming link average faecal glucocorticoids (fGCs) to average grooming rates over a period of time, with resolutions ranging from one month (Beehner et al., 2005; Crockford et al., 2008; Fürtbauer et al., 2014) to two months (Ellis et al., 2019; Shutt et al., 2007) to three months (Engh et al., 2006a). These studies have been instrumental in illustrating the presence (or absence) of the hypothesised negative relationship between grooming and HPA-axis activity but establishing causality in these cases is challenging. Rather than demonstrating HPA-axis activity decreased in direct response to grooming, they demonstrate correlations between grooming and HPA-axis activity (Shutt et al., 2007; Wooddell et al., 2017). Hence, individuals that groom more may show reduced HPA-axis activity, or individuals with lower HPA-axis activity to begin with, may spend more time grooming.

There are, however, exceptions in which studies use a time-lagged approach to test whether changes in grooming metrics are followed by changes in HPA-axis activity. For instance, Wittig et al. (2008) found female baboons who increase the concentration of the grooming network (i.e., focussed their grooming on fewer individuals) from one week to the next (week -2 to week -1), show a decrease in fGCs from week -1 to week 0, suggesting a causal link. In Barbary macaques, continuous grooming data collected on day -1 did not predict fGCs on the following day (Edwards et al., 2013). More recently, the use of urinary glucocorticoids (uGCs), which are better suited for measuring short-term changes in HPA-axis activity (Behringer and Deschner, 2017), has further opened up the possibility for investigating direct consequences of grooming. For instance, Wittig et al. (2016) found that grooming (or resting) with a bond partner within an approximately 2-hour window reduced uGCs relative to the baseline. These two aforementioned studies (Edwards et al., 2013; Wittig et al., 2016) are, to my knowledge, the only examples of continuous data collection (rather than using averaged rates) of grooming being time-matched to fGCs and uGCs. Methods which allow grooming data to be collected continuously, such as collar-mounted accelerometers (Chapter 1), would allow to time-match fGCs and uGCs measurements to grooming data to investigate potential direct effects.

In this chapter, I investigate the short-term and longer-term associations between grooming and HPA-axis activity. First, following the traditional approach, I test whether focal and accelerometer-identified grooming rates correlate with mean fGCs. I also test whether average daily grooming bout length and frequency derived from accelerometer data is correlated with mean fGCs. Some studies have found long-term negative associations between grooming rates (giving and receiving) and GCs (Engh et al., 2006a; Gust et al., 1993; Shutt et al., 2007; Wooddell et al., 2017) while others have not (Beehner et al., 2005; Wittig et al., 2008), which could be due to differences in study systems or the context in which the grooming was taking place (see e.g., discussion in Wittig et al., 2008). Second, I test whether accelerometer-identified giving and receiving grooming time, bout length and bout frequency time-matched to uGC and fGC measures negatively predict GCs. Based on the available literature on behavioural indices of reduced stress during and in the immediate aftermath of receiving (Aureli et al., 1999; Boccia et al., 1989; Goosen, 1981; Schino et al., 1988) and giving (Aureli and Yates, 2010; Ueno et al., 2015) grooming, I predict both giving and receiving grooming to be associated with lower fGCs and uGCs.

Methods

Study site and subjects

The study was conducted on a troop of wild chacma baboons consisting of approximately 50 individuals (n=21 adults) in Da Gama Park, Western Cape, South Africa (-34.15562°N, 18.39858°E) between July and November 2018. Here, I focus on n=10 females for which I have continuous accelerometer-identified grooming data (Chapter 1) which can be time-matched to fGCs and uGCs.

Behavioural data from direct observations

Grooming data was collected during 30-minute focal follows (Altmann, 1974) between August and November 2018. Giving and receiving grooming were recorded in detail to the nearest second. If the grooming interaction was still ongoing by the end of the 30-min focal period, the focal observation was continued until the end of the grooming bout

(Chancellor and Isbell, 2009). Rates were calculated by dividing the total time spent giving or receiving grooming by the total observation time (time during which the focal was visible). For more details on focal data collection, see Chapter 2. For the long-term analysis, I used the focal follows collected across approximately 2.5 months (between 03/08/2018 and 15/10/2018) from n=7 females (n=3 pregnant females were excluded from the analysis; see '*Statistical analysis*'). This resulted in 126 hours of focal data, mean±SD = 11.5±1.7 hours from 24±8 focal follows per female.

Behavioural data from accelerometers

Giving and receiving grooming was obtained from collar-fitted tri-axial accelerometers. Random forest models were trained and validated using video-labelled accelerometer data collected while the baboons were wearing the collars. For more details on the extraction of grooming from accelerometer data using machine learning, see Chapter 2.

For the long-term analysis, I used the accelerometer-identified receiving, giving and overall grooming rate, mean daily bout length and mean daily frequency for n=7 females (excluding n=3 pregnant females, see '*Statistical analysis*'). Rates were calculated by dividing the total number of seconds receiving or giving grooming during the day divided by total daytime (time between sunrise and sunset). To obtain mean daily grooming bout length, I added the daily mean bout lengths together and divided this by the total number of days for each individual (number of days dependent on how long collars were active for; see Table II – S2 in Chapter 2). Similarly, mean daily grooming bout frequencies was calculated by adding together the total number of grooming bouts per day and dividing it by the number of days. Because accelerometer data was collected for variable durations for each individual (Table II – S2), the number of accelerometer days varied (mean±SD=55±18 days). Only full days of accelerometer data were used for calculations.

For the short-term analysis, in which grooming was matched to uGCs and fGCs (see '*Matching grooming to GCs*'), I used accelerometer-identified total durations of giving and receiving grooming within the relevant time-windows preceding sample collection (i.e., 'Peak period' in Fig. V - 1). From this total duration, I also calculated mean bout length and total bout frequency. Mean bout length was the mean number of minutes engaged in continuous receiving or giving grooming within a given time window. Bout frequency was the total number of new bouts within a given time-window. For more details on grooming quality, see Chapter 4.

Hormone data

For the present analysis which focusses on n=10 female baboons for which there is continuous accelerometer-identified grooming data, n=176 fGCs and n=133 uGCs measures could be matched (collar period between 30/7/2018 to 14/10/2018; exact duration of collar period differs between individuals; see Table II – S2 in Chapter 2).

To obtain faecal and urinary glucocorticoid metabolite concentrations (fGCs and uGCs respectively), faecal extracts were analysed for immunoreactive 11β-hydroxyetiocholanolone (Heistermann et al., 2006) and urine samples were analysed using commercial enzyme-linked immunosorbent assay kits (ELISA; IBL, Hamburg, Germany; Cat.-no.: RE52241). fGCs are expressed in ng/g and uGCs in ng/ml. For further details on sample collection, processing and laboratory analyses see Chapter 3.

Due to co-variation between receiving grooming and hour of the day which was identified during the preliminary analysis for this chapter (VIF > 2), I used corrected uGCs values which take into account the diurnal decline in uGCs throughout the day (Wittig et al., 2016). This allowed me to run the model without including hour of sample collection as a fixed effect (see Chapter 3). Based on the estimate obtained in Chapter 3 for the full female model, there was an average decrease of 11.5% in logged uGCs per hour. I used the following formula:

$$\text{uGC} + (11.5*h)/100$$

where the h represents the number of hours since 6:00 (the earliest hour of sample collection; all samples were collected between 6 and 18 hours). Corrected log-transformed uGCs values were used as the response variable in all uGCs models (see Fig. V - S1 for log-transformed and corrected log-transformed uGC-values plotted against hour of collection).

Matching grooming to GCs

Long-term relationship between grooming and fGCs

To investigate the long-term relationship between grooming and GCs, I correlated individual average grooming rates from focal data and accelerometers to individual fGCs averaged over a 2.5 month focal-period (mean±SD = 26±4 samples per individual) and a period adjusted for accelerometer duration (see Table II – S2 in Chapter 2) (mean±SD = 23±6 samples per individual) respectively, for n=7 females.

Short-term effects of grooming on uGCs and fGCs

To time-match fGCs and uGCs to grooming data, (i) a time lag needed to be accounted for and (ii) a grooming time-window needed to be established. The peak excretion in faeces of infused steroids in captive female baboons (*Papio cynocephalus cynocephalus*) was 36.4 hours after steroid infusion (Wasser et al., 1994). Accordingly, baboon studies in the wild have used a 2-day lag between fGCs and the variable of interest (Bergman et al., 2005; MacLarnon et al., 2015), which also corresponds to the biological validation for the Da Gama troop (Chapter 3), thus I used a (i) 2-day time lag. Because fGCs provide a cumulative measure of HPA-axis activity (Behringer and Deschner, 2017), a single grooming event is unlikely to be captured in fGCs, thus a meaningful time period which reflects a 'grooming state' needs to be considered. Following previous work which time-matched behavioural data to fGCs (Edwards et al., 2013), I used a (ii) time-window that corresponds to the time-lag for GC excretion into faeces. Thus, I test the effect of grooming recorded over a 2-day block (days -2 and -3), preceding a 2-day lag (day -1 and day 0) from sample collection; see Fig. V - 1a). Due to the confusion between receiving grooming and resting at night (Chapter 2; Fig. II -S7), only day-time grooming was used for the fGCs analysis.

The peak excretion in urine of infused steroids in captive female baboons was 4.5 hours, which corresponded to the first urine void (Wasser et al., 1994). Similar work conducted on chimpanzees found peak excretion to occur between ±2 hours (the first void) and 4.8

hours (the second void) (Bahr et al., 2000). Considering that urine excretion rates and volumes vary depending on hydration levels (White et al., 2010), events occurring earlier than 4.5 hours before voiding could be reflected in uGCs in baboons. As such, I used a (i) 2-hour time lag to ensure potentially relevant behavioural data was not excluded. I based the grooming time-window on previous work matching grooming to uGCs in chimpanzees, which considered a period of 135 minutes (Wittig et al., 2016). Here, I use (ii) a 2-hour window (which matches the time lag, as done for fGCs; see Fig. V – 1c). To verify whether results for receiving grooming would differ if only day-time grooming was used (receiving grooming and resting are more prone to confusion at night; Chapter 2; Fig. II - S7), I ran an additional analysis excluding samples for which the ‘Peak period’ (Fig. V - 1) included night hours (leaving n= 80 urine samples collected after 11:00). Results for receiving grooming are comparable (Table V – S3)

Statistical analysis

All analyses were run in R Studio version 1.4.1717. For the LMMs, I used the R package ‘lmerTest’ (Kuznetsova et al., 2017). Response and predictor variables were transformed to meet normal distribution where necessary (see Table V – S2 for transformations). Normality assumptions were visually confirmed by plotting residuals in Q-Q plots using the R function ‘qqnorm’. To test for collinearity between predictor variables, I used the R package ‘car’ (Fox et al., 2012). All predictors included in the models had Variation Inflation Factors (VIFs) below 1.5 (VIF < 3 is considered a stringent cut-off to rule out collinearity: Zuur et al., 2010).

Effect of grooming on GCs

To test for the long-term relationship between grooming and fGCs, I used Spearman’s correlations to test whether mean giving, receiving and overall grooming rates (both focal and accelerometer-identified) and average fGCs were correlated (n=7 females). I also tested whether daily mean bout length and bout frequency were correlated with average fGCs. As gestation is associated with increased fGCs (see Chapter 3; Gesquiere et al., 2008; Weingrill et al., 2004), and reproductive state cannot be controlled for in simple correlations, I excluded n=3 pregnant females from these analyses.

To test for the short-term effect of grooming on (log-transformed) fGCs (LMM1), I fitted total duration of giving and receiving grooming across days -2 and -3 relative to sample collection (Fig. V - 1a) as a fixed effect. To test how quality of grooming affected fGCs (LMM2), I ran another model testing for the effect of mean bout length and bout frequency across days -2 and -3 relative to sample collection (Fig. V - 1a). In both models (LMM1, LMM2), I controlled reproductive state (pregnant versus non-pregnant), day length, and urine contamination (see Chapter 3). Baboon ID and Date were fitted as random intercepts. I used day-time data only, due to the differences in activity budgets between night and day (Fig. IV – S1 in Chapter 4).

To test for the short-term effect of grooming on log-transformed, corrected uGCs (see '*Hormone data*'), I fitted total time spent giving and receiving grooming (LMM3) and grooming bout length and frequency (LMM4) within the 2-hour time-window before the 2-hour lag-period as a fixed effect (Fig. V - 1c). In each model, I controlled for rain day (yes/no) and collection method (Salivette or pipette) (see Chapter 3). Baboon ID and Date were fitted as random intercepts.

Effect of GCs on grooming

The finding that grooming during the 'Peak period' (see Fig. V – 1a & 1c) was positively associated with fGCs and uGCs (see *Results*: LMM1 – LMM4), prompted further analysis. A possible interpretation is that there may have been an underlying stressor causing a behavioural (grooming) and physiological (fGCs/uGCs) response (e.g., 'tend-and-befriend': Taylor et al., 2000), which resulted in this positive association. In this case, one would expect that periods of increased physiological stress (as indicated by higher fGCs and uGCs), should be marked by more grooming generally, and that more grooming should follow, not just precede (LMM1-LMM4), high HPA-axis activity. To investigate this, I tested whether giving and receiving grooming during the 2-day 'Lag period' for fGCs (Fig. V - 1b) or the 2-hour 'Lag period' for uGCs (Fig. V – 1d) were predicted by fGCs (LMM5; LMM6) and uGCs (LMM7; LMM8). Grooming that took place during excretion-lag period should, by definition, no longer affect the fGC/uGC measure. Rather, grooming that took place during the 'Lag period' should reflect the grooming that took place following the HPA-axis activity captured in the sample. Absence of a relationship in LMM5-LMM8 would suggest that HPA-axis activity did not affect grooming. In this analysis, I control for predictors of grooming time identified in Chapter 4, namely day length (time between sunrise and sunset) and number of rain hours (number of hours in which it rained during the day).

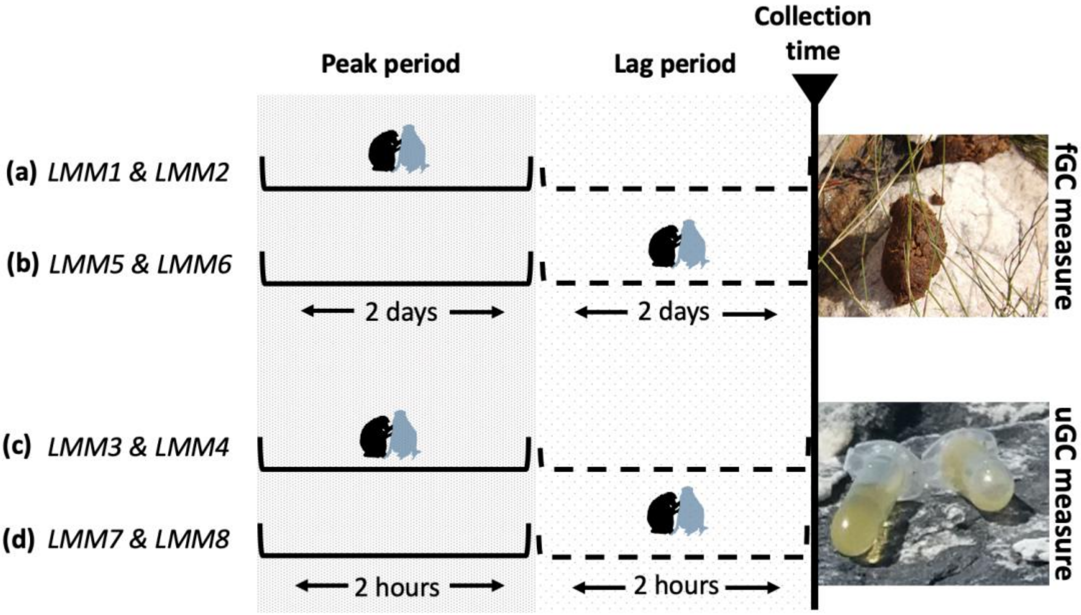


Figure V - 1: Conceptual illustration of matching grooming to GCs. To test whether grooming affected GCs (LMM1-LMM4), I quantified grooming during the period in which HPA-axis activity would be reflected in **(a)** fGCs and **(c)** uGCs, here: the 'Peak period' (term from: Wittig et al., 2015). The length of the 'Peak period' was adjusted to the excretion time-lag of the sample (2 days for fGCs; 2 hours for uGCs). The period after the 'Peak period', labelled the 'Lag period', constitutes the excretion time-lag of the sample (see above). HPA-axis activity during the 'Lag period' should no longer be reflected in the fGCs and uGCs. Rather, the 'Lag period' follows the HPA-axis activity captured in the sample. Thus, to test the effect of HPA-axis activity on grooming (LMM5-LMM8), I quantified grooming during the 'Lag period' **(b)** & **(d)**.

Results

Long-term links between grooming and fGCs

Giving grooming, receiving grooming and total grooming rates were negatively correlated with mean fGCs for n=7 female chacma baboons in both focal and accelerometer-identified grooming data (Fig. V - 2a-c). Moreover, accelerometer-identified mean daily number of bouts (Fig. V - 2 d-f) and mean daily bout lengths (Fig. V - 2 g-i) for giving, receiving and overall grooming were also negatively correlated with fGCs for n=7 females. Most correlations were not statistically significant, but the negative correlations between overall grooming rates and mean fGCs were marginally insignificant (Fig. V - 2c), as was the correlation between mean grooming bout lengths and mean fGCs (Fig. V - 2i).

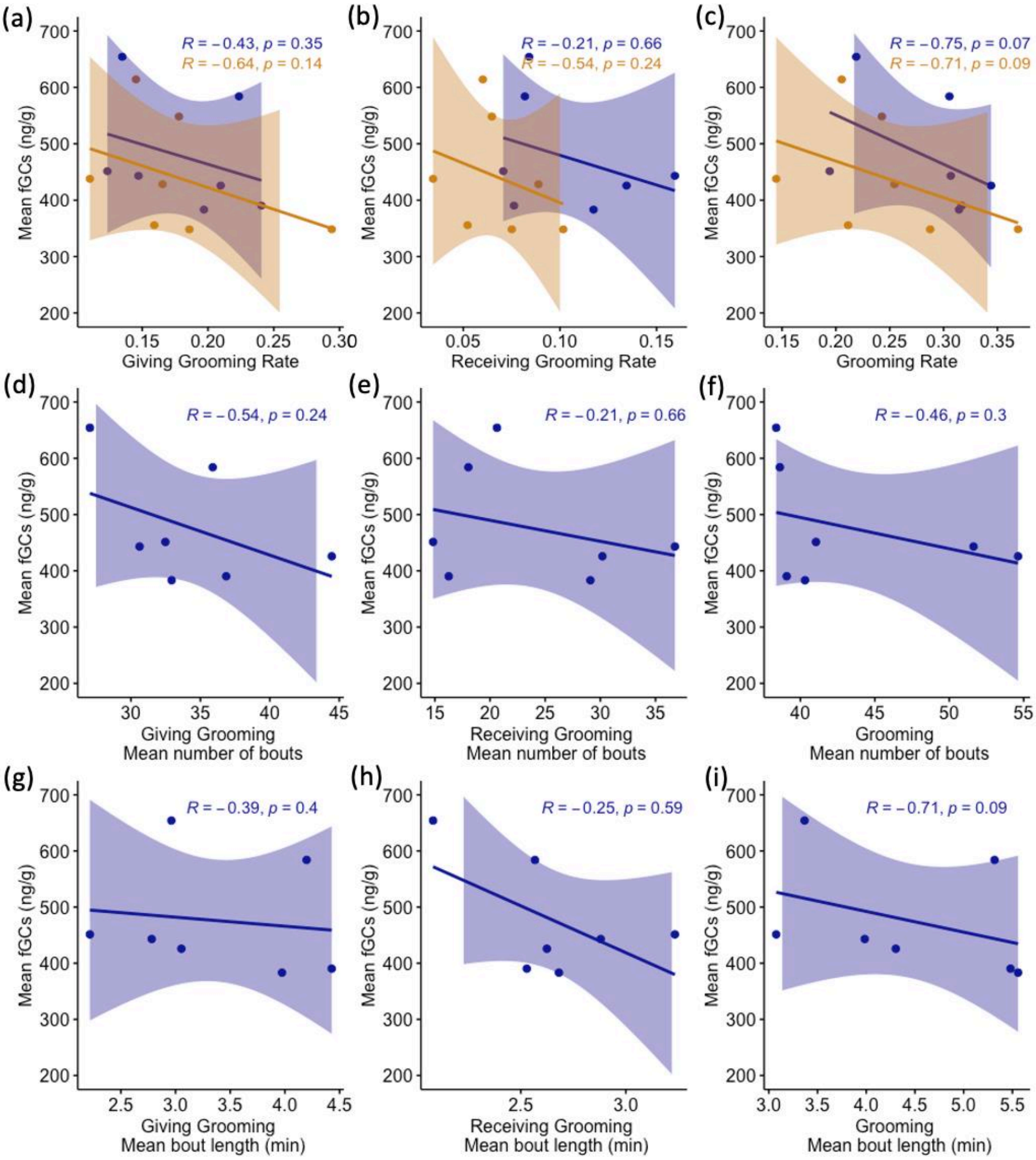


Figure V – 2: Long-term associations between grooming and fGCs Spearman's correlation between focal (orange) and accelerometer-identified (blue) rates of **(a)** giving grooming, **(b)** receiving grooming, **(c)** overall grooming; daily mean bout numbers of **(d)** giving grooming, **(e)** receiving grooming, **(f)** overall grooming; daily mean bout length of **(g)** giving grooming, **(h)** receiving grooming and **(i)** overall grooming and mean fGCs for n=7 female chacma baboons.

Short-term effects of grooming on fGCs

Both receiving and giving grooming across days -3 and -2 relative to sample collection were positively associated with fGCs (Fig. V - 3a; Table V - 1; LMM1). Both giving grooming mean bout length and frequency predicted higher fGCs, whereas receiving grooming bout length and frequency did not predict fGCs (Fig. V - 3b; Table V - 1; LMM2).

Table V – 1: Effect of grooming on fGCs Effect of grooming across days -3 and -2 relative to faecal sample collection on log-transformed fGCs for n=10 female chacma baboons based on n=176 samples from 46 unique dates. Controlling for day length (hours), reproductive state (pregnant versus non-pregnant) and urine contamination of faecal sample (yes/no). Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Grooming duration (LMM1)				
Giving Grooming (hrs)	0.091	0.032	2.837	**0.006**
Receiving Grooming (hrs)	0.087	0.037	2.368	**0.020**
Day length (hrs)	-0.199	0.060	-3.301	**0.002**
Pregnant (Y)	0.349	0.117	2.971	**0.004**
Urine contamination (Y)	0.051	0.080	0.629	0.530
Grooming quality (LMM2)				
Giving Grooming Mean Bout Length (min)	0.105	0.039	2.661	**0.009**
Giving Grooming Bout Frequency	0.005	0.002	2.616	**0.010**
Receiving Grooming Mean Bout Length (min)	0.057	0.041	1.387	0.167
Receiving Grooming Bout Frequency	0.002	0.002	1.158	0.251
Day length (hrs)	-0.192	0.061	-3.165	**0.002**
Pregnant (Y)	0.386	0.116	3.334	**0.001**
Urine contamination (Y)	0.058	0.081	0.708	0.480

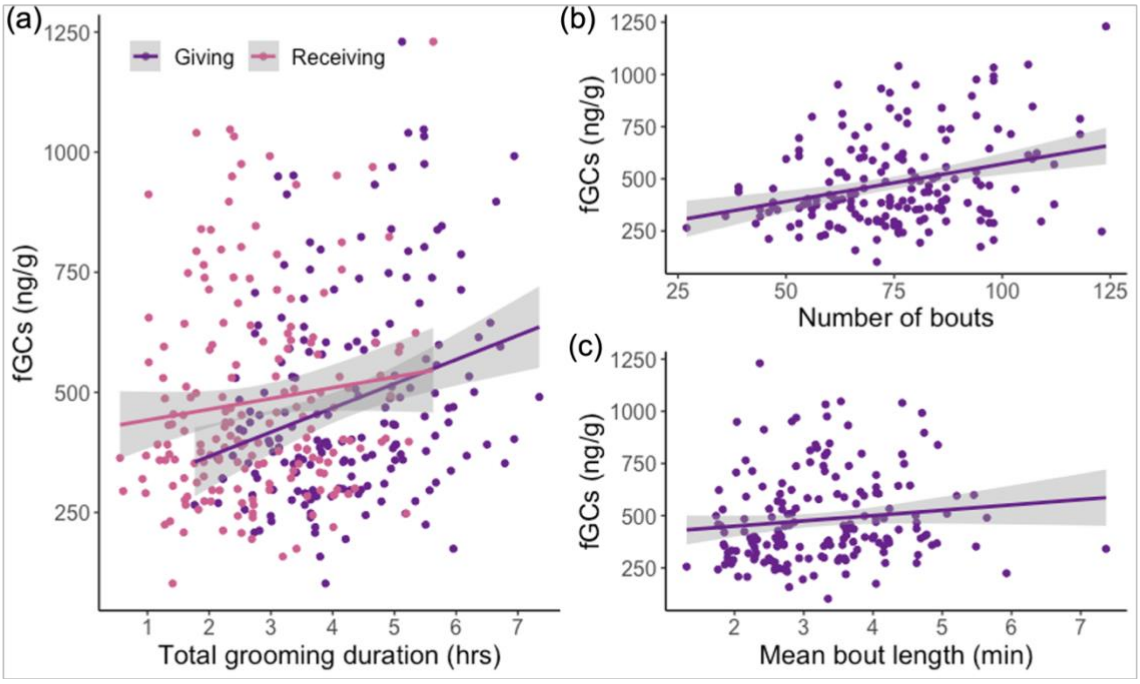


Figure V – 3: Effect of grooming on fGCs Effect of **(a)** duration spent giving (purple) and receiving (pink) grooming **(b)** number of grooming bouts and **(c)** mean giving grooming bout length across days -3 and -2 (relative to sample collection) on fGCs (ng/g) for n=10 female chacma baboons. Dots present real datapoints, the solid line is the linear regression line (with 95% confidence intervals.

Short-term effects of grooming on uGCs

Time spent giving grooming during the 2-hour period prior to the lag-period (Fig. V - 1) was positively associated with uGCs, but time spent receiving grooming was not (Fig. V - 4a; Table V - 2; LMM3). Giving grooming bout frequency was positively associated with uGCs (Fig. V - 4b; Table V - 2; LMM4) but giving grooming bout length was not (Table V - 2; LMM4).

Table V – 2: Effect of grooming on uGCs Effect of grooming on time-corrected log-transformed uGCs during the 2-hour grooming window, using n=133 samples collected from n=10 female chacma baboons across n=42 unique dates. Controlling for rain day (yes/no) and collection method (Salivette vs. pipette). Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Grooming duration (LMM3)				
Giving Grooming (hrs)	1.324	0.412	3.217	**0.002**
Receiving Grooming (hrs)	0.102	0.225	0.454	0.651
Rain day (Y)	0.204	0.147	1.391	0.169
Collection method (Salivette)	-0.225	0.139	-1.625	0.107
Grooming quality (LMM4)				
Giving Grooming Mean Bout Length (min)	0.027	0.069	0.396	0.693
Giving Grooming Bout Frequency	0.192	0.084	2.290	**0.024**
Rain day (Y)	0.188	0.150	1.255	0.212
Collection method (Salivette)	-0.261	0.141	-1.856	0.069

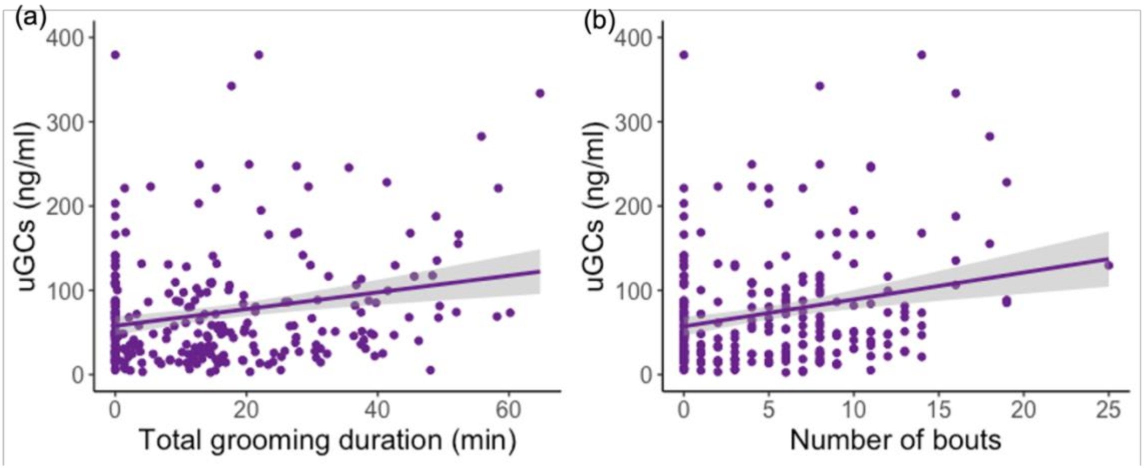


Figure V – 4: Effect of grooming on uGCs Effect of **(a)** time spent giving grooming and **(b)** number of giving grooming bouts in the 2-hour window preceding the two-hour lag on uGCs (ng/ml). Dots present real datapoints (three outliers > 500 ng/ml not shown), the solid line is the linear regression line with 95% confidence intervals.

Does HPA-axis activity predict grooming?

Based on the finding that more giving and receiving grooming were followed by higher fGCs (Table V - 1) and more giving grooming was followed by higher uGCs (Table V - 2), I tested whether higher HPA-axis activity was followed by more grooming. For this I matched the grooming which took place during the lag-period (see Fig. V – 1) and matched it to the fGCs and uGCs. I found no effect of giving grooming on fGCs (Table V – 3) or uGCs (Table V - 4) or of receiving grooming on fGCs (Table V – 3) or uGCs (Table V - 4).

Table V – 3: Effect of (f)GCs on grooming Effect of HPA-axis activity (as reflected in fGCs) on giving grooming and receiving grooming during the 2-day lag period (day 0 and day -1), controlling for known predictors of grooming activity: day length and hours of rain per day, for n=10 female chacma baboons based on n=176 samples from n=46 unique dates. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Giving Grooming (LMM5)				
fGCs (logged)	-0.010	0.033	-0.311	0.756
Day length (hrs)	0.158	0.038	4.185	**<0.001**
Hours of rain	0.014	0.014	0.993	0.329
Receiving Grooming (LMM6)				
fGCs (logged)	0.061	0.042	1.454	0.148
Day length (hrs)	-0.024	0.044	-0.558	0.579
Hours of rain	0.017	0.016	1.067	0.293

Table V – 4: Effect of (u)GCs on grooming Effect of HPA-axis activity (as reflected in time-corrected log-transformed uGCs) on giving grooming and receiving grooming during the 2-hour lag period, controlling for known predictors of grooming activity: day length and hours of rain per day, for n=10 female chacma baboons based on n=133 samples from n=42 unique dates. Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Giving Grooming (LMM7)				
Corrected uGCs (logged)	-0.037	0.174	-0.215	0.830
Day length (hrs)	0.017	0.005	3.226	**0.003**
Hours of rain	-0.093	0.125	-0.749	0.457
Receiving Grooming (LMM8)				
Corrected uGCs (logged)	-0.087	0.221	-0.393	0.696
Day length (hrs)	0.011	0.007	1.535	0.134
Hours of rain	-0.100	0.175	-0.574	0.569

Discussion

The aim of this chapter was to identify the short-term effects of grooming on uGCs and fGCs to establish whether grooming itself directly modulates HPA-axis activity which - at longer time scales - negatively correlates with grooming rates (Gust et al., 1993; Shutt et al., 2007). In line with previous work, I found that higher rates of grooming (from accelerometer and focal data) were negatively (but non-significantly) correlated with lower mean fGCs (Fig. V - 2). In contrast, when directly matching grooming to uGCs and fGCs, I found that giving grooming (total time and grooming bout frequency) was associated with higher fGCs (Fig. V - 3) and uGCs (Fig. V - 4). Mean giving grooming bout length was also positively associated with fGCs (Fig. V - 4c). Receiving grooming was positively associated with fGCs (Fig. V - 3a), but not uGCs. Together, these findings suggest a short-term cost associated with grooming whilst in the long-term grooming is associated with reduced HPA-axis activity, likely due to the benefits of investing in social bonds. Alternatively, the short-term positive association between increased HPA-axis activity and grooming could reflect a behavioural and physiological response to a stressor. Both possibilities are discussed below.

Co-occurring physiological and behavioural responses to a stressor could be explained by the ‘tend-and-befriend’ theory (Taylor et al., 2000). Namely, the response to a stressor may be to upregulate HPA-axis activity which motivates ‘tending’ (providing nurturing support) and ‘befriending’ (strengthening social networks) to reduce distress (Taylor et al., 2000). For instance, female chacma baboons who lost a close relative had increased fGCs and expanded their grooming network and rates in the following month (Engh et al., 2006a), after which fGCs returned to baseline. To test whether this might be the case here, I tested whether more grooming took place during the lag-period in response to increased HPA-axis activity (as captured in the fGC and uGC measures), using a 2-hour window for uGCs and a 2-day window for fGCs, but this was not the case (Table V - 3; Table V - 4). This suggests that grooming did not increase in response to higher HPA-axis activity. One potential caveat, especially for uGCs, is that the time-window in which grooming was expected to increase is rather short. It is possible that grooming is less of an ‘acute’ behavioural response to elevated HPA-axis activity, particularly in the wild where other activities may take priority (Dunbar et al., 2009), and grooming increases may therefore only be detectable at broader time scales (e.g., see Engh et al., 2006a, who used 3-month scales). Nevertheless, the results do not support a 'tend-and-befriend' interpretation and point towards a causal relationship between grooming and uGCs/fGCs.

Several papers have called upon a re-examination of the costs and benefits of grooming (Ostner and Schülke, 2018; Russell and Phelps, 2013), particularly giving grooming (Semple et al., 2013; Shutt et al., 2007). Giving grooming can be costly, as it may reduce vigilance (Cords, 1995; Maestripieri, 1993; Mooring and Hart, 1995) and may carry energetic costs, as picking through the fur of a conspecific is laborious and may require cognitive resources due to concentration (Russell and Phelps, 2013; Silk, 1982). There might also be opportunity costs as grooming necessarily detracts time from other activities (Dunbar et al., 2009). Moreover, giving grooming may expose the groomer to increased aggression by the recipient of the grooming interaction (Carne et al., 2011; Schino and Alessandrini, 2015), who could be frustrated by the termination of the grooming bout (Schino et al., 1988; but see: Aureli and Yates, 2010; Gumert and Ho, 2008). Grooming could also lead to interference of others (e.g., competition for grooming partners: Mielke et al., 2017; Schino and Lasio, 2018). In mandrills *Mandrillus sphinx*, low-ranking individuals preferentially groom 'safe areas' (rump and back), which avoid eye contact and would allow time to flee in case of aggression by the recipient (Schino and De Angelis, 2020) and in Barbary macaques *Macaca sylvanus*, self-scratching increased after giving grooming, potentially indicating a state of increased anxiety (Semple et al., 2013). These behavioural studies support the interpretation that increased GCs after giving grooming may be driven by psychological stress and emphasize that, at least in hierarchical societies, the consequences of grooming can be unpredictable (Schino and Alessandrini, 2015).

Receiving grooming was also associated with higher fGCs, but not uGCs. This is an unexpected result considering that, unlike giving grooming, most studies are equivocal about the relaxing effects of being groomed (Aureli et al., 1999; Boccia et al., 1989; Ueno et al., 2015). However, many of these studies were conducted in captivity (Aureli et al., 1999; Boccia et al., 1989) or in provisioned groups (Ueno et al., 2015), where the context may have differed from wild systems (Calisi and Bentley, 2009). First, similar factors may be at play here as for giving grooming in terms of opportunity costs and proximity to potential aggression or interferences from by-standers (see above). Second, out of the 10 collared females, 7 had dependent infants of varying ages (one female gave birth during the collar period), which can affect grooming relationships (Frank and Silk, 2009; Henzi and Barrett, 2002). Baboon mothers often receive unsolicited attention due to infants attracting other females (Altmann, 2001; Silk et al., 2003b), and will receive grooming by individuals who are motivated to handle their infants (Fig. V - S2; Frank and Silk, 2009; Henzi and Barrett, 2002). As such, lactating females may not have as much control over who they groom with, which could increase HPA-axis activity (Crockford et al., 2008). Indeed, lactating females who received higher rates of grunts (a signal of benign intent often preceding friendly interactions: Cheney et al., 1995) had higher fGCs, while the pattern was reversed for females in other reproductive states (Crockford et al., 2008). As such, it is possible that receiving grooming poses a stressor for lactating females, which could explain the positive association between fGCs and receiving grooming found here. Finally, while fGCs analyses were limited to measures of day-time receiving grooming, the potential confusion between resting and receiving grooming could also mean that fGCs increased after more time ‘sitting very still’ (Chapter 2).

Not only total giving grooming time, but also the frequency of giving grooming bouts was positively associated with fGCs and uGCs (Fig. V – 3c; Fig V – 4b). This relationship could be interpreted in several ways. Frequent, short bouts could reflect more interrupted grooming. For instance, macaques that were exposed to human disruptions engaged in shorter and more interrupted grooming bouts (Kaburu et al., 2019), which could reduce the ‘value’ of the grooming interaction as long bouts are considered to be of higher quality (Fruteau et al., 2009) and are more likely to be reciprocated (Franz, 1999). However, given that mean giving grooming bout length was also positively associated with fGCs (Fig. V – 3b), this trade-off between length and frequency is not supported here. Rather it seems that total time giving grooming, frequency of bouts and mean length of bouts all predict increased HPA-axis activity. A higher number of grooming bouts could suggest that females were distributing grooming across a wider network rather than focussing on fewer partners. While I cannot conclude this definitively without information on grooming partners associated to the accelerometer-identified grooming (females could be frequently grooming the same individuals), I found a moderate correlation between giving grooming bout frequency and total number of unique grooming partners recorded during focal observations (Fig. V – S3), suggesting that giving grooming frequency may indeed be indicative of a larger network. More diffuse grooming networks have been associated with higher fGCs previously (Crockford et al., 2008; Wittig et al., 2008), potentially because these grooming networks provide less stable and predictable support (Crockford et al., 2008). This could explain the short-term negative effect of grooming frequency on GCs found here, as individuals may be grooming more frequently, but with less predictable partners.

My findings suggest that there may be a short-term physiological ‘cost’ (increased HPA-axis activity) associated with grooming, and in particular giving grooming, which is offset in the long-term (lowered HPA-axis activity) as socially incurred favour pays off. The long-term benefits of incurring social tolerance or access to resources through giving grooming (Barrett et al., 1999b; Kaburu and Newton-Fisher, 2015) may explain why long-term rates of giving grooming are associated with reduced HPA-axis activity (found here Fig. V - 2; Shutt et al., 2007), despite the short-term increase in fGCs and uGCs (Fig. V – 3 & Fig. V – 4). Comparing the ‘act’ of giving grooming to the long-term benefit of giving grooming, may clarify these contrasting patterns in HPA-axis activity. For instance, in Barbary macaques, victims in aggressive interactions groom the aggressor to reduce the likelihood of renewed aggression (McFarland and Majolo, 2011). In vervet monkeys, time spent giving grooming was positively correlated with the duration of tolerance around food resources by the dominant grooming recipient (García et al., 2021). The authors described this period of tolerance as an hourglass where the remaining sand was proportional to the amount of grooming given (García et al., 2021). These examples highlight how the state of the groomer is likely far from ‘relaxed’, as they are actively engaging in a mitigation strategy against exposure to imminent aggression.

Conclusions

Using different methodological approaches when investigating hormone-behaviour links has previously yielded different results, e.g., when comparing time-matched fGCs and long-term average fGCs in relation to auto-grooming (Edwards et al., 2013). Here, I show how using high-resolution grooming data from accelerometers can reveal the short-term physiological consequences of grooming and how, rather than sub-serving the previously documented long-term decrease in HPA-axis activity (Gust et al., 1993; Shutt et al., 2007; Wooddell et al., 2017), giving grooming, and to a lesser extent receiving grooming, is associated with an increase in HPA-axis activity. This is an unexpected relationship which needs to be considered within the wider sociality-health-fitness realm. It suggests that social bonds which can ultimately affect survival (Snyder-Mackler et al., 2020), are maintained by a process (grooming) which increases HPA-axis activity in the short-term. Further investigation into whether this result is generalisable across different contexts within this study troop, as well as across primate groups which experience different socio-ecological selective pressures, would inform how widespread this phenomenon is.

Appendix

Table V – S1: Overview of supplementary material for Chapter 5

Content	Tables & Figures
S1: Methods	
Transformation of response and predictor variables	Table V – S2
Correction of logged uGCs	Fig. V – S1
S2: Results	
LMM3 without night-time receiving grooming	Table V – S3
S3: Discussion	
Female-infant attraction	Fig. V – S2
Grooming partner * Grooming frequency correlation	Fig. V – S3

Table V – S2: Transformations of response and predictors variables in LMMs

Model	Response variable	Predictor variables
fGCs – Grooming duration (LMM1)	Log-transformed fGCs	Raw giving and receiving grooming (hrs)
fGC – Grooming quality (LMM2)	Log-transformed fGCs	Raw giving and receiving grooming bout length (min) and bout number
uGCs – Grooming duration (LMM3)	Log-transformed, time-corrected uGCs	Sqrt-transformed giving and receiving grooming (hrs)
uGCs – Grooming quality (LMM4)	Log-transformed, time-corrected uGCs	Sqrt-transformed giving and receiving grooming bout length (min) and bout number
Giving Grooming – fGCs (LMM5)	Sqrt-transformed giving grooming (hrs)	Log-transformed fGCs
Receiving Grooming – fGCs (LMM6)	Sqrt-transformed receiving grooming (hrs)	Log-transformed fGCs
Giving Grooming – uGCs (LMM7)	Sqrt-transformed giving grooming (hrs)	Log-transformed, time-corrected uGCs
Receiving Grooming – uGCs (LMM8)	Sqrt-transformed receiving grooming (hrs)	Log-transformed, time-corrected uGCs

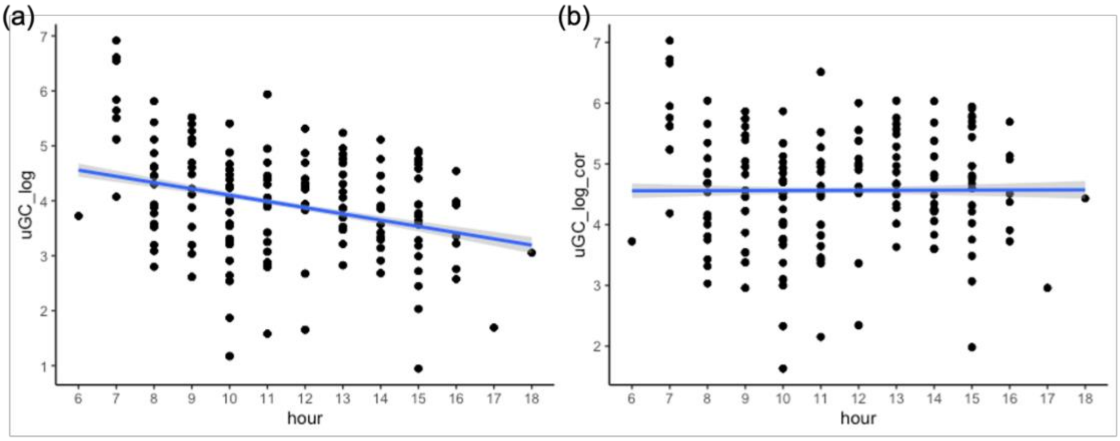


Figure V – S1: (a) raw uGCs values **(b)** corrected logged uGCs value (11.5% decrease in logged uGCs per hour based on estimate from full female model presented in Chapter 3).

Table V-S3: Effect of grooming on uGCs Effect of receiving grooming on time-corrected log-transformed uGCs during the 2-hour grooming window (limited to day time), using n=80 samples collected from n=10 female chacma baboons across n=38 unique dates. Controlling for rain day (yes/no) and collection method (Salivette vs. pipette). Significant effects are in bold.

Predictor variable	**Estimate**	**SE**	**T**	***p***
Grooming duration (LMM3)				
Receiving Grooming (hrs)	0.193	0.388	0.498	0.620
Rain day (Y)	-0.044	0.189	-0.235	0.816
Collection method (Salivette)	-0.386	0.175	-2.202	**0.031**

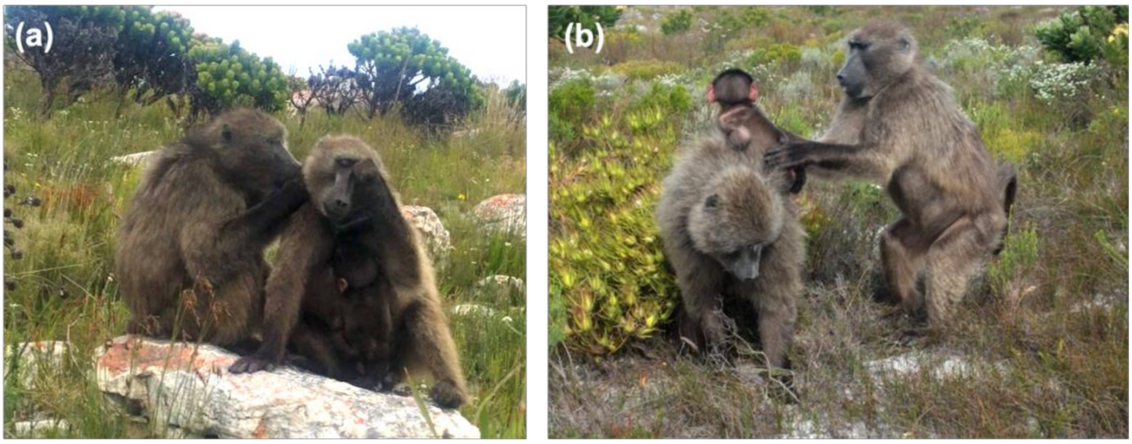


Figure V – S2: (a) F19 with ±2-month-old infant being groomed by F16. **(b)** F13 foraging, with her ±3-month-old infant being handled by F11. Photo Credit: Charlotte Christensen.

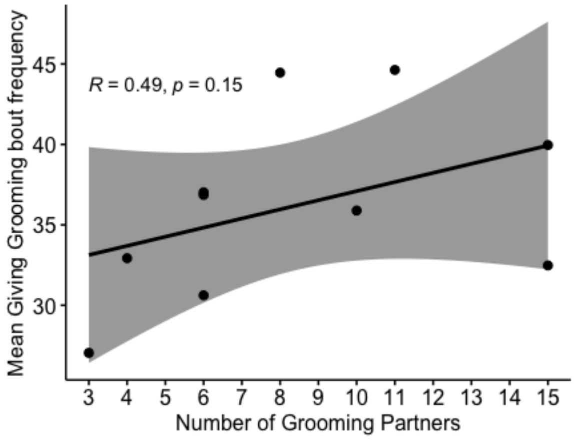


Figure V – S3: Spearman correlation between the total number of unique grooming partners each female was observed with during the collar period in relation to her mean daily giving grooming bout number for n=10 female chacma baboons.

Chapter 6: General Discussion

"Natural selection is an efficient process that does not often tolerate excessive amounts of slack in the biological system. Thus, the fact that such a high proportion of an animal's day can be devoted to grooming others suggests that there is a substantial benefit to be gained from doing so."

Dunbar, 2010, pg. 261

PC: Charlotte Christensen

Chapter 6: General Discussion

Thesis synthesis

The overarching objective of this thesis was to investigate the direct link between grooming and HPA-axis activity in chacma baboons living at a southerly latitude. To achieve this, I used accelerometer-identified grooming and non-invasive sampling of urinary and faecal glucocorticoids (uGCs and fGCs, respectively).

As allo-grooming has, thus far, not been successfully identified from tri-axial acceleration signals (but see: Fehlmann et al., 2017a), my first aim was to identify receiving and giving grooming from video-labelled accelerometer data using a supervised machine learning approach (**Chapter 2**). The identification was successful with a high overall performance for both giving and receiving grooming (78 and 82%, respectively) which allowed me to calculate grooming durations and frequencies for n=12 baboons (n=680 baboon days). Second, I established whether known predictors of HPA-axis activity were associated with GC variation in this study troop (**Chapter 3**). In line with previous findings for Western Cape baboons, I found that pregnancy and shorter (winter) days were associated with higher fGCs. uGCs, in contrast, were negatively associated with rain days and time of day (driven by circadian pattern). The two sample types thus captured predictors with different temporal profiles, which is often assumed (Behringer and Deschner, 2017; Touma and Palme, 2005) but has never explicitly been tested. Third, I established how total grooming time, bout frequency and bout length were affected by socio-ecological context (**Chapter 4**). I found that shorter days and days with more rain hours were associated with less giving grooming (driven by both shorter and fewer bouts per day), demonstrating how environmental factors can impose temporal bottlenecks on social behaviour. After more rain hours during the day, giving grooming increased at dusk, suggesting baboons may compensate for 'lost' social time. Finally, I tested whether receiving and giving grooming affected fGCs and uGCs by directly matching grooming to subsequent (using a matrix-appropriate time-lag) GC-measures (**Chapter 5**). Contrary to my predictions, I found that grooming, in particular giving grooming, was associated with higher uGCs and fGCs, and higher HPA-axis activity did not prompt an increase in subsequent grooming. This suggests that grooming may constitute a stressor, at least in this study troop. In contrast, grooming rates averaged over the entire study period were negatively correlated with fGCs. Together, these findings highlight that the long-term benefits typically associated with grooming (downregulated HPA-axis activity), are not reflected in the short-term mechanisms associated with grooming (upregulated HPA-axis activity). High-resolution accelerometer data can help unravel the proximate consequences of grooming to better understand its role within the larger sociality-fitness-link.

Proximate mechanism versus ultimate outcomes

The mechanisms that link sociality to fitness in primates are currently understudied (Ostner and Schülke, 2018). While grooming, a major aspect of social life in primates (Dunbar, 1991; McFarland, 2018; Silk et al., 2006b), seems like a positive social interaction on the surface, its benefits should not be taken as self-evident (Ostner and Schülke, 2018; Russell and Phelps, 2013). Indeed, given that grooming has been linked to increased aggression from conspecifics (Schino and Alessandrini, 2015; Schino and De Angelis, 2020) and decreased vigilance (Cords, 1995; Maestripieri, 1993), and is in trade-off with other activities (Dunbar et al., 2009), it is possible that grooming has associated, short-term costs, rather than benefits. The increase in GCs following grooming (Chapter 4) supports this interpretation, with grooming potentially imposing a social stressor (exposure to aggressive conspecifics) or an energetic cost, as grooming reduces the time for energy-intake (feeding) or energy-conservation (resting). These pressures are likely reduced in captive or semi-free ranging primates, as food is provided, predators are absent, and group compositions are often artificially manipulated to reduce social conflict (Olsson and Westlund, 2007; Stevens and Carlson, 2008). In such contexts, the ‘hedonistic’ benefits of grooming may become more apparent, reflected in reduced behavioural indicators of stress and lowered heart rate (Aureli et al., 1999; Boccia et al., 1989; Schino et al., 1988). Establishing whether grooming in captivity is linked to reduced GCs in the short-term (as found in human studies on physical touch: Ditzen et al., 2007; Field et al., 2005), would help to confirm whether this is the case. If so, this may be an example of a potential sociality-fitness mechanism which does not necessarily translate from captivity to the wild (Calisi and Bentley, 2009; Hofmann et al., 2014). This does not exclude the possibility that grooming may have tension-reducing effects in wild primate populations, too. For instance, many field primatologists have observed their study subjects appearing progressively more relaxed as they are being groomed (pers.

obs.; Dunbar, 2010; Sade, 1965). However, given my findings, this might not be an accurate depiction of most grooming interactions.

Short-term increases in HPA-axis activity after grooming may seem contradictory in the sociality-health-fitness realm, but animals regularly engage in fitness-relevant activities that raise allostatic load during various life-history stages, such as breeding, migration and infant-rearing (for reviews see: Crespi et al., 2013; Romero, 2002). Increases in HPA-axis activity (particularly in the short-term) are usually not maladaptive (see *General Introduction*), but rather allow the organism to cope and respond appropriately to the challenge at hand (Sapolsky et al., 2000). In contrast, the long-term effects of social bonds on HPA-axis modulation are perhaps the ones that are important to health and fitness.

Proposed mechanisms by which social bonds may provide fitness benefits include agonistic support (which can aid in protection and rank attainment), resource access (through tolerance and cooperative defence), reduced predation risk, and thermoregulation (see Ostner & Schülke, 2018 for a review). In contrast, recent reviews have posited that HPA-axis modulation cannot be an ultimate goal of social bonds, but rather serves as a mechanism that promotes prosocial behaviour (Beehner and Bergman, 2017; Brent et al., 2014; Higham, 2016; Ostner and Schülke, 2018). However, given that HPA-axis modulation has consequences for health and survival (Aguilera, 2011; Campos et al., 2021), it stands to reason that behaviours which help keep GCs within an adaptive range (‘normal reactive scope’: Romero et al., 2009) should be under positive selection (Wittig et al., 2016). The findings from Chapter 4 do not suggest that grooming reduces HPA-axis activity in the short-term, hereby leading to overall reduced HPA-axis activity in the long-term as previously proposed (Aureli and Yates, 2010; Russell and Phelps, 2013). Rather, individuals who regularly groom to maintain social bonds may have reduced HPA-axis activity compared to individuals that do not, because having social bonds may change the way in which an individual perceives and responds to stressors (Hennessy et al., 2009; Hostinar et al., 2014) or because social bonds provide access to resources/other ‘commodities’ (see above) which reduce exposure to stressors that would otherwise increase HPA-axis activity (e.g. aggression, inclement weather, lack of food, etc.). This is supported by the broader patterns emerging from this (Chapter 5) and other (longer-term) studies which show decreased HPA-axis activity is associated with increased grooming time (Engh et al., 2006a; Gust et al., 1993; Shutt et al., 2007) and other aspects of grooming such as grooming network concentration (Crockford et al., 2008; Wittig et al., 2008) and grooming partner identity (Fürtbauer et al., 2014; Wittig et al., 2016).

Socio-ecology shapes the sociality-fitness link

Understanding the proximate mechanisms that drive social behaviour is important for understanding which aspects of sociality improve fitness (Ostner and Schülke, 2018), and by extension which aspects of sociality might be linked to reduced HPA-axis activity. The explanation is unlikely to be 'one size fits all' across primates (Ostner and Schülke, 2018). Indeed, different aspects of social bonds and/or grooming relationships may become relevant in the same populations under different contexts. For instance, female chacma baboons with focussed grooming networks have lower GCs under stable conditions (Crockford et al., 2008), but when they lose a close relative, females who expand their network and groom more have lower GCs (Engh et al., 2006a). In white-faced capuchin monkeys, offspring of socially integrated females have better survival rates than offspring of less integrated females under stable conditions, but during male take-over, the pattern is reversed, possibly because infants of more central females were more likely to be targeted by immigrant males (Kalbitzer et al., 2017).

The socio-ecological context of the baboons on the Western Cape may affect the sociality-fitness link differently compared to other baboon populations. For instance, the work on Kenyan and Botswanan baboon populations suggests that females form durable, strong social bonds (Silk et al., 2012; Silk et al., 2010a) which result in longer life-spans (Silk et al., 2010b) and higher infant survival (Silk et al., 2003a; Silk et al., 2009). In contrast, female baboons from De Hoop on the Western Cape form social bonds that show seasonal cyclicity (Henzi et al., 2009), suggesting that rather than forming long-term social bonds, grooming associations may be the product of 'short-term optimisation'. Notably, the number of weak rather than strong social bonds are associated with higher infant survival in De Hoop (McFarland et al., 2017). This suggests that under certain socio-ecological conditions a broader network of weak bonds may be an adaptive social strategy (McFarland et al., 2017). How might this apply to the Da Gama troop (on the Western Cape) and why is it relevant to HPA-axis modulation?

Ecologically, living on the Western Cape entails distinct seasonal changes in daylength, rainfall and temperature (Hill et al., 2003; van Doorn et al., 2010), with increased HPA-axis activity recorded in baboons during short, cold winter days (Chapter 2; Chowdhury et al., 2021; Weingrill et al., 2004). Low temperatures may require huddling for thermal benefits (Gilbert et al., 2010) and larger social networks may help to do this more effectively. Indeed, in vervet monkeys (McFarland et al., 2015) and Barbary macaques (Campbell et al., 2018; McFarland and Majolo, 2013) individuals are more likely to survive cold spells and receive thermoregulatory benefits if they have many social bonds, rather than strong social bonds. From a social pressure perspective, chacma baboons have relatively high rates of infanticide (Fischer et al., 2019) particularly on the Cape Peninsula where alpha males turnover is frequent (Beamish, 2009; Kansky and Gaynor, 2000) and show high rates of male-female aggression (Kalbitzer et al., 2015). The threat of infanticide/aggression may mean that females benefit from increasing their network of potential agonistic support, particularly with males which can provide ‘protective bonds’ against infanticide (Beehner et al., 2005; Palombit et al., 2001; Van Schaik and Aureli, 2000). A meta-analysis across 14 primate species showed that grooming predicts agonistic support (Schino, 2007) and playback experiments in chacma baboons showed that females are more likely to approach the recruitment calls of a recent grooming partner (Cheney et al., 2010). As such, the socio-ecological variables (cold, short days and high aggression/infanticide risk) may require a social strategy that is more focussed on ‘working the crowd’ (see: Josephs et al., 2016) relative to more equatorial baboon populations.

While I did not investigate the number of grooming partners per se, the positive correlation between number of giving grooming bouts per day and number of total grooming partners (Chapter 5), suggests that more frequent grooming bouts may be linked to a larger network, and that this may be a social strategy in the females of the Da Gama troop. Average individual GCs were negatively (though not significantly) correlated with average grooming bout frequency (Chapter 5). If socio-ecology favours short-term optimisation (Henzi et al., 2009) and the Da Gama females are engaging in more short-term biological market type grooming interactions (Barrett et al., 1999b), it could further help explain why GCs were increased rather than reduced after grooming. In chimpanzees, an important aspect of whether GCs are reduced after grooming, is whether the grooming partner is a close bond (Wittig et al., 2016). If grooming interactions take place across a wide network, rather than focussed on long-term social bonds, they may indeed not reduce HPA-axis activity in the short-term, but only once the 'investment' is realised in the long-term (see '*Proximate mechanism versus ultimate outcomes*'). The baboon collars contained both a tri-axial accelerometer and a GPS-logger (see e.g., Bracken et al., 2021; McCann et al., 2021). Thus, GPS-data could be used to identify proximate dyads during periods where grooming is detected in the accelerometer signal and be used to further investigate grooming-partner identity (at least between the subset of females for which both data-streams are available).

Future directions: investigating context

Stressful contexts have been shown to promote the seeking of positive social interactions in human and non-human animals (Taylor, 2006; Taylor et al., 2000). While I did not find support for higher fGCs and uGCs being followed by more grooming (Chapter 5), it is still worth considering what potential role underlying stressors played during the study period. There were two potential stressors: male-male fighting over dominance and baboon-management. Below, I consider how these may have affected grooming-GCs patterns, as a potential avenue for future investigation.

First, the two adult males of the troop were competing for dominance, which was associated with aggression between the males, re-directed aggression towards females, and infanticide attempts (one of which was successful; pers. obs.). While there was no definitive rank reversal, the beta-male initiated and 'won' some of the agonistic interactions, resulting in a period of repeated challenges. Moreover, as previously mentioned, 7 out of 10 collared females had dependent infants, who were at risk of becoming the target of infanticide attempts: a stressor which is reflected in higher female fGCs (Engh et al., 2006b; Wittig et al., 2008). It is possible that increases in grooming and fGCs/uGCs reflect a common stressor (e.g., male fights, infanticide attempts), and that grooming under these circumstances is indeed 'stressful' as it may be an active strategy to form alliances during periods of heightened aggression (Polo and Colmenares, 2012; Weingrill, 2000).

Second, the study troop, like many other troops on the Cape Peninsula, are herded (using pain-aversion techniques) towards natural spaces by a team of field rangers to minimise conflict between humans and baboons (van Doorn and O'Riain, 2020). Previous work on this troop showed that herding alters baboon activity budgets substantially, with high intensity herding days resulting in decreased foraging and increased social behaviours (predominantly grooming) (van Doorn and O'Riain, 2020). As such, grooming may not entail the same level of 'agency' on high intensity herding days as it does when activity budgets are not dictated by management. This could be an additional explanation for the positive relationship between grooming and fGCs/uGCs in the short-term, as grooming under high herding intensity may be 'stressful'.

Considering the relatively short duration of the present study (5 months, with accelerometer data for approximately 2.5 months), it was not possible to distinguish stressful from non-stressful periods in ways that were categorically different. For instance, there was no 'peaceful period' to compare to a period of alpha-male rank instability (e.g., Wittig et al., 2008) or periods in which infanticide was not a risk (e.g., Engh et al., 2006b). Similarly, there was no period during which rangers were not present (e.g., a management strike: van Doorn and O'Riain, 2020). However, these two continuous stressors did vary in intensity from day-to-day and could have affected activity budgets, including grooming, and their physiological correlates. A more detailed investigation of stressors, using GPS-identified male-male chases (Fürtbauer et al., in prep) or herding data recorded using direct observations, could reveal whether grooming and GCs increase in tandem to these stressors. Indeed, studying the *absolute* grooming-uGCs/fGCs relationship without information on potential stressors (as I did in this thesis) could mask changes that occur in *relative* terms. This might be important, as demonstrated in a study on chimpanzees, where resting is associated with the same levels of uGCs during non-stressful contexts as grooming is during stressful contexts (Wittig et al., 2016). As such, grooming could indeed have had buffering effect, but this would only be evident in relative terms when comparing uGCs/fGCs in stressful and non-stressful context. Establishing whether the overall negative relationship between grooming and GCs identified in Chapter 4 is robust across contexts would be informative.

Challenges and opportunities of working with 'high-resolution data'

In this thesis, I used high-resolution (second-by-second) accelerometer data to study baboon grooming at a finer and more continuous scale than would have been possible using direct observations. To qualify as 'big data', a dataset must contain information of such high volume and variety that it requires specific analytical methods and technology in order to extract 'value' from it (De Mauro et al., 2015). Indeed, the accelerometer-files were too large to open in Excel and the processing time of the entire baboon dataset (n=58,747,636 rows of data) comprised about 2 months using a 20-core PC. Logistics aside, a more important challenge throughout this PhD has been thinking about how to match second-by-second grooming data to changes in GC-levels which are dynamic and continuously influenced by a range of internal and external factors (Sapolsky et al., 2000; Spencer et al., 2018). While it would be theoretically possible to extract information on the behaviour that took place before the voiding of a faecal sample at the 131,040th second (i.e., 36.4-hour peak excretion: Wasser et al., 1994), this information would have no biological bearing on the fGCs recovered from said sample. Thus, the task exists in determining what summary measures can be calculated from high-resolution data that would be relevant to the baboon's endocrine state as reflected in uGCs and fGCs. How large or restrictive does a time-window need to be to capture grooming which could reasonably affect physiological state, but which avoids capturing information that is no longer relevant to the physiological state? Particularly with grooming, a 'non-catastrophic event' (*sensu* Crockford et al., 2008), the effect on GCs may not be as acute. In this thesis, I used time-windows that corresponded to the given GC excretion lag-time of the sample matrices, as had previously been done (Edwards et al., 2013; Wittig et al., 2016). This revealed relatively short-term effects of grooming on GCs but not in the direction I expected. Further exploratory analyses looking at larger time-windows revealed similar results/trends, so exploring the 'adequate' time-window for capturing grooming may be warranted. Finally, having the luxury of a large dataset means being selective about which questions to address, as there are many ways in which the data could be used.

While high-resolution data allows to tackle new and exciting questions, including in the field of socio-endocrinology (Fig. I - 1), it also poses a challenge in that it is impossible to verify each data point. This is relevant for the use of accelerometer-identified grooming, and indeed other behaviours, as using machine-learning over direct observations introduces some uncertainty (i.e., behavioural identification from accelerometers has, to my knowledge, never reached 100% precision and recall). An observer can conclude with 100% certainty that a baboon was being groomed at a specific point in time, but each second which is identified as 'receiving grooming' from the accelerometer data has a ~18% chance of being another behaviour (Table II – 2). While this caveat exists for all behaviours identified using the random forest model, the similarity between 'receiving grooming' and 'resting' (Fig. II – 1; Table II – S7) likely led to more misidentifications in the overall dataset than the random forest metrics suggest. The finding that 'receiving grooming', rather than 'resting', increases during the night (Chapter 2), during days with more rain hours (Chapter 4) and in pregnant females (Chapter 4), signals that rather than identifying 'receiving grooming' and 'resting', the random forest model identifies 'being very still' and 'being still', respectively. While it may indeed be the case that 'being very still' during the day mostly occurs when baboons are receiving grooming (see Discussion in Chapter 2; Table II – S5; Fig. II – S7), hereby explaining the relatively high accuracy obtained using the training data (~23 hours), this assumption may not hold across all contexts for the full study period (16, 319 hours). Thus, caution when interpreting results based on the full data set is warranted (as has been done in Discussions of Chapter 2, Chapter 4, and Chapter 5).

Future studies, or further exploration of this particular dataset, could investigate ways to distinguish receiving grooming and resting with more certainty. Using GPS-identified dyads may help, i.e., if two baboons are spatially close and are classified as giving and receiving grooming respectively, this may further help extract 'true' receiving grooming. In the present study, GPS recorded continuously which results in high positional accuracy (Moriarty & Epps, 2015; here within 5 meters: Bracken et al., 2021; McCann et al., 2021). However, given that GPS positional error tends to increase during stationary behaviours (e.g., grooming) (Gunner et al., 2021), the identified 'dyads' could in reality be sitting several meters apart. Moreover, baboons often groom in small sub-groups (Washburn & DeVore, 1961), and it is not uncommon to see several females grooming and resting in proximity without necessarily grooming one another (pers. obs.). Additionally, this approach would be limited to grooming interactions where both participants have active collars. Alternatively, accelerometers have been deployed on different body parts to target or tease apart similar (from an accelerometery point-of-view) behaviours (Brown et al., 2013). For instance, mandible- and head-mounted accelerometers deployed on seals have been used to distinguish between feeding and vocalising (*Leptonychotes weddellii;* Naito et al., 2010) and between resting and being alert (*Halochoerus grypus*; Shuert et al., 2018), respectively. Arm-mounted accelerometers have been used in captive baboons (May et al., 1996) and wrist-mounted accelerometers are currently being tested in wild baboons (Max Planck, 2021). Self-directed behaviours (e.g., scratching) decline while receiving grooming (Schino et al., 1988) and can increase during resting (Castles, et al., 1999; Semple et al., 2013), thus wrist-mounted accelerometers may add a layer of information that could help distinguish between the two behaviours. In the present dataset, additional behaviours such as body-shakes and self-scratching were removed from the resting category (see Chapter 2) but adding these back into the random forest model may provide a more biologically valid 'profile' of resting that is more distinct from receiving grooming. Finally, additional sensors such as heart-rate loggers are becoming more widely used in birds and mammals (Butler et al., 2004; Twiss et al., 2021), but to my knowledge not in wild primates. Receiving grooming has been linked to reduced heart rate in captive primates (Aureli et al., 1999; Boccia et al., 1989) and could thus be potentially used to validate receiving grooming. However, resting, specifically when sleeping, is similarly linked to reduced heart rate (Boccia et al., 1989). Moreover, heart rate only slows down over several minutes of being groomed (Boccia et al., 1989), and so might only be appropriate when identifying relatively sustained grooming bouts, and not second-by-second grooming data. In conclusion, resting and receiving grooming fall into a category of stationary behaviours that present challenges for identification using tri-axial acceleration signals alone (Williams et al., 2015). Collar-mounted tri-axial accelerometers do allow to estimate these behaviours to some extent (Chapter 2), but continued efforts to improve detection will allow to leverage the benefits of continuous grooming data with more certainty.

What do high-resolution data streams add to the field of socio-endocrinology? All the advantages laid out in the *General Introduction* (Fig. I - 1) contributed to answering the questions in Chapters 3 and 4. First, time-matching samples to continuous grooming data allowed to establish not only whether there was a link between grooming preceding GC-state but also whether GC-state predicted the grooming that followed. While it is generally established that there is a bi-directional relationship between hormones and behaviour (Oliveira, 2004; Packard et al., 2011), studies usually focus on one direction (social behaviour to GCs: Creel et al., 2013; Hennessy et al., 2009) over the other (GCs to social behaviour: Raulo and Dantzer, 2018). Continuous data-streams thus allow for a more comprehensive investigation of the grooming-GCs (and vice versa) link. Here, I showed that more grooming was followed by higher GCs, but higher GCs were not followed by more grooming. Second, the high-resolution data allowed me to investigate details about grooming interactions in relation to predictors of interest (e.g., environmental data in Chapter 3; GCs in Chapter 4). The duration of grooming bouts may be indicative of their quality (Fruteau et al., 2011), while the frequency may be indicative of spreading grooming across a wider network (Chapter 4; see above), although this needs to be further examined. While I did not find a trade-off between grooming bout length and frequency, the possibility of investigating 'quality vs. quantity' – and how this may change across contexts and affect GCs – is possible with high-resolution data. Third, being able to monitor night-time grooming also opens questions regarding the temporal profile of grooming. While day-time grooming may be limited by other activities that must take place during the diurnal window, sleep-site grooming could represent a period where social relationships are maintained (as findings in Chapter 3 suggest). Finally, having continuous data for several individuals simultaneously allows to monitor changes in grooming and GCs across contexts and compare how individuals respond, behaviourally and physiologically, to the same environmental changes.

Accelerometer-identified grooming could become a more widely used tool, and high-resolution grooming data could be used to augment experimental studies. For instance, 'stressors' could be presented, and associated grooming-GC patterns could be compared to non-stressful control trials (see e.g., Gustison et al., 2012; Wittig et al., 2016). Moreover, time-series approaches where samples are collected repeatedly from one individual along a continuous timeline (see e.g., Wallner et al., 1999) could shed more light on the bidirectionality between grooming and GCs.

Closing thoughts

In socio-endocrinology, and the sociality-health-fitness research field more broadly, the investigation of mechanisms underpinning social behaviours and markers of health is becoming more widely called for (Ostner and Schülke, 2018; Snyder-Mackler et al., 2020; Snyder-Mackler and Snyder-Mackler, in press). New technology, such as accelerometer-identified social behaviours, may provide the tools to answer some of these questions in more detail; I have only started to scratch the surface in this thesis. The irony of studying the role of social touch on physiological stress levels during a pandemic in which official guidelines advise that at least one meter distance be kept between people (World Health Organisation, 2021) is not lost on me. Nor is the timeliness of the question: which aspects of sociality are important to health and survival (Ostner and Schülke, 2018)? Research on the effects of social isolation on mental and physical health has been quick to emerge since the start of 2020 (Pancani et al., 2021; Robb et al., 2020), as were the proposed solutions to remain in social contact while minimising the risk of COVID-19 transmission (Razai et al., 2020; Wu, 2020), including ‘sociable robots’ which can provide tactile reassurance (Eckstein et al., 2020). While humans have evolved under selective pressures that differ from those shaping grooming relationships in chacma baboons, it is interesting to consider the robustness of the sociality-fitness link (Snyder-Mackler et al., 2020). What continues to be investigated is how social animals, including humans, achieve these benefits within the parameters of their socio-ecological context.

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Reprints of publications

Below are reprints of publications which have come from the data collected during the 2018 baboon field season (Bracken et al., 2021; Bracken et al., 2022; Fürtbauer et al., 2020; McCann et al., 2021) to which I have contributed.

Chapter 3 formed the basis of a paper titled: "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*)" published in General and Comparative Endocrinology, 2022.

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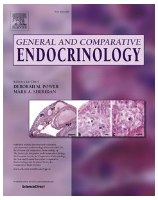

Research paper

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*)

Charlotte Christensen [a,*], Anna M. Bracken [a], M. Justin O'Riain [b], Michael Heistermann [c], Andrew J. King [a], Ines Fürtbauer [a]

[a] Biosciences, School of Biosciences, Geography and Physics, Faculty of Science and Engineering, Swansea University, SA2 8PP Swansea, UK
[b] Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa
[c] Endocrinology Laboratory, German Primate Centre, 37077 Göttingen, Germany

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ABSTRACT

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* Corresponding author.
E-mail address: c.christensen.974205@swansea.ac.uk (C. Christensen).

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et al., 2000).

Biomedical research has shown that prolonged activation of the HPA-axis can have negative consequences as the physiological mediator itself (i.e., GCs) begins to disrupt normal bodily functions (Kirby et al., 2009; Korte et al., 2005; Sapolsky, 2002; Spencer et al., 2010). However,

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et al., 2020; Heistermann and Higham, 2015; Higham et al., 2020; Preis et al., 2018; Sadoughi et al., 2021), we can expect an increase in the use of uGCs in future studies of HPA-axis functioning in wild animals. It is therefore necessary to investigate how measuring uGCs compares as a tool for measuring HPA-axis activity, relative to the more frequently 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 generally fGCs capture the cumulative secretion of GCs over longer time periods (many hours/days: Behringer and Deschner, 2017), while uGCs

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troglodytes: Emery Thompson, 2005; musth *Loxodonta africana*: Ganswindt et al., 2002). These differences may be linked to methodological factors (e.g., uneven representation of reproductive categories for each sample type; see Emery Thompson, 2005), however, potential effects of sample matrix are not discussed. To establish whether variation in fGCs 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., 2011; Levy et al., 2020) and environmental predictors (Gesquiere et al.,

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

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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:

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 methanol (Palme et al., 2013). Faecal suspensions were vortexed (1500 rpm, 10 min) in a Hercuvan TT-2500-VM Multi-Tube Vortex Mixer and centrifuged (3000 rpm, 10 min) in a VWR Mega Start 1.6 centrifuge. Subsequently, the supernatant was decanted into two safelock Eppen-

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facturer's instructions. The majority of samples were measured undiluted ($n = 343$ samples) and samples with concentrations above the 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.e., the density of urine relative to the density of distilled water, using the following formula: $uGC_{SG} = uGC_{ng/ml}*(SG_{pop}-1)/(SG-1)$, where SG_{pop} is the mean SG value for the population (1.020) (see e.g., Fürtbauer et al., 2020; Miller et al., 2004). SG corrections offer advantages over creati-

1995) in non-human primates. For lactation, the categorisation may differ based on whether the underlying stressor is hypothesised to be 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 is still caring for offspring vulnerable to infanticide (social definition). In our study n = 2 females were cyclic but also had infants that were targeted/injured by the beta male (pers. obs.), thereby falling into both the

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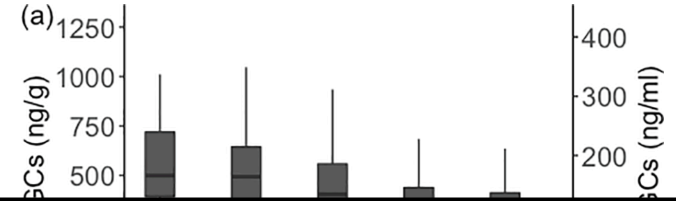
(July - November), AM/PM (before/after 12PM, to account for potential effects of circadian cortisol rhythms; Coe and Levine, 1995; Fries et al., 2009), sex (male/female, to control for potential sex-differences in baseline GCs; Touma and Palme, 2005) and urine contamination (n = 55 samples; see Palme, 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).

To investigate responses to daily weather parameters, the main model was run with the same dataset (n = 603 samples, n = 17; LMM3), where rain, minimum temperature (°C) and day length (minutes be-

monthly changes in fGCs, suggesting a gradual decrease from winter to summer months (Fig. 1a; Supplementary Material: Table S3). The main model (LMM3) was significantly different from the null model ($\chi 2 = 114.29$, $p < 0.001$). 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;



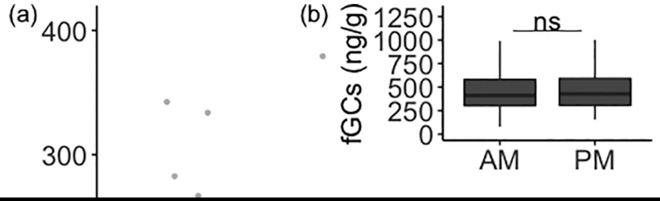


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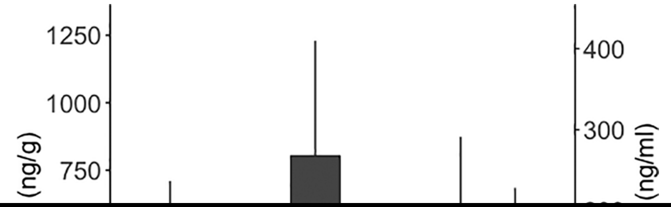
Fig. 2b). fGCs were significantly negatively correlated with day length (Table 2; Fig. 1). Minimum temperature and rain days did not predict fGCs (Table 2). fGCs were significantly higher in pregnant females

Reproductive state (lactating)*	−0.147	0.208	−0.705	0.483
Reproductive state (cycling)*	−0.063	0.217	−0.292	0.771
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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dictors with different temporal profiles, although acknowledged in several review papers (Behringer and Deschner, 2017; Creel, 2001; 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 implications for investigating stressors of different temporal nature in future research, focussing on the use of urine for GC measurements. uGCs may become increasingly used as they can be quantified alongside

positive effect on uGCs. Unlike studies where rainfall is used as a proxy for food availability (Foley et al., 2001; Pereira et al., 2006; Pride, 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

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

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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 for uGCs face the risk of overall patterns (which are informative for long-

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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 limitation will be crucial to consider, particularly in studies of shorter

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

Anna M. Bracken, et al. ***[full author details at the end of the article]***

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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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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).

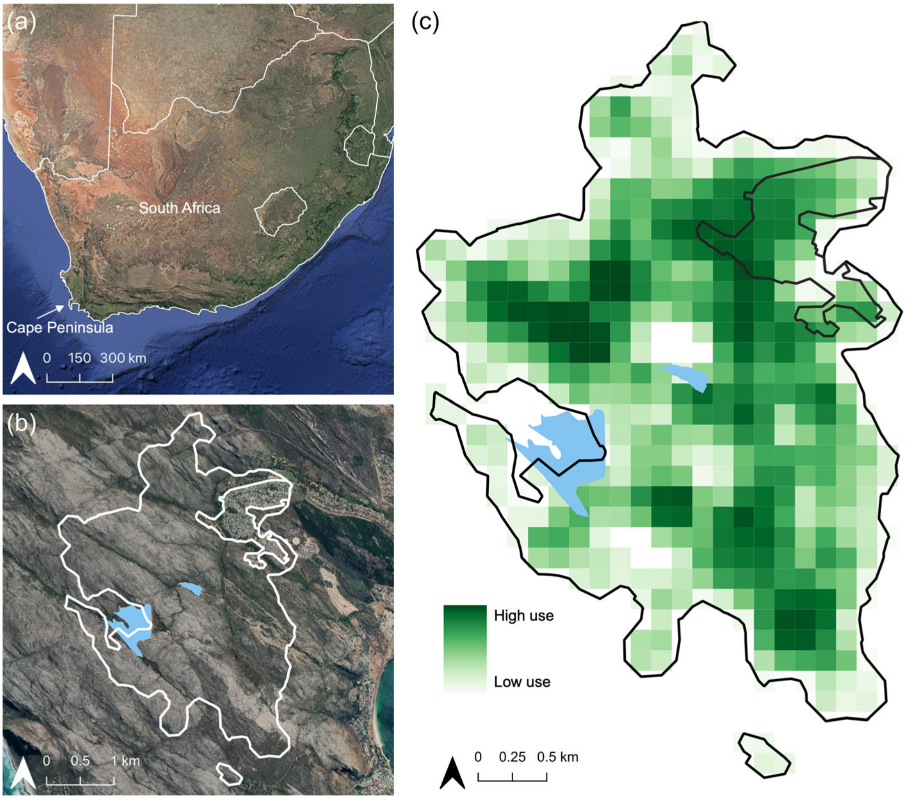

Fig. 1 Study site and baboon group overall space use, between July and September 2018. **a** The location of the Cape Peninsula in South Africa (−34.161, 18.403). **b** 95% kernel home range of the baboon group (outer white outline) and the defined urban space (inner white outline). **c** 95% kernel 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

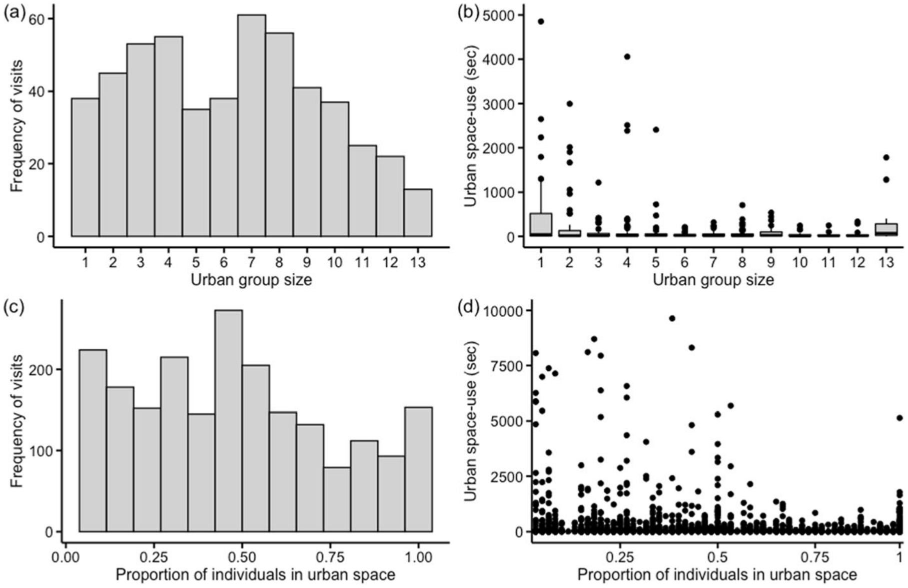

Fig. 2 Urban space use of a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Frequency of visits to urban space. **b** Seconds spent in urban space, for different baboon group sizes. **c** Frequency of visits to urban space as a function of the proportion of collared 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.

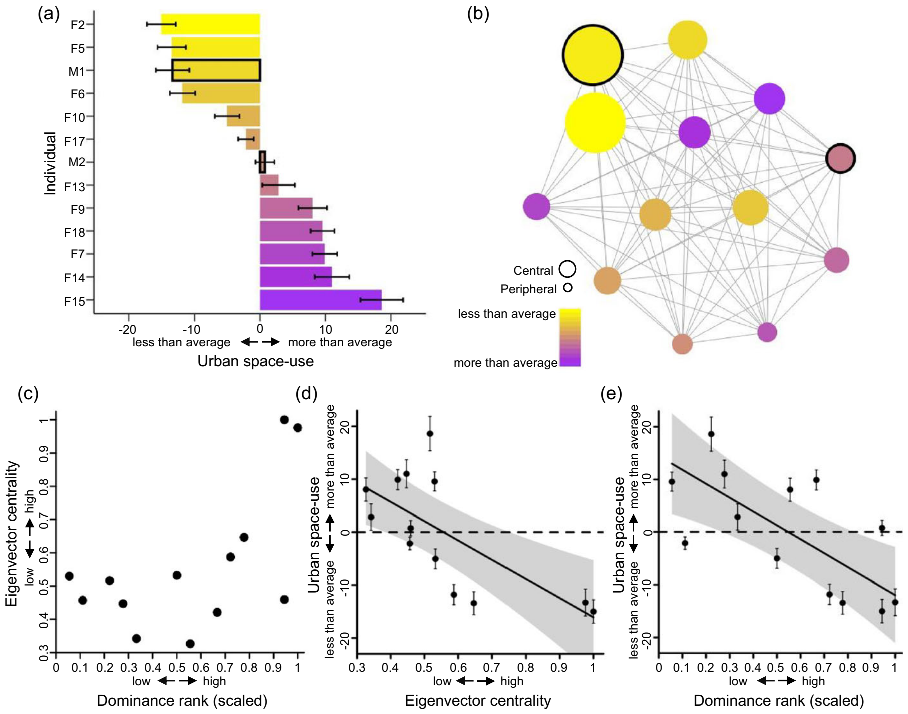

Fig. 3 The influence of social factors on variation in urban space use for a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Individual mean ± SE difference in urban cell use. **b** Baboon social network with increasing circle size indicating higher eigenvector 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.

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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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Affiliations

Anna M. Bracken[1] · **Charlotte Christensen**[1] · **M. Justin O'Riain**[2] · **Gaëlle Fehlmann**[1,3] · **Mark D. Holton**[1,4] · **Phil W. Hopkins**[4] · **Ines Fürtbauer**[1] · **Andrew J. King**[1]

✉ Anna M. Bracken
967936@swansea.ac.uk

[1] Department of Biosciences, College of Science, Swansea University, Swansea, UK

[2] Department of Biological Sciences, Institute for Communities and Wildlife in Africa, University of Cape Town, Cape Town, South Africa

[3] Present address: Cognitive and Cultural Ecology Group, Max Planck Institute of Animal Behavior, Radolfzell, Germany

[4] College of Science, Swansea University, Swansea, UK

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Author for correspondence:
Anna M. Bracken
e-mail: a.m.bracken.967936@swanse

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

Anna M. Bracken[1], Charlotte Christensen[1], M. Justin O'Riain[2], Ines Fürtbauer[1] and Andrew J. King[1]

[1]Department of Biosciences, Faculty of Science and Engineering, Swansea University, Swansea, UK
[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

AMB, 0000-0002-5183-3139; CC, 0000-0001-7697-9903; MJO, 0000-0001-5233-8327; IF, 0000-0003-1404-6280; AJK, 0000-0002-6870-9767

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

[redacted]

baboons to urban-forage [12], which can result in negative interactions between baboons and people [13–16].

The City of Cape Town contracts a private company that deploys field rangers whose objective is to deter baboons' from urban space using aversive conditioning

[9,15]. This management effort reduces the time the baboons spend in urban space [9,17], but can contribute to significant within-group variation in behaviour and space-use [9,13]. For example, in the group we study here, a combination of management effort and socioecological factors creates opportunities for

[redacted]

If association networks are interrupted and modular then we 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 coordination among local neighbours in clusters may be increased). We therefore predicted more variable group travel speeds, turning angles and alignment across all indi-

sphericity, using the package ‘swaRm’ in R [67]. Convex hull 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 strength [46,59], calculated based upon baboon associations in urban and natural space. Association networks were constructed

[redacted]

space (the natural dataset was 48× larger than the urban dataset; 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 iteration, averaged each coefficient (across iterations) and calculated 95% confidence intervals for the bootstrapped data.

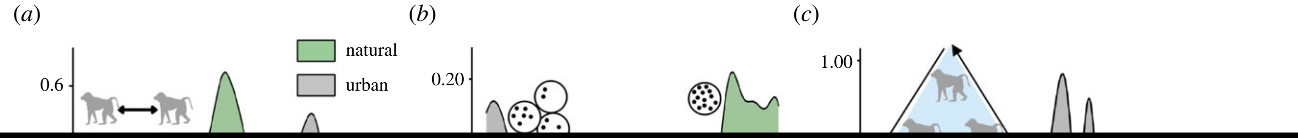
displaying lower density and higher modularity (density = 0.718; $Q = 0.429$) compared to the network in natural space (density = 1; $Q = 0.118$), reflecting lower cohesion in urban space (figure 1) where baboons are further apart (figure 1*a*,

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 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 italics (*p*-values below 0.05).)

[redacted]

was present in urban and natural space (electronic supplementary material, figure S3a,b) but this relationship was weaker in urban space (mean speed × urban space: estimate ± 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

spatial association networks (figure 2*a*,*c*) (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, $p = 0.921$).



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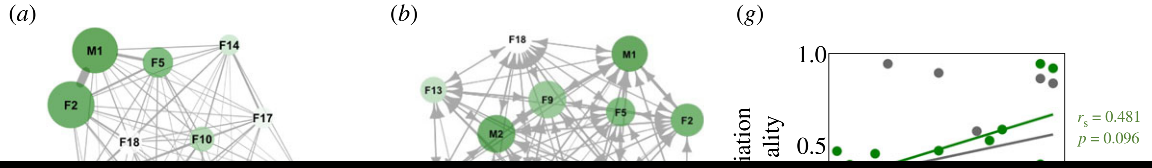
in turn.

Baboon social cohesion and association networks were significantly reduced in urban space, supporting our first hypothesis. This finding is in line with recent research

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



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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]

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.

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

Ines Fürtbauer[a,b,*], Charlotte Christensen[a,b], Anna Bracken[a,b], M. Justin O'Riain[b], Michael Heistermann[c], Andrew J. King[a,b]

[a] *Department of Biosciences, College of Science, Swansea University, SA2 8PP Swansea, UK*
[b] *Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa*
[c] *Endocrinology Laboratory, German Primate Centre, 37077 Göttingen, Germany*

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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

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[*] Corresponding author at: Department of Biosciences, College of Science, Swansea University, SA2 8PP Swansea, UK.
E-mail address: i.fuertbauer@swansea.ac.uk (I. Fürtbauer).

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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).

Monitoring energetic condition in wild animals, without relying on [redacted] 2012). Therefore, devising novel methods to better understand the drivers for wild animals to live and forage within and adjacent to urban and rural landscapes is crucial to developing management plans that ultimately seek to improve the welfare of people and wildlife and the conservation value of the latter (Fehlmann et al., in press).

Here, we investigate variation in uCP levels in wild, male and female, chacma baboons (*Papio ursinus*) living at the urban edge on the 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 during a period of provisioning compared to the periods before and

work was approved by local authorities and Swansea University's Ethics Committee (IP-1314-5).

2.2. Urine sample collection and storage

N = 315 urine samples (mean ± SD = 18.5 ± 3.5 per individual; Table 1) were collected opportunistically throughout the day and immediately 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]

centrations.

the assay and duplicate 50 µl aliquots of diluted samples and 5α-pregnane-3ß-ol-20-one standard (4.8–625 pg/50 µl) were combined with labelled conjugate (50 µl) and antiserum (50 µl) and incubated overnight at 4 °C. After incubation, the plates were washed four times after which TMB substrate solution was added and the plates incubated at room temperature in the dark for another 60 min. The enzyme reaction

[redacted]

allow including males) and collection method (Salivette vs. pipette) were controlled for as fixed effects (see LMM2).

Second, a LMM was used to investigate the effects of various predictors on uCP levels (n = 315 samples, n = 17 individuals; LMM2). Collection method (Salivette/pipette), standardized dominance rank (continuous, see above), sex (male/female; to control for potential sex 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 November. Due to winter rainfall, annually flowering grasses are mainly available in winter whereas fruits and flowers are most abundant in spring and summer (Johnson, 1993; Milton, 2004). An inter-

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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) and female (n = 15) chacma baboons (LMM2). Significant effects are highlighted in bold (n = 315 samples). See text for further details.

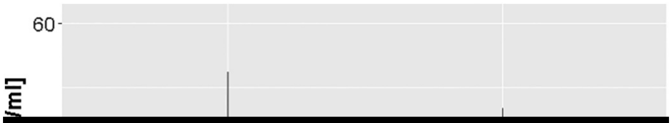

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Fig. 2. Effect of season on uCP levels in wild chacma baboons. UCP was significantly higher during winter (July and August) and summer (November) than during spring (September and October). Notches display 95% confidence intervals around the median (black line). Grey dots represent individual data points (n = 1 data point for 'Winter' not shown; uCP = 228.9 ng/ml).

plementary material).

4. Discussion

Where there is human activity, there is likely to be predictable access to food, which is attractive to wildlife (Baruch-Mordo et al., 2013). Studies have demonstrated that animals can reap benefits from access to human foods, including higher reproductive success through decreased birth intervals and increased infant survival (Altmann and 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;

[redacted]

Nigeria, for instance, experience a quicker return to menstrual cycling and increased reproductive output (Higham et al., 2009).

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

(primates: Nowak et al., 2017; Naughton-Treves et al., 1998; Tweheyo et al., 2005; black bears: Lewis et al., 2015; African elephants: Osborn, 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 com-

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found no significant difference in uCP concentrations in human and macaque urine transferred onto synthetic Salivettes and matched controls (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

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

R. McCann[1] · **A. M. Bracken**[1] · **C. Christensen**[1] · **I. Fürtbauer**[1] · **A. J. King**[1]

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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*

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R. McCann
rebecca.mccann55@hotmail.co.uk

A. J. King
a.j.king@swansea.ac.uk

[1] Department of Biosciences, Singleton Park Campus, Swansea University, Swansea, UK

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).

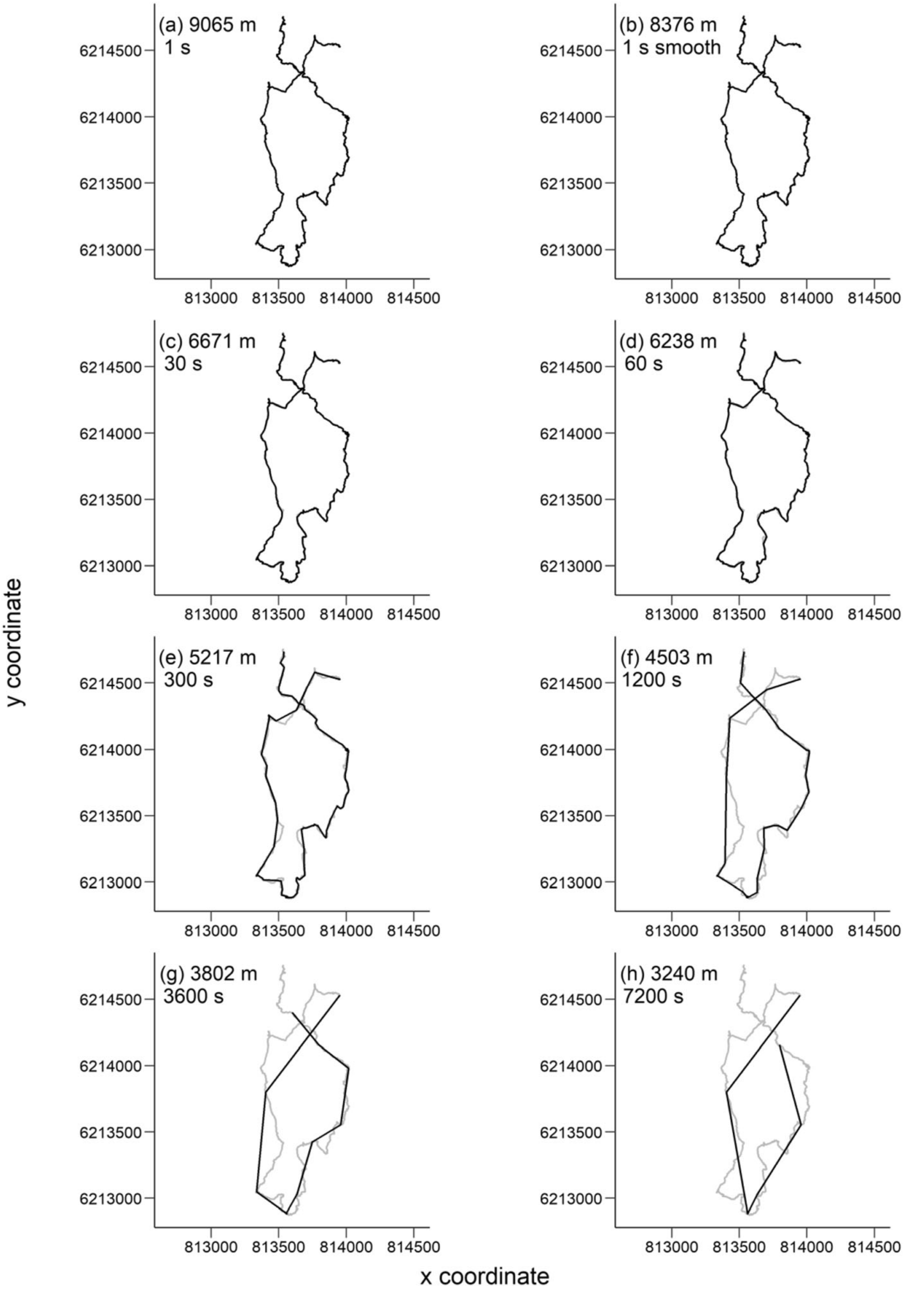

Fig. 1 Path traveled (black line) by one adult female chacma baboon between 06:18 and 18:00 UTC on August 4th, 2018 in Cape Town, South Africa, estimated using a GPS sampling interval of **(a)** 1 s, **(b)** 1 s smoothed, **(c)** 30 s, **(d)** 60 s, **(e)** 300 s, **(f)** 1200 s, **(g)** 3600 s, and **(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

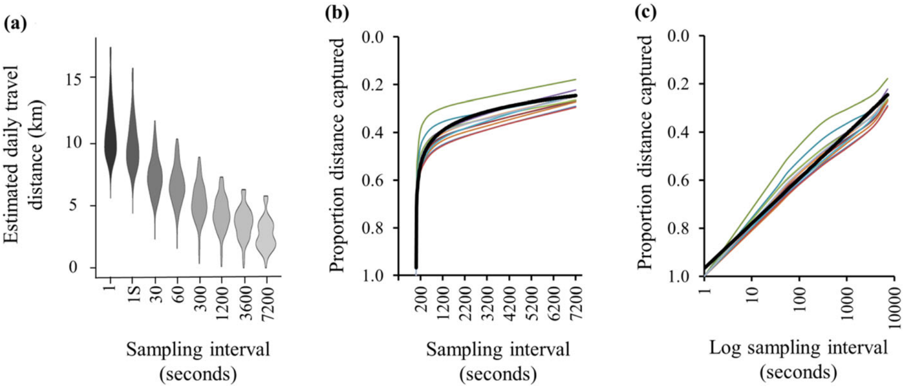

Fig. 2 **(a)** Kernel probability density of daily travel distances by 12 chacma baboons over 11–12 days, in Cape Town, South Africa, measured using GPS sampling intervals ranging one fix per second to one fix per 7200 s; smoothed 1-s data (1S) are also shown. **(b)** Comparison of the estimated distance 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

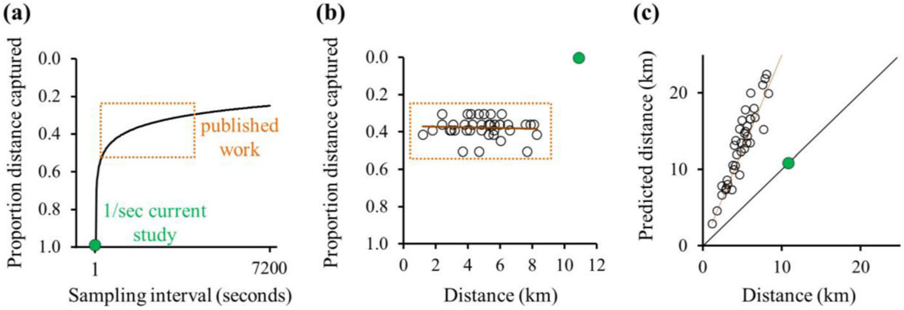

Fig. 3 **(a)** Comparison of the estimated distance calculated with one fix per second GPS (filled circle) compared to less frequent GPS sampling intervals, expressed as a proportion. The dashed box indicates the range of GPS sampling interval (300–3600 s) used in 38 published groups' daily travel distances (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.

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

Anna M. Bracken, et al. *[full author details at the end of the article]*

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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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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).

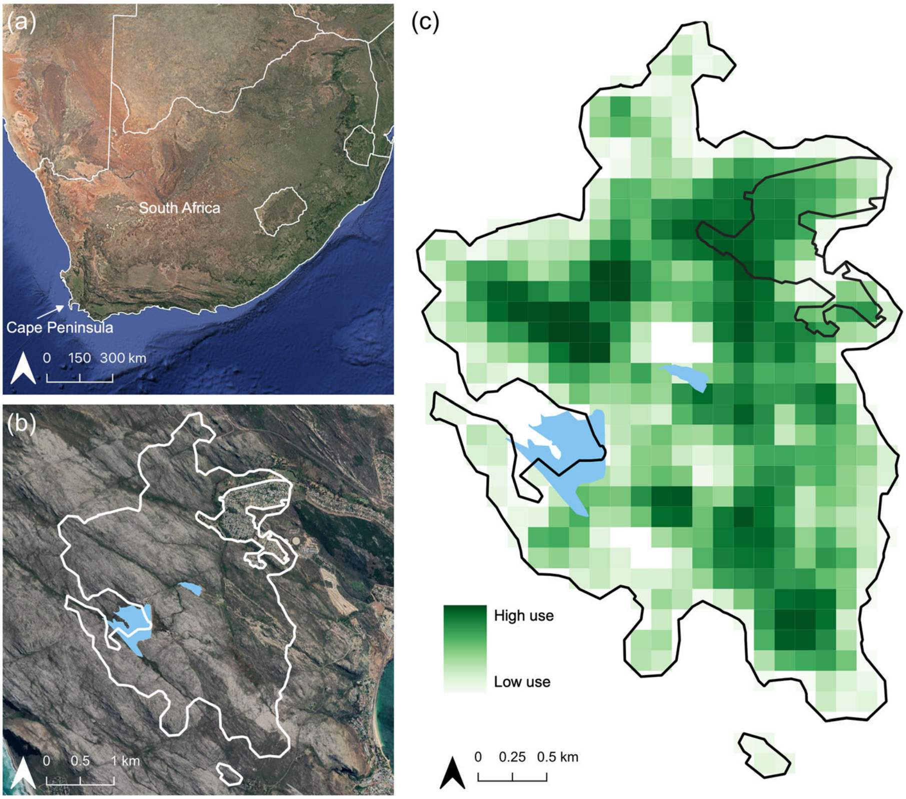

Fig. 1 Study site and baboon group overall space use, between July and September 2018. **a** The location of the Cape Peninsula in South Africa (−34.161, 18.403). **b** 95% kernel home range of the baboon group (outer white outline) and the defined urban space (inner white outline). **c** 95% kernel 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

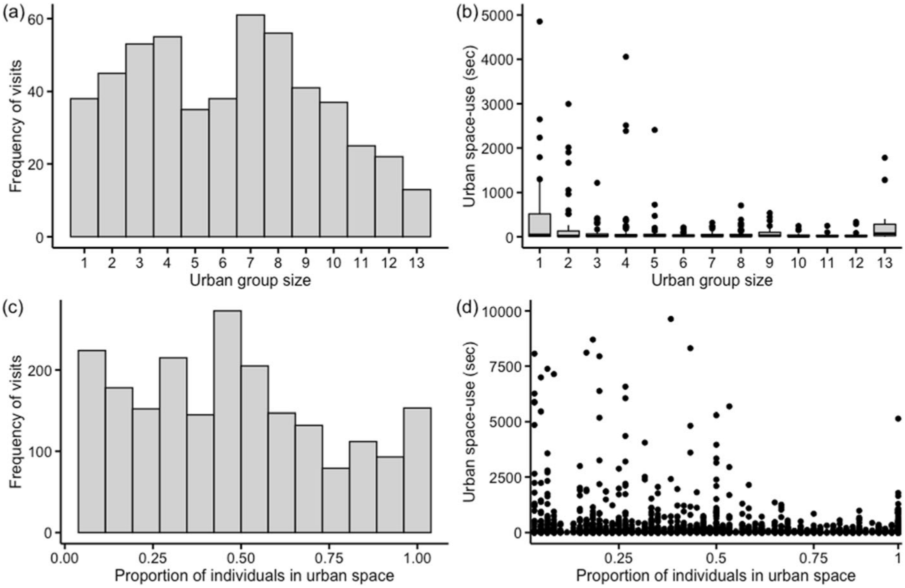

Fig. 2 Urban space use of a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Frequency of visits to urban space. **b** Seconds spent in urban space, for different baboon group sizes. **c** Frequency of visits to urban space as a function of the proportion of collared 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.

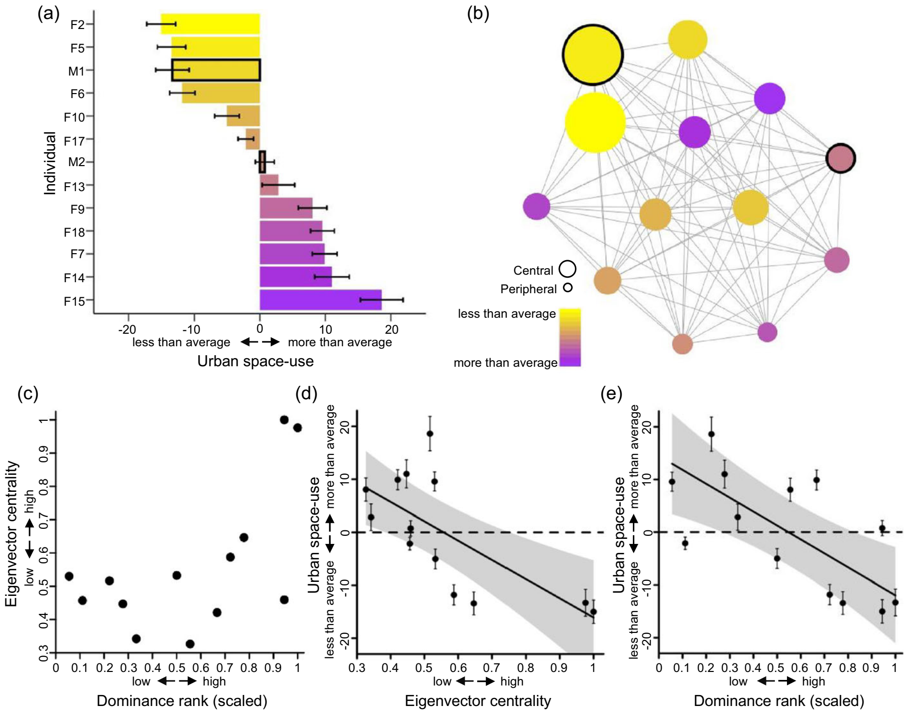

Fig. 3 The influence of social factors on variation in urban space use for a baboon group living in Cape Town, South Africa, between July and September 2018. **a** Individual mean ± SE difference in urban cell use. **b** Baboon social network with increasing circle size indicating higher eigenvector 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.

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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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Affiliations

Anna M. Bracken[1] · **Charlotte Christensen**[1] · **M. Justin O'Riain**[2] · **Gaëlle Fehlmann**[1,3] · **Mark D. Holton**[1,4] · **Phil W. Hopkins**[4] · **Ines Fürtbauer**[1] · **Andrew J. King**[1]

✉ Anna M. Bracken
967936@swansea.ac.uk

[1] Department of Biosciences, College of Science, Swansea University, Swansea, UK

[2] Department of Biological Sciences, Institute for Communities and Wildlife in Africa, University of Cape Town, Cape Town, South Africa

[3] Present address: Cognitive and Cultural Ecology Group, Max Planck Institute of Animal Behavior, Radolfzell, Germany

[4] College of Science, Swansea University, Swansea, UK

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Author for correspondence:
Anna M. Bracken
e-mail: a.m.bracken.967936@swansea.ac.uk

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

Anna M. Bracken[1], Charlotte Christensen[1], M. Justin O'Riain[2], Ines Fürtbauer[1] and Andrew J. King[1]

[1]Department of Biosciences, Faculty of Science and Engineering, Swansea University, Swansea, UK
[2]Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

AMB, 0000-0002-5183-3139; CC, 0000-0001-7697-9903; MJO, 0000-0001-5233-8327;
IF, 0000-0003-1404-6280; AJK, 0000-0002-6870-9767

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*)—

[redacted]

whose objective is to deter baboons' from urban space using aversive conditioning

[9,15]. This management effort reduces the time the baboons spend in urban space [9,17], but can contribute to significant within-group variation in behaviour and space-use [9,13]. For example, in the group we study here, a combination of management effort and socioecological factors creates opportunities for

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area [52,53], shape [54,55] and spread [56–58] of the group when in natural and urban space, and built networks describing patterns of spatial associations among individuals [46,59]. If association networks are interrupted and modular then we 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 coordination among local neighbours in clusters may be increased). We therefore predicted more variable group travel speeds, turning angles and alignment across all indi-

To test for differences in social cohesion when baboons were in urban and natural space we calculated: (i) convex hull area and perimeter; (ii) mean nearest neighbour distance; (iii) mean distance to the group centroid; and (iv) group stretch and sphericity, using the package ‘swaRm’ in R [67]. Convex hull 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 strength [46,59], calculated based upon baboon associations in urban and natural space. Association networks were constructed using the ‘Spatsoc’ package in R [69]. Baboon GPS fixes were grouped spatio-temporally, where individuals within 5 m and 1 min of one another were assumed to be in association using the ‘chain rule’ [70]. Network edges were weighted using the

[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 iteration, averaged each coefficient (across iterations) and calculated 95% confidence intervals for the bootstrapped data. We 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 group centroid, speed of the group centroid and mean

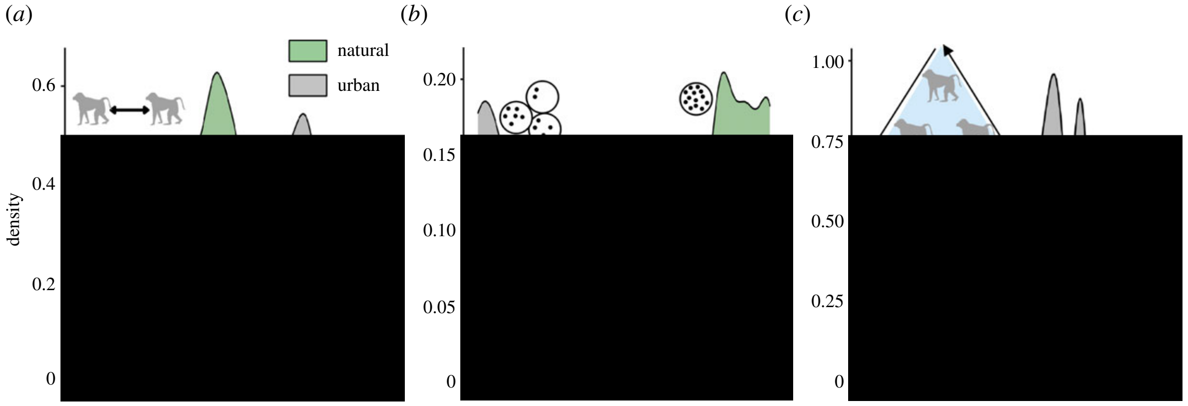
0.718; $Q = 0.429$) compared to the network in natural space (density = 1; $Q = 0.118$), reflecting lower cohesion in urban space (figure 1) where baboons are further apart (figure 1*a*,

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 the natural log scale. With the exception of 'stretch', positive estimates indicate a parameter increase in urban space and negative estimates indicate a parameter

[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, $p = 0.921$).



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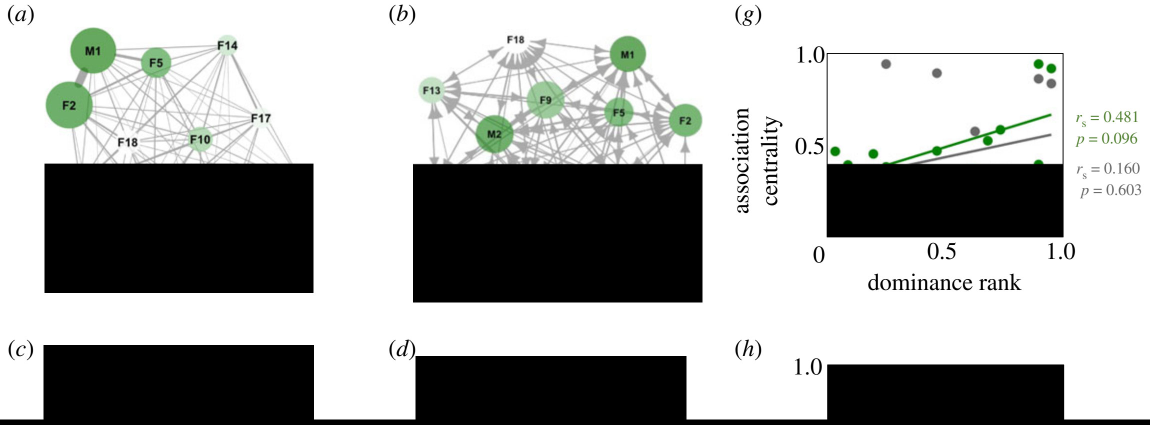
Baboon social cohesion and association networks were significantly reduced in urban space, supporting our first hypothesis. This finding is in line with recent research

actions at the dyadic level in urban space. Moreover, the spread of the group in urban space had an uneven distribution. Individuals were often seen in dispersed subgroups,



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

ation 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.

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 space, leadership roles as predicted by dominance rank remained stable. This finding therefore offers partial support

[redacted]

burg-Peshkin *et al.* [64] 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, we 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, our results demonstrate how chacma baboons in the Cape Peninsula have adapted to exploit urban space,

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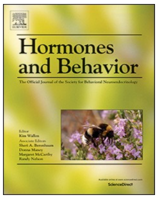

Energetics at the urban edge: Environmental and individual predictors of urinary C-peptide levels in wild chacma baboons (*Papio ursinus*)

Ines Fürtbauer[a,b,*], Charlotte Christensen[a,b], Anna Bracken[a,b], M. Justin O'Riain[b], Michael Heistermann[c], Andrew J. King[a,b]

[a] *Department of Biosciences, College of Science, Swansea University, SA2 8PP Swansea, UK*
[b] *Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa*
[c] *Endocrinology Laboratory, German Primate Centre, 37077 Göttingen, Germany*

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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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[*] Corresponding author at: Department of Biosciences, College of Science, Swansea University, SA2 8PP Swansea, UK.
E-mail address: i.fuertbauer@swansea.ac.uk (I. Fürtbauer).

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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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male, chacma baboons (*Papio ursinus*) living at the urban edge on the 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

Table 1) were collected opportunistically throughout the day and immediately 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)			
			Male	Cyclic	Pregnant	Lactating

[redacted]

measured with a manual handheld refractometer, using the following correction formula: $uCP_{SG} = uCP_{ng/ml} * (SG_{pop} - 1) / (SG - 1)$, where SG_{Pop} is the mean SG value for the population (1.019) (see e.g. Miller et al., 2004). All uCP values reported are the SG corrected uCP concentrations.

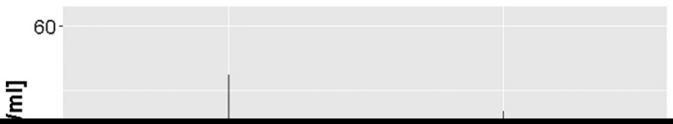
including baboons, to assess female reproductive status (Wasser et al., 1988; Graham et al., 2001).

Prior to EIA, faecal extracts were diluted 1:30–1:300 with assay buffer to bring the hormone concentrations into the working range of the assay and duplicate 50 µl aliquots of diluted samples and 5α-pregnane-3ß-ol-20-one standard (4.8–625 pg/50 µl) were combined with labelled conjugate (50 µl) and antiserum (50 µl) and incubated overnight at 4 °C. After incubation, the plates were washed four times after which TMB substrate solution was added and the plates incubated at room temperature in the dark for another 60 min. The enzyme reaction was finally stopped by adding 50 µl of 2 M H_2SO_4 to each well and

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 November. Due to winter rainfall, annually flowering grasses are mainly available in winter whereas fruits and flowers are most abundant in spring and summer (Johnson, 1993; Milton, 2004). An interaction between season and rank (which would be expected if compe-

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) and female (n = 15) chacma baboons (LMM2). Significant effects are high-



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nificantly higher during winter (July and August) and summer (November) than during spring (September and October). Notches display 95% confidence 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).

to human foods, including higher reproductive success through decreased birth intervals and increased infant survival (Altmann and 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 et al., in press; Lowry et al., 2013), research into the energetic correlates are largely lacking. In this study we investigated predictors of variation in uCP, a proxy for energy balance (Emery Thompson, 2016), in chacma baboons living at the urban edge on the Cape Peninsula. We (1) discuss the implications of our findings and (2) provide future di-

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the energetic constraints of lactation are dampened by the consumption of high-energy human foods. Female olive baboons feeding on crops in Nigeria, for instance, experience a quicker return to menstrual cycling and increased reproductive output (Higham et al., 2009).

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 et al., 2012; McCabe et al., 2013). Furthermore, the effects of reproductive state on uCP may vary across seasons; however, investigating such interactions requires a larger data set where the same females are sampled in different reproductive states and across seasons.

conjunction with the ripening of palatable crops in agricultural areas are key drivers in attracting animals to human-modified landscapes (primates: Nowak et al., 2017; Naughton-Treves et al., 1998; Tweheyo et al., 2005; black bears: Lewis et al., 2015; African elephants: Osborn, 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

[redacted]

Our study also highlights methodological aspects of uCP as a non-invasive marker of energy status. In contrast to a recent study that found no significant difference in uCP concentrations in human and macaque urine transferred onto synthetic Salivettes and matched controls (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

tical support.

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

R. McCann[1] · **A. M. Bracken**[1] · **C. Christensen**[1] · **I. Fürtbauer**[1] · **A. J. King**[1]

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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*

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✉ R. McCann
rebecca.mccann55@hotmail.co.uk

✉ A. J. King
a.j.king@swansea.ac.uk

[1] Department of Biosciences, Singleton Park Campus, Swansea University, Swansea, UK

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).

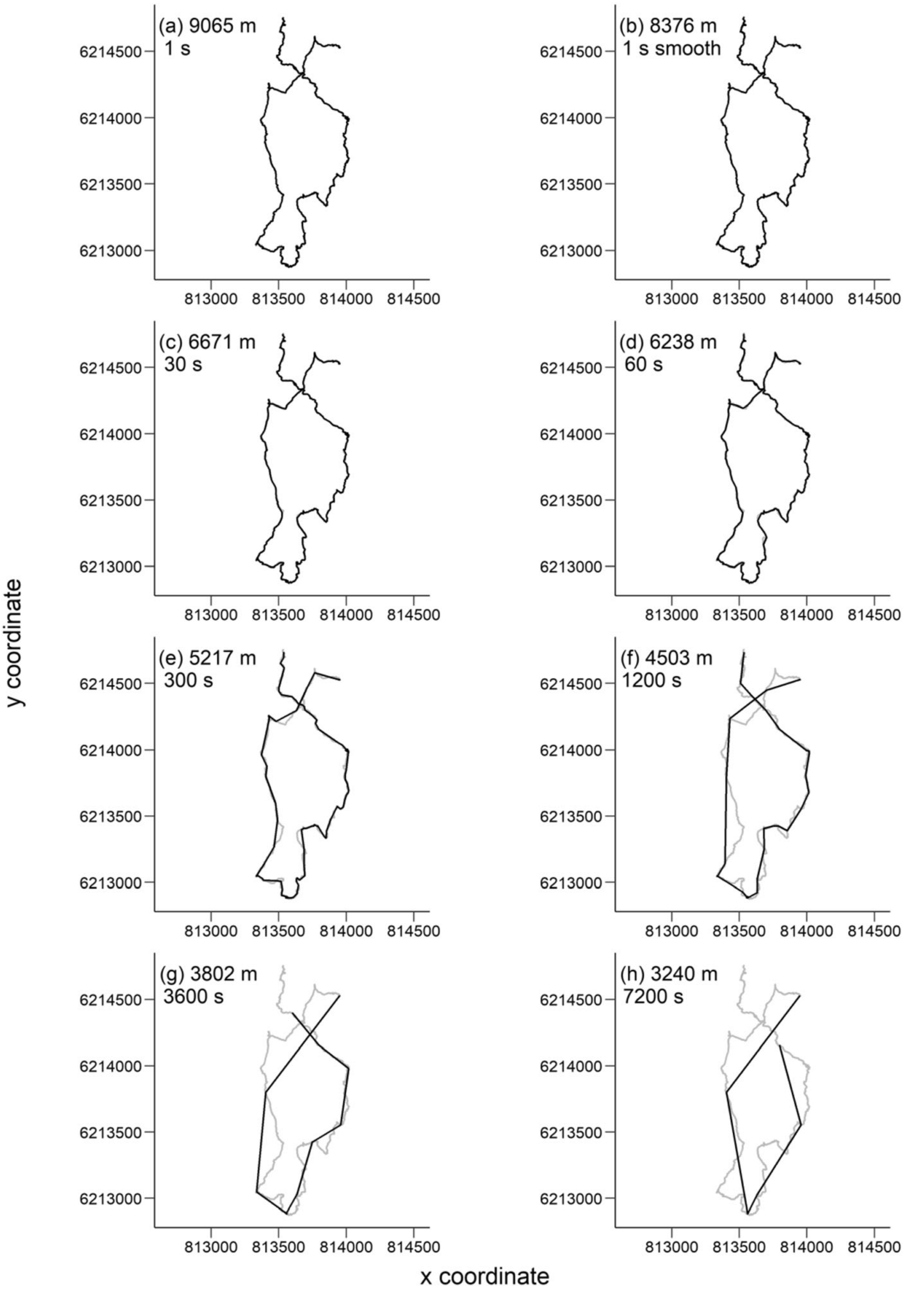

Fig. 1 Path traveled (black line) by one adult female chacma baboon between 06:18 and 18:00 UTC on August 4th, 2018 in Cape Town, South Africa, estimated using a GPS sampling interval of **(a)** 1 s, **(b)** 1 s smoothed, **(c)** 30 s, **(d)** 60 s, **(e)** 300 s, **(f)** 1200 s, **(g)** 3600 s, and **(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

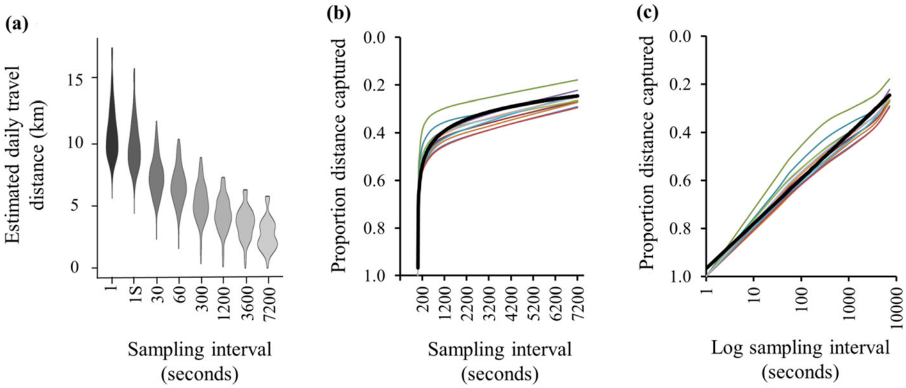

Fig. 2 **(a)** Kernel probability density of daily travel distances by 12 chacma baboons over 11–12 days, in Cape Town, South Africa, measured using GPS sampling intervals ranging one fix per second to one fix per 7200 s; smoothed 1-s data (1S) are also shown. **(b)** Comparison of the estimated distance 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

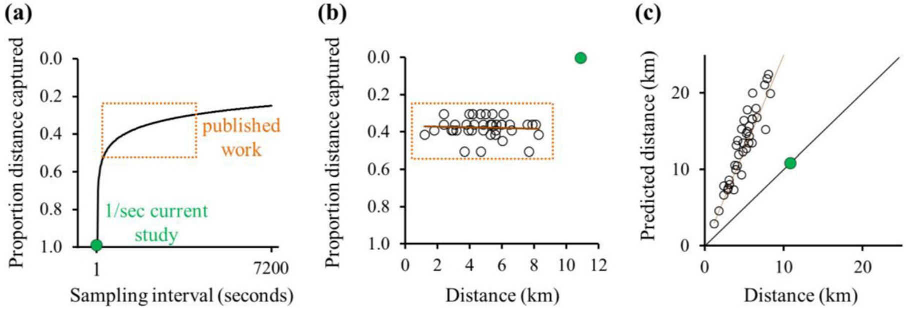

Fig. 3 **(a)** Comparison of the estimated distance calculated with one fix per second GPS (filled circle) compared to less frequent GPS sampling intervals, expressed as a proportion. The dashed box indicates the range of GPS sampling interval (300–3600 s) used in 38 published groups' daily travel distances (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.

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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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