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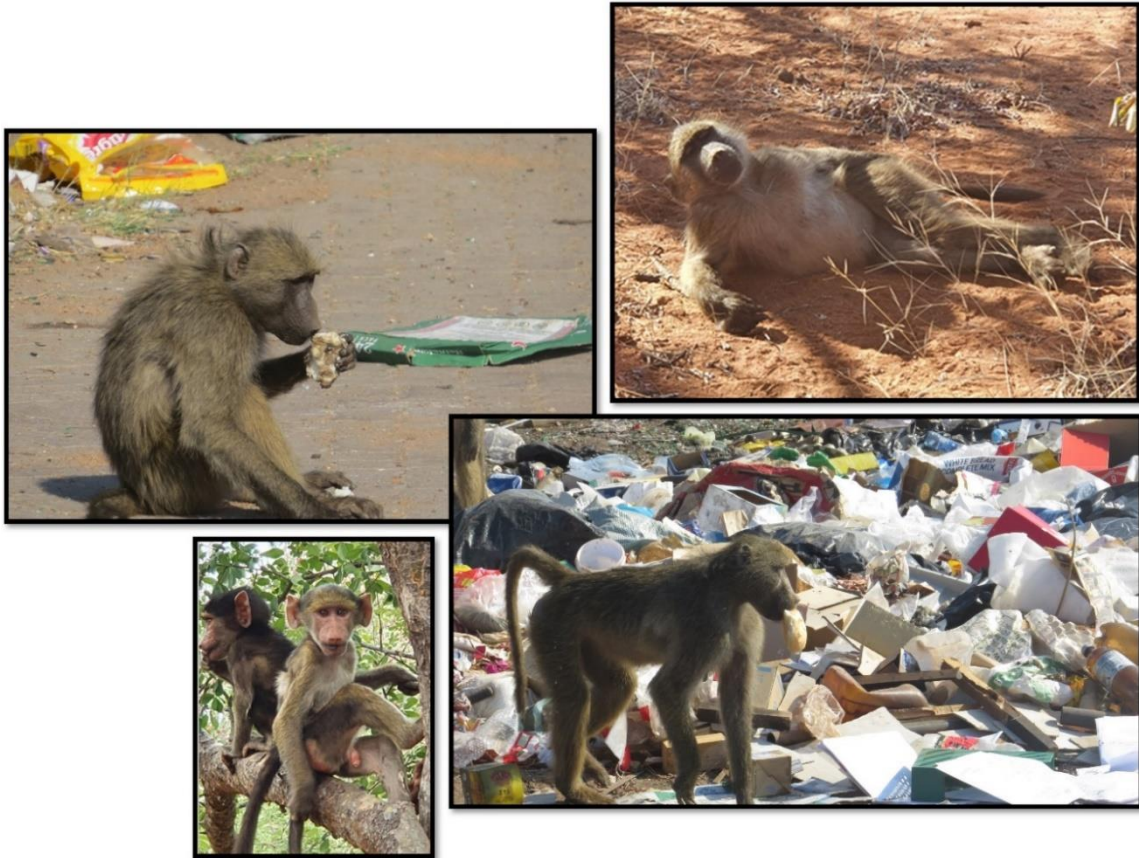
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# BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES TO ANTHROPOGENIC FOOD SOURCES IN CHACMA BABOONS



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**Thesis submitted to Durham University for the degree of Doctor of Philosophy**

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# Behavioural and physiological responses to anthropogenic food sources in chacma baboons

Md Mokhlesur Rahman

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## Abstract

Human impact on primate habitats is increasing across the range countries. As a result, many primates are sharing their habitats with humans. This proximity to humans is often accompanied with the incorporation of human foods into primate diets. The effects of human foods, and how primates modify their behaviours and physiology according to these changing food habits, are therefore becoming increasingly important to understand. This study aimed to increase our understanding of the impacts of human foods on primates by studying a baboon group that feeds on a human rubbish dump, investigating their behavioural plasticity and physiological changes.

This study was conducted on a habituated chacma baboon (*Papio ursinus*) group in Alldays, South Africa. The group regularly visits a garbage dump from where they gained food on a daily basis. Behavioural (activity budget, ranging distance), physiological (glucocorticoid and thyroid hormone levels) and ecological (food availability) data were collected over a 12-month period. A novel method combining the estimated number of dumped bags and sampling of their content, was used to estimate dump food availability. Similar data on other baboon groups from across the African continent, both wild-feeding and anthropogenic foragers, were compiled from the literature to enable comparison of the impacts of dump-feeding.

The study results showed that the activity budgets of the Alldays Dump Group were dominated by resting, which was significantly higher than wild foraging baboons; whereas feeding time was significantly lower than for both wild foraging and other anthropogenic foraging baboons. The group spent an average of three hours per day in the dump, which varied according to dump food availability. They spent almost half of their total foraging time on dump foods. Home range size and daily travel length were significantly decreased compared to wild foraging baboons. Baboons showed more behavioural anxiety when they were in the dump compared to their natural habitat, presumably driven by the concentrated and desirable nature of dump resources and consequently increased intragroup feeding competition. The results also showed that the thyroid and glucocorticoid hormone levels, which measure baboons' energetic physiology, varied with food availability. Thyroid hormone levels, which are an index of basal metabolic rate, were positively related to food availability, and negatively related to distance travelled suggesting similar relationships with energy acquisition and energy expenditure, respectively. Unexpectedly, glucocorticoid levels, or physiological stress levels, were positively related to natural but not dump food availability and only related to psychosocial stress in females. Persecution events increased both behavioural anxiety and physiological stress levels in the baboons, with some evidence of a cumulative effect of two fatal shooting incidents occurring in relatively quick succession, and a faster recovery in terms of behavioural anxiety than physiological stress.

Significant differences in activity budgets and ranging patterns for the Alldays Dump Group compared to other baboon populations suggest that dump feeding might be an extreme form of anthropogenic feeding, in terms of positive energetic benefits and limited negative impacts. However, there were some significant costs in terms of physical injury and death associated with living close to the human population surrounding the dump resources, emphasising that there are always trade-offs between the benefits and risks of living in human-modified habitats.

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## **Statement of copyright**

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## **Dedication**

To my lovely wife- Tahmina, and our son- Hasnain, who I missed the most !



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# Chapter 1. General introduction

Human urbanisation and industrialisation have had a negative impact on biodiversity (Hunter 2007), through destruction and fragmentation of natural habitat (Ewers and Didham 2007, Arroyo-Rodríguez and Dias 2010), land transformation (Stone et al. 2015) and increasing human populations (Hunter 2007). As a result of the land use changes, many animals live closer to humans as we extend our ranges further into their habitats (Humble and Hill 2016, Chowdhury et al. 2020). Increasing spatial overlap between humans and wildlife causes decreasing wild food supplies for wildlife, as well as limiting their access to space, water, nesting sites and safe habitats (Humble and Hill 2016). Some animals such as small mammals and small birds have adapted to live and thrive in new environments, with the resources and threats of the human-modified habitats (Hunter 2007, Hulme-Beaman et al. 2016). Many large-bodied and habitat-specific mammals are greatly affected by the anthropogenic modification of land use patterns and their populations are declining markedly (Karanth et al. 2010). However, some mammals, such as primates, have adapted through evolutionary and selective processes to live in challenging habitats (Gesquiere et al. 2008).

Non-human primates (hereafter primates) that live in human-modified habitats face a number of ecological constraints including restricted home range (Strum 2010, Tesfaye et al. 2013), reduced food availability (Chaves et al. 2011) and increased inter and intra-species competition (Warren et al. 2011, El Alami et al. 2012). These ecological constraints may affect their diet, reproduction and ultimately survival (Menon and Poirier 1996). To overcome these constraints, many primates display remarkable dietary flexibility in response to habitat variation and seasonally fluctuating food resources, including the capability to incorporate human-derived foods into their diet (Altmann and Muruthi 1988, Warren et al. 2011, Grueter et al. 2013, Lewis and O’Riain 2017,

Khatun et al. 2018); such species also become habituated to living in close contact with humans (Sha et al. 2009). Such flexibility is core to their ability to adapt to varied or changing ecological circumstances. Investigating this flexibility is therefore key to furthering our understanding of human-wildlife interactions, the impact of habitat change and conservation efforts, as well as fundamental evolutionary biology.

## **1.1 Human-primate interfaces**

In anthropogenic habitats, human-primate interfaces appear in multiple contexts such as during primate crop foraging, human provisioning, research activities and ecotourism. Broadly, humans and primates have similar physiological needs and often exploit the same plant resources (Riley 2007b, Hockings et al. 2020). These common interests may draw primates to human cultivated crop fields (Strum 2010, McKinney 2011, Warren et al. 2011). In addition, similarities between species allow humans to share their own food with primates, as frequently observed at temple sites and tourist spots (Seth and Seth 1986, Medhi et al. 2007, Ilham et al. 2018). Research activities and primate-related ecotourism also bring humans and primates into closer proximity (Unwin and Smith 2010, Maréchal et al. 2011, Maréchal et al. 2016b). Up to now, detailed examination of the utilization of garbage/rubbish bins by primate species has received limited attention (Altmann and Muruthi 1988, Sha and Hanya 2013). However, this can be a potential source of human-primate interface in human modified habitats.

Most of the above-mentioned human-primate interfaces commonly result in the incorporation of human foods into primate diets. These foods are obtained from crop fields, foraging on bins and garbage pits, or are offered by tourists, animal lovers or pilgrims (Altmann and Muruthi 1988, Kamal et al. 1997, Higham et al. 2009b, Maréchal et al. 2011, Ilham et al. 2018). Maize, barley, potatoes, sweet potato, sorghum, beans, butternut squash, tomato, ground nuts, millet, wheat, rice, pumpkin, cabbage, lentils, cauliflowers, mango, roots, cassava, tuber crops, different fruits, and other crops are foraged on by different primate species across their ranges (Naughton-Treves et al. 1998, Hill 2000, Tweheyo et al. 2005, Strum 2010, Khatun et al. 2013, Ghimire and Chalise 2019, Wiafe 2019, Alemayehu and Tekalign 2020, Findlay and Hill 2021, Jaleta and Tekalign 2023). Primate foods from garbage dumps or refuse bins include leftover fruits and vegetables, processed foods such as jam, baked items, milk and the contents of styrofoam food boxes, and plastic food packages (Altmann and Muruthi 1988, Sha and Hanya 2013). Provisioning and/or

tourist provisioned items include varieties of fruits, vegetables, dried items, nuts, cakes, biscuits (Medhi et al. 2007, Unwin and Smith 2010, McKinney 2011, Schurr et al. 2012).

## **1.2 Stressors, stress response, stress and anxiety**

The definitions of stressor, stress response, stress and anxiety used by researchers vary. Here I describe the definitions used in this thesis. An unpredictable stimulus or noxious event that requires some changes to maintain stability, is termed a stressor; and the behavioural, hormonal and physiological responses to any stressor are called stress responses (Romero 2004). There are ambiguities and controversies between authors defining the term stress. However, McEwen and Wingfield (2003) redefined the stress concept focusing on the impact of stress. By their definitions, stress can be defined as an event that threatens an individual and which requires an urgent energetic response to overcome. Put simply, if a stimulus or threat pushes the animal beyond a certain limit of what an animal can handle within its normal range (called allostatic overload (Romero et al. 2009)), and which requires physiological and/or behavioural responses to overcome, can be considered as a stressor. On the other hand, anxiety is physiological state, triggered by stimuli that cause negative emotional reactions (Coleman and Pierre 2014). Anxiety can be considered as a subset of stress, related to animals' psychology.

Stressors trigger the hypothalamic-pituitary-adrenal (HPA) axis to release catecholamines (e.g. epinephrine and norepinephrine) and glucocorticoids such as cortisol and corticosterone (Beehner and Bergman 2017). The catecholamines are responsible for the immediate stress response (the fight-flight-freeze) while glucocorticoids respond more slowly (Sapolsky et al. 2000, Beehner and Bergman 2017). In vertebrates, glucocorticoid hormones are increasingly being used as indicators of physiological stress (Romero 2004) which can be detected non-invasively from urine and faecal samples (Hodges and Heistermann 2003).

Self-directed behaviours such as scratching, self-grooming, yawning and body shaking can be used as indices of animals' anxiety (Maestriperi et al. 1992), has and have been used in many different non-human primate species in a variety of contexts (Castles et al. 1999, Higham et al. 2009a, Maréchal et al. 2011, Pearson et al. 2015). Agonistic interactions between individuals can lead to a rise in animals' anxiety levels (Maestriperi et al. 1992, Castles and Whiten 1998). Vigilance and excessive fear (measured by aggression) can also be good indicators of anxiety in

primates (Coleman and Pierre 2014). In this study, I used behavioural measures of SDBs, aggression and vigilance to measure overall anxiety, and faecal measures of glucocorticoid hormones to measure physiological stress levels.

### **1.3 Benefits and costs of having human foods in primates' diet**

Most human foods tend to be energy rich, palatable, easily digestible, spatiotemporally predictable and sometimes readily available in greater amounts than natural foods (Muruthi et al. 1991, Saj et al. 1999, Ilham et al. 2018). The inclusion of high-quality human foods in a primate's diet has significant positive impacts on their reproductive functions (Altmann and Muruthi 1988, Saj et al. 1999, McKinney 2011, El Alami et al. 2012). For example, a crop foraging baboon group had reduced infant mortality (Higham et al. 2009b, Warren et al. 2011), shorter inter-birth intervals (Higham et al. 2009b, Strum 2010, Warren et al. 2011), and shorter postpartum amenorrhea (Higham et al. 2009b, Warren et al. 2011) than a non-crop foraging baboon group, and overall, the health condition of crop foraging groups was better (Altmann et al. 1993, Warren et al. 2011). Thus, crop foraging, or human-derived food provides both energetic and reproductive advantages to primates.

There are some costs associated with access to human foods, however, such as higher intragroup aggression (Ram et al. 2003, El Alami et al. 2012, José-Domínguez et al. 2015, Ilham et al. 2018), resulting in different levels of injury (McKinney 2011). Food supplemented primate groups carry more parasites (Weyher et al. 2006, Warren et al. 2011) and antibiotic resistant bacteria (Rolland et al. 1985) than wild feeding counterparts. A supplemented feeding group of red howler monkeys (*Alouatta macconnelli*) had poorer health due to several physical injuries and intestinal parasite infections (McKinney et al. 2015). Provisioning increases the chances of cross-species disease transmission from humans and their livestock (Altmann and Muruthi 1988, McKinney et al. 2015). Provisioning was also related to infant mortality in Tibetan macaques, *M. thibetana* (Berman et al. 2007)).

In addition to some health risks, behavioural anxiety, measured by self-directed behaviours, SDBs (Maestriperi et al. 1992) is also associated with accessing human foods. For example, a provisioned group of Barbary macaques in the Middle Atlas Mountains, Morocco, showed strong positive association between anxiety and receiving foods from tourists (Maréchal et al. 2011).

Provisioning is also indirectly a cause of rising anxiety levels through aggression. For example, members of the provisioned primate group spent significantly more time in aggressive interaction than their wild counterparts (El Alami et al. 2012, José-Domínguez et al. 2015, Ilham et al. 2018), which is considered one of the main causes of rising anxiety levels (Maestriperi et al. 1992, Castles and Whiten 1998, Troisi 2002, Maréchal et al. 2011). Living close to humans and having access to human-derived foods could thus have some potential negative consequences in specific contexts.

#### **1.4 Causes and consequences of persecutions in human modified habitat**

In human-modified habitats, interactions between people and wildlife range from mutually beneficial to harmful (Humble and Hill 2016). The harmful and conflicting interactions are often referred to as human-wildlife conflicts. Conflicts between humans and wildlife occur when the needs of wildlife impact negatively on the objectives of humans, or vice versa (Dickman and Hazzah 2016). As a result of such conflicts, affected people tend to persecute the wild animals involved (Torres et al. 2018). Human persecution is different from hunting, because in hunting the hunter looks for a product (meat, trophy, and game), while for persecution, the aim is to threaten or eradicate the animals involved or even the species (Zimmermann et al. 2010). In many cases the persecuted species are less charismatic; for example, chacma baboon (*Papio ursinus*) in South Africa (Stone et al. 2015). Negative consequence for humans of interactions with wildlife include attacks on humans, destruction of properties and transmission of disease to domestic animals, and even to humans (Torres et al. 2018).

#### **1.5 Physiological responses to anthropogenic and ecological factors**

Primates' behavioural responses to anthropogenic and ecological factors can be measured through direct behavioural observations and measuring ecological parameters. Living in human modified habitats and feeding on human foods are often associated with energetic benefits to primates, which positively impact life-history parameters and reproductive output (Higham et al. 2009b, Warren et al. 2011).

In addition, living close to humans may be associated with physiological stress, which can be measured by glucocorticoid levels (Maréchal et al. 2011, Maréchal et al. 2016b). Assessing

physiological responses is challenging. It may involve repetitive trapping and measuring parameters such as weight, energy intake, energy expenditure, and body temperature (Gesquiere et al. 2018b). However, non-invasive techniques of hormone analysis enable the measurement of physiological responses using faecal or urine samples (Whitten et al. 1998, Hodges and Heistermann 2003). Using this technique, physiological responses to a range of anthropogenic and environmental factors have been studied in several species (Weingrill et al. 2004, Gesquiere et al. 2008, Thompson et al. 2010, Ahlering et al. 2011, Carnegie et al. 2011, Lodge et al. 2013, Cristóbal-Azkarate et al. 2016). Two hormones of particular interest, as they reflect aspects of energy balance, are cortisol (excreted as glucocorticoid metabolites) and thyroid hormone.

## 1.6 Glucocorticoid and thyroid hormones

During periods of energetic stress, e.g. when food is limited, increased secretion of cortisol upregulates glucose metabolism and provides the necessary energy (Sapolsky et al. 2000). Cortisol secretion is also associated with psychosocial stress that potentially requires energy to overcome (Engh et al. 2006b, Wittig et al. 2008, Carnegie et al. 2011). For example, in response to social threats, increased glucocorticoid levels are related to the releasing of energy for aggressive displays (Beehner et al. 2005).

Thyroid hormone, regulate the rate of energy use for basal metabolism (Kim 2008). When food is limited, thyroid hormone is downregulated to conserve energy and the opposite applies when food is plentiful (Cristóbal-Azkarate et al. 2016, Schaebs et al. 2016, Gesquiere et al. 2018b). However, thyroid hormone does not seem to be associated with psychosocial causes (Ayres et al. 2012). Cortisol is secreted during the period of energy deficiency, whereas, thyroid hormone is secreted in both during positive energy balance (energy intake exceeds energy expenditure) and negative energy balance (opposite to positive energy balance). Thyroid hormone, thus, allows more detail and fine measure of energetic condition in regulation by different factors (Gesquiere et al. 2018b). Therefore, assessing glucocorticoid and thyroid hormones together is informative about energetic and stress responses to both ecological and social factors.

After contributing to metabolic activity, both hormones are excreted from the body through urine and faeces (Whitten et al. 1998, Sapolsky et al. 2000, Wasser et al. 2010). So, the effects of



anthropogenic, ecological and social factors on primates can be assessed through measuring glucocorticoid and thyroid hormones from faecal samples.

## 1.7 Research gaps and aims of this study

*Papio* is one of the most widespread primate genera, and *Papio* spp. inhabit a diverse range of habitats in sub-Saharan Africa (Van Doorn et al. 2010). Their success in colonising these habitats is attributed to several factors which include dietary flexibility (Beamish and O'Riain 2014), social integrity (Kalbitzer et al. 2015), reproductive flexibility (Bergman et al. 2005), high levels of behavioural plasticity (Fehlmann et al. 2017) and high adaptability across terrestrial and arboreal habitats (Beamish and O'Riain 2014). Within this genus, the chacma baboon species ranges over much of southern Africa, including South Africa, Botswana, Zimbabwe, Namibia, Angola, Mozambique and Zambia (Sithaldeen 2019). The species is adaptable to challenging arid and semi-arid habitats (Gesquiere et al. 2008).

Much research has been focused on behavioural and ecological aspects of wild feeding chacma baboons, including activity patterns (Davidge 1978a, Marais et al. 2006, Lewis and O'Riain 2017, Ellwanger 2020); behavioural ecology (Stoltz and Saayman 1970, Davidge 1978b, Whiten et al. 1987, Hill and Dunbar 2002, Hill et al. 2003); feeding and foraging behaviours (Gaynor 1994, Segal 2008, Henzi et al. 2011, Lewis and O'Riain 2017); group size and habitat use (Marais et al. 2006, Henzi et al. 2011); social strategies (Ellwanger 2020); leadership and coordination of social behaviours (King 2008); spatial ecology (Pebsworth et al. 2012, Lewis and O'Riain 2017, Slater et al. 2018); cause and consequences of mortality (Beamish 2010) and effects of permanent injury on behaviour and diet (Beamish and O'Riain 2014).

Some studies have investigated the physiological responses to different psychosocial and ecological stressors in chacma baboons. These responses are measured through glucocorticoid levels. Increased faecal glucocorticoid metabolite levels have been reported for social instability, male immigration and infanticide (Engh et al. 2006b); dominance, reproductive state and environmental factors (Weingrill et al. 2004); effect of new alpha male (Beehner et al. 2005); social stressors and coping mechanisms (Bergman et al. 2005, Crockford et al. 2008); predation effect (Engh et al. 2006a); and social behaviours and grooming networks (Wittig et al. 2008, Kalbitzer et al. 2015). Nevertheless, no study has yet measured physiological energetic responses of chacma

baboons, through assessing thyroid hormones. Only one study, to my knowledge, has done so on a sister species, yellow baboon (*P. cynocephalus*), showing a positive relationship between thyroid hormone with natural food availability (Gesquiere et al. 2018b).

The behaviour and ecology of various baboon species has been studied in anthropological contexts in relation to crop foraging (Nagel 1973, Anderson 1981, Eley et al. 1989, Warren 2003, Higham 2006, Strum 2010, Hoffman and O’Riain 2011); tourist and human provisioning (Boug et al. 1994, Kamal et al. 1997, Hoffman 2011, Kaplan et al. 2011) and garbage feeding (Altmann and Muruthi 1988, Muruthi et al. 1991, Van Doorn et al. 2010). In every case, anthropogenic foods were an essential part of the diet and the high-quality foods provided energetic benefits to the baboon groups. Like crop foraging and provisioning, garbage foraging is important to study because of co-occurrence of primates and humans is increasing across the range countries (Humble and Hill 2016). But, compared to other garbage feeding mammalian taxa such as raccoons (Totton et al. 2002, Totton et al. 2004), mongooses (Gilchrist and Otali 2002, Otali and Gilchrist 2004), bears (Lewis et al. 2015, Teampanpong 2021), foxes (Reshamwala et al. 2018), research to date on garbage feeding primates/baboons is very limited.

Human-derived foods have some properties such as high energetic value, they are easily digestible, and clumped in distribution. Due to these properties, baboons that have access to human foods may differ in various ways to natural foraging baboons or baboons that do not have access human foods. Inspecting the dietary flexibility in relation to different environmental conditions involves a combination of behavioural and physiological factors, but these are rarely investigated together.

Thus, this study is designed to investigate both behavioural and physiological responses of a group of garbage feeding chacma baboons in South Africa, using behavioural observation techniques and physiological measures derived through non-invasive hormone analysis of faecal samples collected in the field. This includes comparison between the baboon population with other baboon studies (natural and anthropogenic feeding) conducted in different habitats, to examine the extent to which human-derived foods contribute to modifying the activity budgets and ranging patterns of the baboon group. This study also evaluates whether the availability and access to anthropogenic foods produce or reduce behavioural anxiety and physiological stress in the baboons, as well as whether the nutritional enrichment provided by garbage dumps gives

energetic benefits to the baboons. This involves the faecal measurement of glucocorticoid and thyroid hormones together for the first time in any anthropogenic foraging wild baboons. This study is therefore novel in its integrated approach to primate dietary flexibility through the cross-disciplinary combination of behavioural and physiological factors.

## **1.8 Outline of this thesis**

Following this introductory chapter, Chapter 2 provides a brief overview of the study area, study species and group, along with details of the behavioural, physiological, ranging and ecological sampling methods. In this chapter I introduce a new technique of estimating food availability in garbage dumps. Chapter 3 describes activity budgets, diet and ranging patterns of the study group. Comparisons between the study group and other naturally foraging and anthropogenic foraging baboons are used to examine the extent to which garbage dumps modify the activity budgets and ranging patterns of the study baboon group. This chapter also compares the feeding behaviour of different age and sex classes within the group who may have different levels of access to the dump foods. Chapter 4 then analyses the effects of dump foods on behavioural anxiety of the baboons taking an integrated approach for assessing overall anxiety levels that combines the measures of known causes and effects of animals' anxiety, and how these measures link with the access to the dump foods. Chapter 5 then focuses on the hormonal responses to stress and energetic factors. Variation in glucocorticoid and thyroid hormone levels are assessed in relation to food availability, behavioural, social and climatic constraints. This chapter also examines whether the hormonal levels vary according to the different energy demanding developmental and reproductive stages of baboons. Chapter 6 then describes two human persecution events experienced by the baboon group towards the end of the study period and investigates their effects on the activity budgets, ranging behaviours, behavioural anxiety and physiological stress levels of the baboons. Finally, in Chapter 7, key findings of previous chapters are brought together within a general discussion. The limitations of this study are also highlighted in this chapter.

## Chapter 2. General methodology

### 2.1 Study area

My fieldwork was conducted in Alldays, one of the largest wards of Blouberg municipality in the Limpopo Province, South Africa (Figure 2.1). Alldays is a small town that serves a large area of private game farms, many of which are known as hunting destinations.

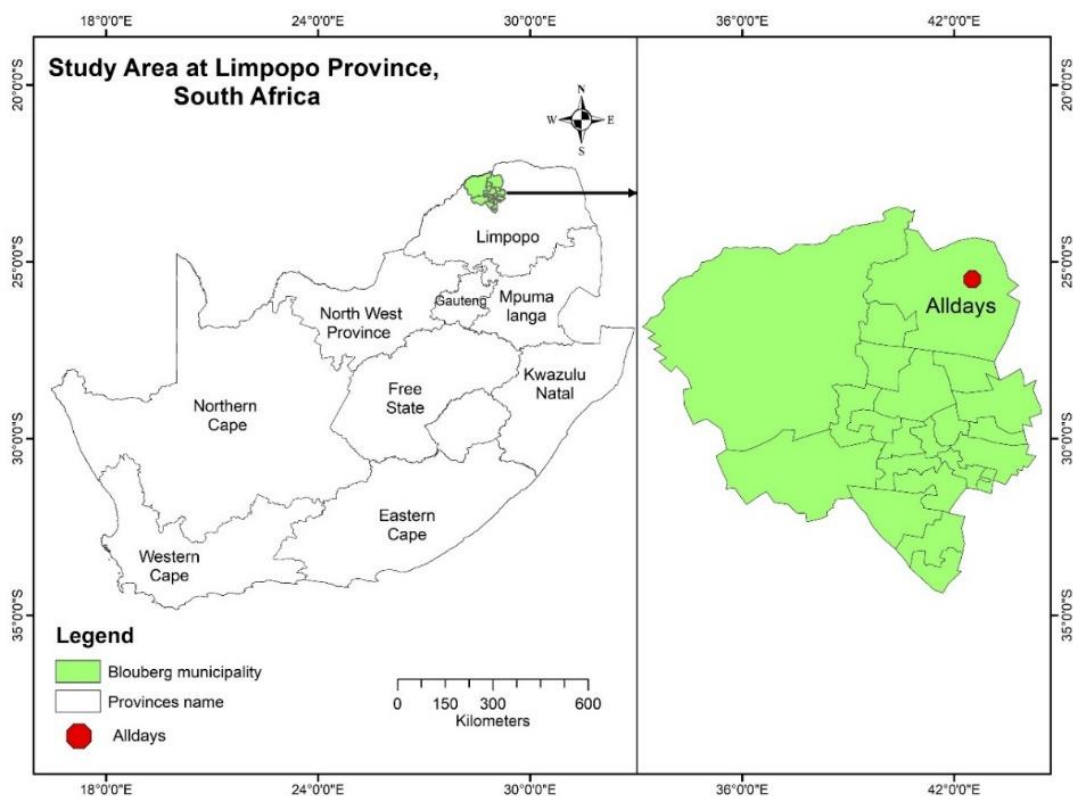


Figure 2. 1. Map of South Africa showing Blouberg municipality under Limpopo province (left), map showing study area within Blouberg municipality (right).

The area is also known for its crop farming, producing large amount of citrus fruits, tomato, squashes, tobacco, pumpkins, onions and potato (Walton et al. 2022). Crops are mainly sold to

national and international markets (Blouberg Municipality 2014-2015). Vegetable crops are mainly planted during the cooler winter season to avoid overly warm temperatures (Agricultural Research Council 2013).

Alldays local landfill site ( $22^{\circ}38'58.3''$  S,  $29^{\circ}07'03.7''$  E), referred to as the garbage dump hereafter, is the focal point of my study site (Figure 2.2). The area of the dump is 41000 square metres, which is protected by nearly two meters high barbed metal fence line (Figure 2.3A). The dump is managed and supervised by the Blouberg local municipality. People usually dump their rubbish in black plastic polybags, although and sometimes bins were carried for dumping. As part of regular town cleaning, the municipality also collected rubbish from the town and deposited it at the garbage dump. A South African Army camp near to the Alldays also dumped their rubbish at the site. The rubbish at the dump included Styrofoam food boxes, plastic food packets, cooked or uncooked vegetables, dried foods, milk or milk product, juice or soft drinks etc. (Figure 2.3B). Along with the kitchen and household waste, people also dumped their garden waste at the site.

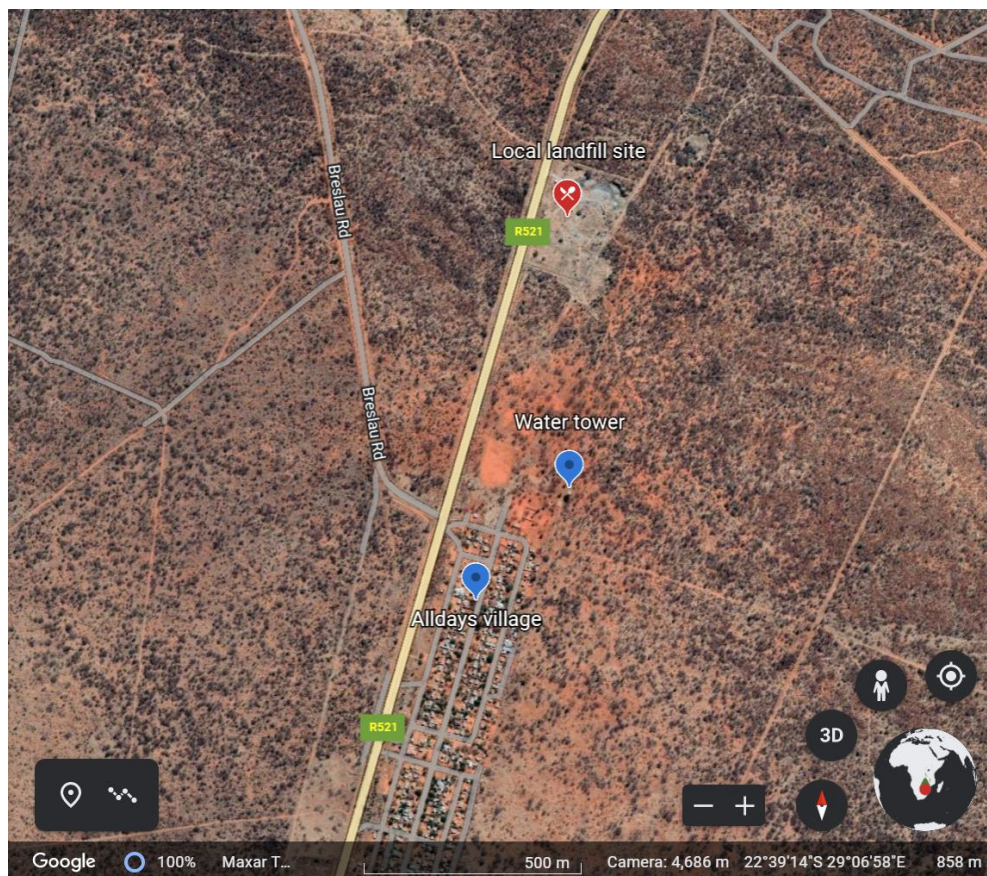


Figure 2. 2. Satellite image of Alldays village, water tower and Alldays garbage dump.



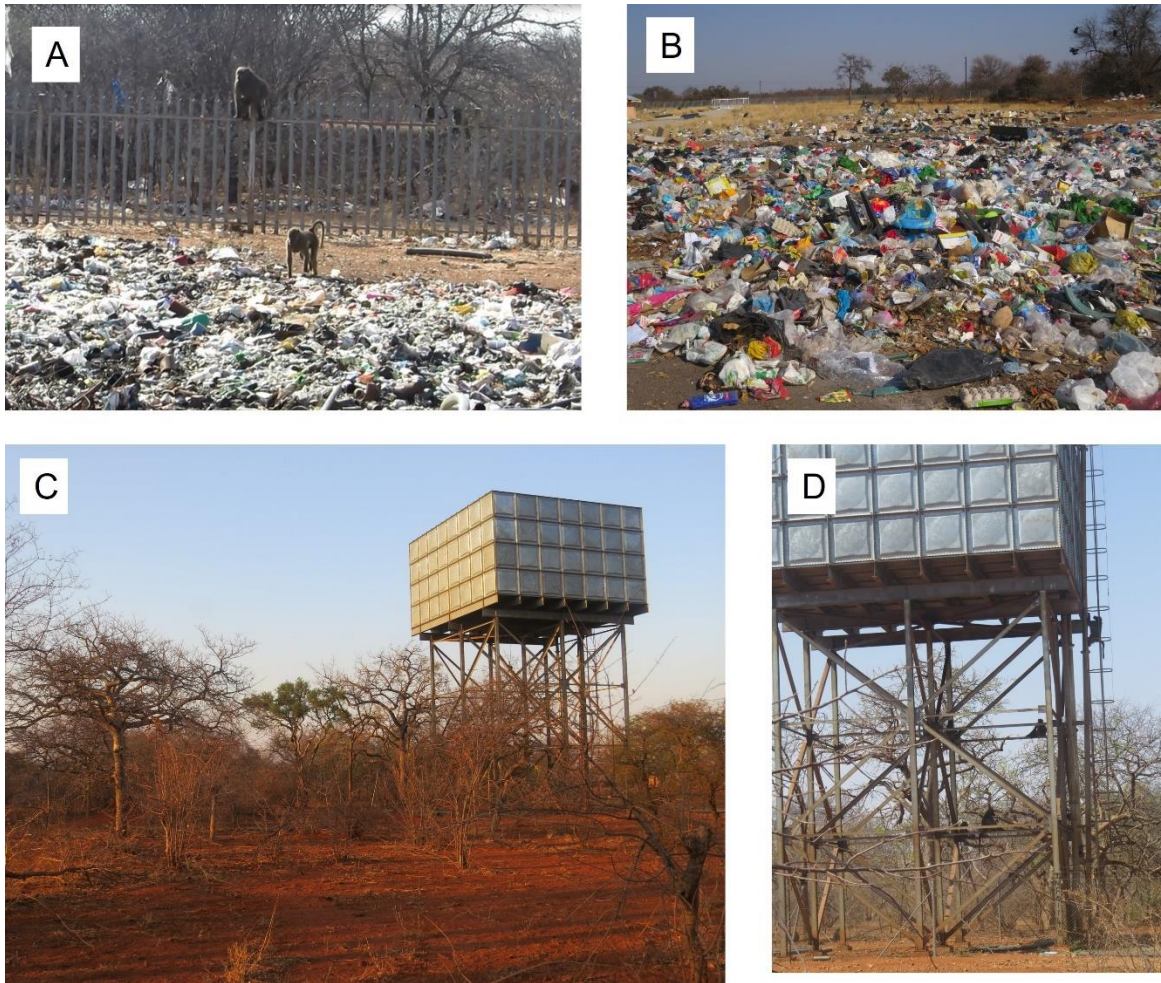


Figure 2. 3. Baboons crossing dump fence line (A); rubbish at dump (B); the water tower, the baboons preferred sleeping site (C) and baboons resting on the water tower at midday (D).

A water tank supplying water to the local community ( $22^{\circ}39'18.60''$  S,  $29^{\circ}07'06.65''$  E) between the dumping site and the nearby village was a regular sleeping site for the baboons (Figure 2.2 and 2.3C,D). The tower is approximately 20 metres in height and covered an area of around 50 square metres. The tower was fenced with barbed wire, though one side of the fence was completely broken. The tower was maintained by some volunteers in the village (mostly middle-aged men), who were responsible for filling the tank and switching it off. The distance of the tower from the garbage dump site is around 450 metres.

### 2.1.1 Climate

The area is characterized by a semi-arid climate with six warm, wet summer months starting from October. The summer season is followed by six months of cooler, drier winter starting in April. Temperatures range from an average daily minimum of 8 °C in July (with a minimum of -4 °C recorded), to an average daily maximum of 32 °C in November (with a maximum of 44 °C recorded, Figure 2.4). Annual rainfall is variable ranging from 380-550 mm per year, most of which falls during the summer months (Findlay 2016). The area is prone to frequent drought and the Mogalakwena River is the only perennial river nearby (reviewed in Findlay 2016).

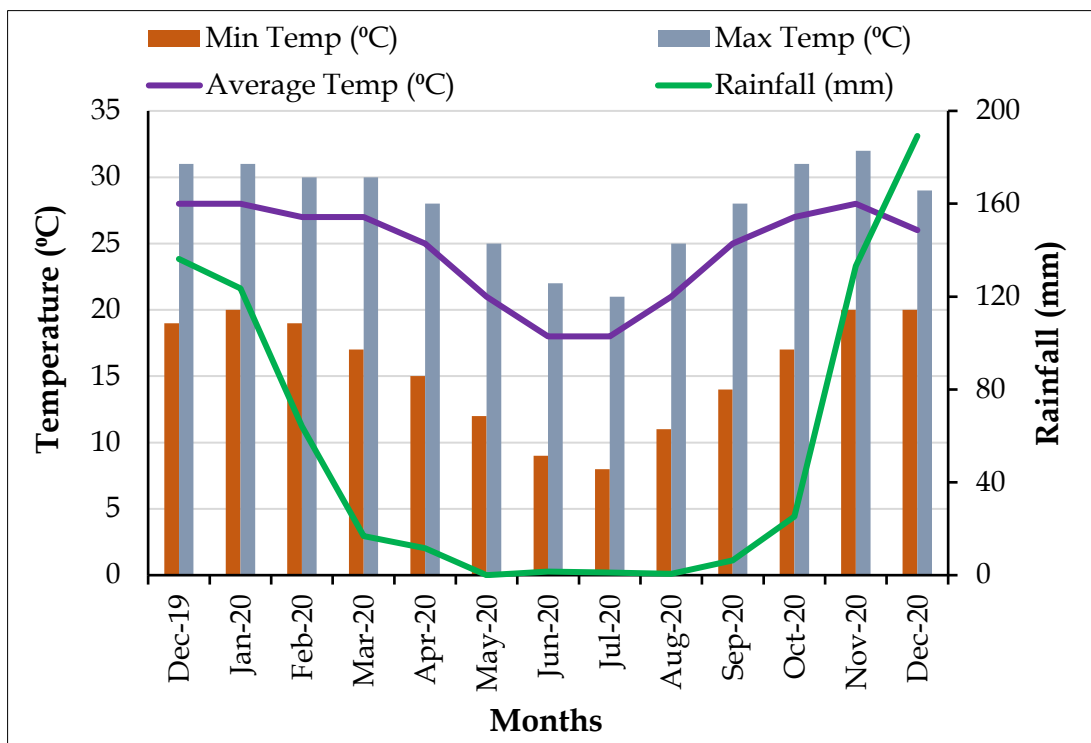


Figure 2. 4. Monthly temperature and rainfall in Alldays throughout the study period. Months are ordered according to the starting time of the study. Data were obtained from Alldays weather station (<https://www.worldweatheronline.com/alldays-weather-history/limpopo/za.aspx>).

### 2.1.2 Vegetation

The Blouberg municipality belongs to savanna type terrestrial biome (commonly referred to as Bushveld) consisting of 11 vegetation types. Most of the Alldays area falls within the Musina

Mopane Bushveld vegetation type. This vegetation type is characterised by undulating to irregular plains with some hills.

## 2.2 Study species

Baboons (*Papio* spp.) are distributed across sub-Saharan Africa and some part of the Arabian Peninsula. Six baboon morphotypes have usually been recognized as full-rank phylogenetic species: hamadryas (*Papio hamadryas*), Guinea (*Papio papio*), olive (*Papio anubis*), yellow (*Papio cynocephalus*), chacma (*Papio ursinus*) and Kinda baboons (*Papio kindae*; Martinez et al. 2019). However, there is still debate regarding the taxonomic status, their phylogenetic relationships, and hybridisation occurring between them (Martinez et al. 2019). My study focussed on chacma baboons.

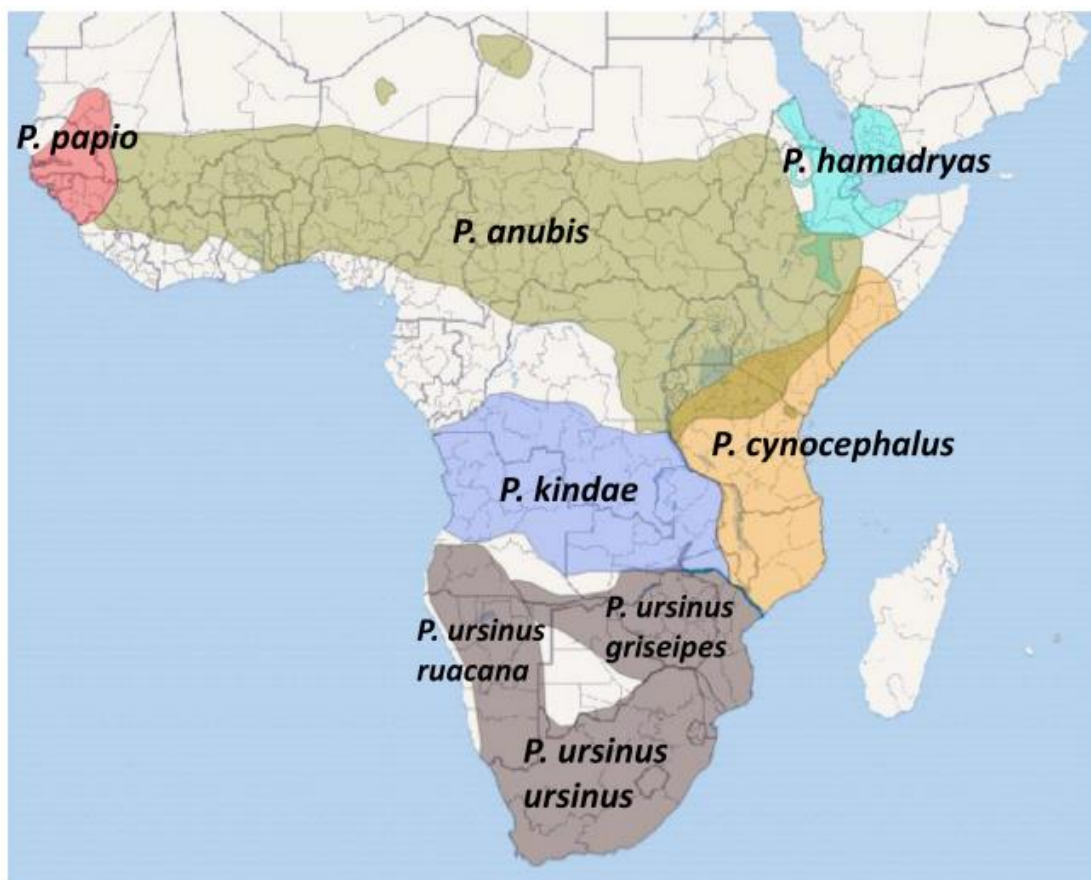


Figure 2. 5. The natural distribution of six baboon species including three subspecies of chacma baboon throughout Africa (image from Martinez et al., 2019).



### 2.2.1 Distribution

The chacma baboon ranges over southern Africa, up to the Zambezi valley (and including south-west Zambia), north-eastern corner of Namibia and southern Angola and at altitudes from sea level to >2,100 m, one region of exclusion is the central Kalahari Desert (Sithaldeen 2019). There are three subspecies of chacma baboon (Figure 2.5): the grey footed chacma, *P. u. griseipes* occurs in south-west Zambia, Botswana (Okavango Delta), Zimbabwe and Mozambique, south of the Zambezi River; the Cape chacma, *P. u. ursinus* occurs in the range south of the Limpopo River, in all provinces in South Africa; and ruacana chacma baboons, *P. u. ruacana* occur throughout Namibia, and in the southern part of Angola (Martinez et al. 2019).

### 2.2.2 Habitat and ecology

Baboons are generally recognized for its great adaptability that can inhabit highly challenging semi-arid tropical habitats (Gesquiere et al. 2008). Chacma baboons occupy all types of woodland, savanna, steppes and sub-dessert, montane regions (such as the high elevations of the Drakensberg), Cape Fynbos and Succulent Karoo (Sithaldeen 2019). In addition, chacma baboons can be found in close proximity to humans in both rural and semi-urban settings (Hoffman 2011).

Chacma baboons use rocky cliffs, hills or tall trees as sleeping site at night or when threatened. The species is dependent on drinking daily, and water availability limits its overall range in Namibia. However, artificial water supplies have allowed substantial expansion of territory (Sithaldeen 2019). The species is an opportunistic omnivore and shows a local preference for leaves, bulbs, shoots, roots, seeds or fruits. Invertebrates, small vertebrates, seashore life, fungi and lichen are eaten as and when available. Occasionally, they take small antelopes or the young of species like impala, antelopes, smaller monkeys, python eggs (Sithaldeen 2019, Allan et al. 2022). Crops (maize, tomatoes, citrus and root crops) are eaten in settled areas (Findlay and Hill 2021).

### 2.2.3 Social structure

Chacma baboons live in multi-male-multi-female groups that can contain over one hundred individuals, with an average group size between 20 and 50 animals (Sithaldeen 2019). Female baboons will often remain with their natal troop for the entirety of their lives, while males usually leave at the onset of adulthood (Barrett and Henzi 2008). As such, baboon societies are primarily

structured around females and their closest kin who may form matrilineal subgroups within the troop (Silk et al. 2006). Female rank is inherited through matrilines; some mothers continue to rank higher than their adult daughters, and others' rank below them (Cheney et al. 2004, Barrett and Henzi 2008). In contrast to the stability inherent to female dominance and rank, male dominance is ephemeral and unstable, with males changing dominance status many times over their lifetimes (Strum 2001). The duration of alpha male tenure can be relatively short (7-8 months) (Cheney et al. 2004). This leads to high levels of infanticide as new males kill existing infants to facilitate the resumption of reproductive cycling in resident females (Palombit et al. 2000).

#### **2.2.4 Body size and maturity**

Chacma baboon is a large, diurnal, and terrestrial primate species. Like other members of *Papio*, chacma baboons are sexually dimorphic in terms of body size, with adult males having the potential of body mass up to 80% more than adult females (Henzi et al. 2003). The average body mass for wild adult male chacma baboon is typically up to 35 kg, whereas females tend to weigh approximately 15 kg (Bulger and Hamilton 1987). Adult males have longer canines that are often used to display a threatening gesture or as weapons in physically aggressive interactions with other males (Hamilton and Bulger 1990). Female baboons exhibit colourful sexual swellings throughout the perineal area that often peak around ovulation (Higham et al. 2008). Male baboons take approximately twice as long as females to reach full sexual maturity and adult body size; 10 years versus 5 years (Altmann et al. 1977). A study on chacma baboons life history and growth found that the growth rates in male and female baboons are quite similar up to 5.5 years, and the growth rates then greatly changed, with male growth accelerating and female growth declining (Johnson 2003). Both growth rates and adult body size are greatly affected by food availability (Altmann and Alberts 2005). In female baboons, the adult stage is signified by the first occurrence of menarche (Altmann et al. 1981), whereas, in males, this is primarily indicated by the enlargement of the testes (Alberts and Altmann 1995).

#### **2.2.5 Reproduction**

Around the time of ovulation, female baboons will often initiate a short term consortship with an adult male and priority of access for males is based on his dominance status (Henzi et al. 2003). During this period, individuals frequently engage in activities such as copulating and grooming

one another. After approximately six months of gestation baboons will usually produce one offspring biannually (Beehner et al. 2006). Lactating females often make strong associations/friendships with an adult male who is likely to be the father of her offspring based on consortships during the reproductive period. Such friendships with males may benefit female baboons by providing the protection of infants from attacks by other males, as well as promoting bonds between male friends and offspring (Palombit 2009).

### **2.2.6 Predators**

Baboons are susceptible to predation from numerous species across their range (Cowlshaw 1994). Throughout Africa, leopards are the primary predator of baboons (Cowlshaw 1994, Cheney et al. 2004). Baboons are most vulnerable at night and at dawn and dusk when they ascend or descend from their sleeping sites. Lions have been found to opportunistically hunt all baboon age-sex classes (Cheney et al. 2004). While spotted hyenas occasionally hunt solitary baboons, there is little evidence to suggest that they pose as a substantial threat (Cheney et al. 2004). Large reptilian predators like crocodile have been also observed to feed on baboons (Cheney et al. 2004). African rock python is also a potential predator of baboons; juveniles are more susceptible to python attack (Tomlin 2016). Martial eagle (Cheney et al. 2004), crowned eagle (Mitani et al. 2001), and Verreaux's eagle (Zinner and Peláez 1999) primarily pose a threat to juveniles, but they are often too small to efficiently hunt adults. Sometimes humans also hunt baboons to eat or sell as bushmeat (Mwangi 2019).

### **2.3 Study group**

There were two baboon groups living close to the Alldays dump site during the study period. One group was large containing approximately 50-60 individuals but did not regularly visit the dump site. The small group contained 18-25 individuals (Table 2.1) and visited the dump almost daily and so was the focus of this study. Prior to my study the group was habituated by two trained field assistants. The assistants started habituation on 25<sup>th</sup> June 2019. For habituation, standard processes and techniques used for wild primate studies (Williamson and Feistner 2003) were followed. The baboon group was fully habituated to the presence of researchers within six months (defined as no flight, avoidance and display behaviours) and I started data collection from December 2019.

Table 2. 1. Composition of the baboon group throughout the study period

Months	Adult male	Adult female	Sub-adult male	Adolescent female	Juvenile	Infant	Total
Dec 19	2	7	1		10	2	22
Jan 20	2	7	1		10	2	22
Feb 20	2	7	1		10	4	24
Mar 20	2	7	1		10	4	24
Apr 20							
May 20	2	7	1		10	5	25
Jun 20	2	6	1	1	9	5	24
Jul 20	2	6	1	2	8	6	25
Aug 20	2	6	1	2	8	6	25
Sep 20	2	6	1	2	6	6	23
Oct 20	2	5	1	2	5	3	18
Nov 20	2	5	1	2	5	3	18
Dec 20	2	5	1	2	5	4	19

Each individual was identified through anatomical and physiognomic characteristics including body size, scars, pigmentations and genital morphology (detail description in the Table 2.2). Each individual has an identity (name), and data were collected against individuals' identity.

Table 2. 2. Age-sex class descriptions for chacma baboons

Age-sex category	Physical description	References
Infant	Body hair black to brown, skin pink at early stage, black pigmentation occurs at the end. Nutritionally dependent on lactating mother, but undergoing weaning at later stage.	(Altmann et al. 1981, Tomlin 2016)
Juvenile	Distinguished by darker body hair; face wrinkles completely disappear; male's scrotum grey and flat at the beginning to becoming round due to the rapid	(Altmann et al. 1981)

	development of testes at the end. Males' canines extend beyond tooth row at end of this period.	
Adolescent/sub-adult female	A short period of around a year. Nearly the size of an adult female, with the onset of the first sexual swellings, nipples pink and buttonlike	(Tomlin 2016)
Sub-adult male	A male baboon that has entered puberty stage but still growing, capable of siring.	(Setchell 2019)
Adult female	Attainment of full body size, sexually mature, categorized as- <ul style="list-style-type: none"> <li>• Cycling- female in any stage of menstrual cycle, recognized by cycling patterns of sex skin turgescence, followed by deturgescence and then menstruation</li> <li>• Pregnant- period of final deturgescence of the menstrual cycle to the birth of an infant. This state is documented by cessation of sexual swellings (&gt; 40 days) without evidence of menstruation (i.e., vaginal bleeding followed by sexual swelling within a week)</li> <li>• Lactating- period of following birth until infant reaches one to one and half year old. This state is easily recognized by the presence and age of an infant.</li> </ul>	(Gesquiere et al. 2008)
Adult male	All secondary sexual characteristics fully developed; musculature expands to full adult size. Approximately double body size that of adult females and reproductively active.	(Akinyi et al. 2017)

### 2.3.1 Preferred feeding and sleeping site

Along with the foraging in the natural habitat, the baboon study group visited the dump site every day, spent some time there and exploring dumped bags which generally contained foods. As the dump is easy to access (although there is a fence line, baboons can easily cross), and the foods there tended to be energy-rich and easily digestible, they used the dump as a preferred feeding site.

The baboon study group used the water tower as their main sleeping site (Figure 2.2 and 2.3C,D) until human persecution events happened towards the end of the study period (Chapter 6). The water tower had numerous metal cross bars between pillars to make a base for the tank. The bars were wide enough for baboons to lie on. The height of the tower allowed baboons to see adjacent areas, and especially to monitor the dump. The tower also provided shelter to protect from rain and sun.

### **2.3.2 Predators and threats**

Outside of the dump, the group often ranged in a large cattle farm, where large predators, e.g. lions, leopards were absent. I found hyena scats in some places on the farm, but I observed no encounters with the baboon group throughout the study period; the scat may have been from brown hyena anyway which are predominantly scavengers in the area (Williams et al. 2018, Faure et al. 2019). People from a nearby village and their pet dogs posed a threat to baboons. People sometimes hunted birds with airguns/ air rifles, which was also a cause of fear for baboons.

## **2.4 Data collection**

### **2.4.1 Data collection period**

I collected behavioural data from 19<sup>th</sup> December 2019 until 4<sup>th</sup> December 2020. Due to the coronavirus pandemic, a national lockdown was imposed in South Africa from 27<sup>th</sup> March 2020, and I could not continue data collection from this date. After getting special permission from the satellite office manager and the police commissioner of Blouberg local municipality, South Africa, I resumed data collection from 18<sup>th</sup> May 2020. No data were collected in April 2020 and there are a lower number of working days and data collection in March and May 2020 than in other months as a result of the restrictions.

### **2.4.2 Behavioural data collection**

Three types of sampling were used to collect the baboons' behavioural data.

#### **Scan sampling**

I collected scan samples (Altmann 1974) from dawn to dusk at 30-minute intervals for a maximum duration of 5 minutes. I recorded the behaviour of all visible individuals (except infants) along

with weather and general information (detailed ethogram in Table 2.3). I gave training to my field assistants on individual identifications and data collection procedures. After two months training when we classified individual identity, age-sex class, and behaviours exactly the same way according to the ethogram then field assistants collected scan data if needed. As it was difficult to identify the sex of juveniles, we collected data on their age only. We thus recorded behaviour for adult males, sub-adult males, adult females, adolescent females and juveniles. Four major behavioural activities were recorded during scan sampling (Table 2.3), as these activities constitute more than 95% of baboon time budgets (Dunbar 1992). We collected scan data from an average distance of 5 to 10 metres. Based on the group's movement we collected data either from front to back (when moving) or left to right (when stationary) to avoid repeated entry of an individual in a scan. If we were not sure about an individual's identity due to the distance or obstacles between baboon and us, we did not include that individual in the scan.

Table 2. 3. Ethogram for data collection during scan sampling

Category	Sub-category	Description
Date		Date of data collection
Number of observers		Number of people following the group
Time		Time when each scan started
<b>Environmental status</b>		
Weather		Clear sky
		Mostly clear sky
		Mostly cloudy
		Cloudy (Overcast)
		Misty
		Light rain
		Heavy rain
Wind		Calm
		Breeze
		Windy

		Very windy
Habitat		Natural
		Human modified (dump)
<b>Individual ID and Age-sex class</b>		
Adult female	7 individuals	Eggo, Leah, Zane, Ruby, Pamela, Fiona and Soshi. (Table 2.2)
Adult male	2 individuals	Hound, Clubto (Table 2.2)
Adolescent female	2 individuals	Hannah and Rosie (Table 2.2)
Sub-adult male	1 Individual	Jamie (Table 2.2)
Juveniles	5-10 individuals	Table 2.2
<b>Activity</b>		
Feeding	Foraging	Actively searching for foods while stationary or moving small distances, processing and handling of food items by hand or mouth
	Cheek pouch feeding	Collecting and temporarily storing foods in a cheek pouch, most often chewing.
	Feeding	Holding, licking or chewing and swallowing food items, but not while moving; drinking water or any liquid Further recordings- Types of food, name of plant species and parts of plants being eating (natural food), categories of dumped foods, approximate quantity eaten
Moving	Walking	Move at a regular pace by lifting and setting down hands and feet
	Running	Very fast movement by lifting and setting down hands and feet swiftly
	Climbing	Ascending or sliding from one tree branch to another
Resting	Resting sitting	Sitting stationary



	Resting lying	Sleeping or lying down, eyes may be closed
	Resting huddle	Sitting very closely with one or more other individuals
Grooming	Groom other/grooming given	Manipulating, nibbling or licking fur of other group members Further data noted- individual identity and age-sex of partner. Partners defined as a pair of individuals engaged together in the same activity.
	Being groomed/grooming received	Manipulating, nibbling or licking fur by any other group members Further data noted- individual identity and age-sex of partner
Other behaviours		I recorded aggression, affiliation, mating, playing, SDBs, vigilance, interspecies interactions as other activities
<b>Others</b>		
Distance from the partner		Estimated distance to the partner (at 1 metre intervals for 0-10m)
Location of the activity	Ground	On the ground
	Near ground	0-2m above the ground
	Lower canopy	2-5m above the ground
	Mid canopy	5-10m above the ground
	Upper canopy	10m or more above the ground
Number of neighbours		The number of other individuals within a 3 metre radius

I collected scan data using a Microsoft Excel spreadsheet programme installed on a portable iPad (Apple Mini5 64 SG) using drop-down lists to record the data. I collected data over 11 months,

giving a total of 2601 scans from 123 days of data collection. My aim was to collect data at least three days per week, 12 days per month, and I tried to collect around the same amount of data in each month. Due to the inaccessibility of the baboons, adverse weather conditions, recruitment of assistants, and personal injuries, there was a lower number of working days and scans collected in December 2019 and January 2020. There were also a lower number of working days and data in March and May 2020 because of the Covid 19 lockdown situation. The mean monthly data collection days was 10 (SD=  $\pm 3$ ) and the mean scan was 217 (SD=  $\pm 82$ ) per month (Figure 2.6).

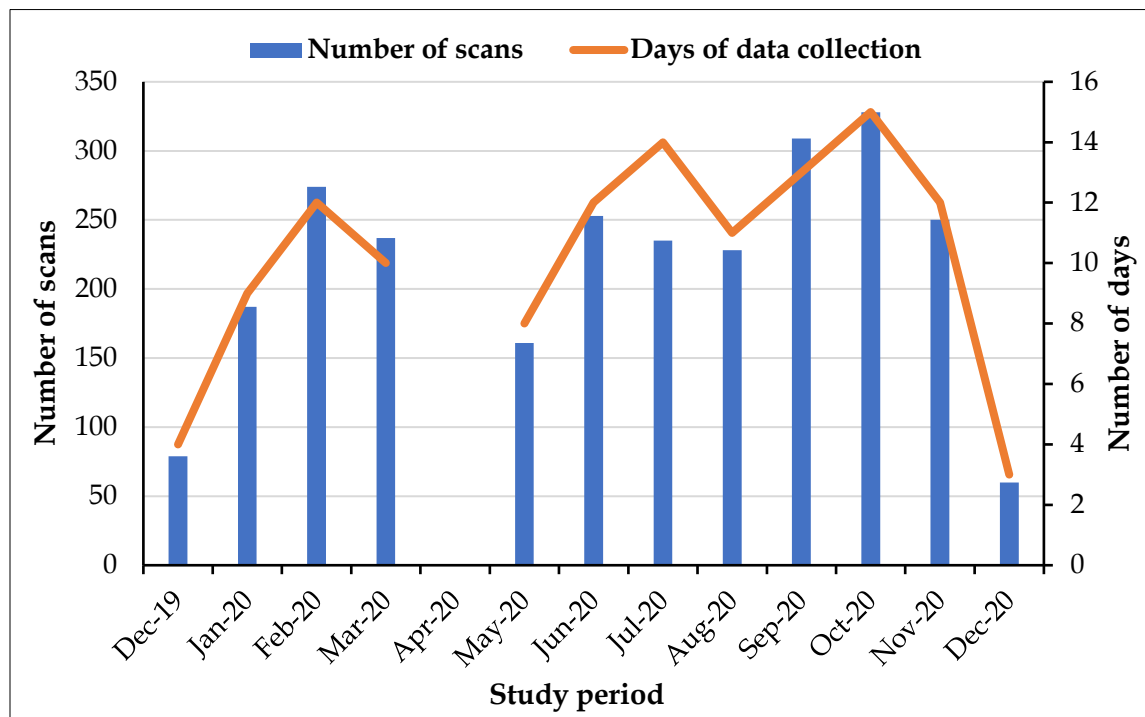


Figure 2. 6. Total number of scan samples collected and number of data collection days across the study period.

There was little variation in the amount of scan data collected at different times of the day. Due to the monthly and/or seasonal variation in daylength hours baboons started their activity earlier in summer days than winter. As a result, there was less data collected from 5 to 6 am in the morning and 6 to 7 pm in the afternoon (Figure 2.7).

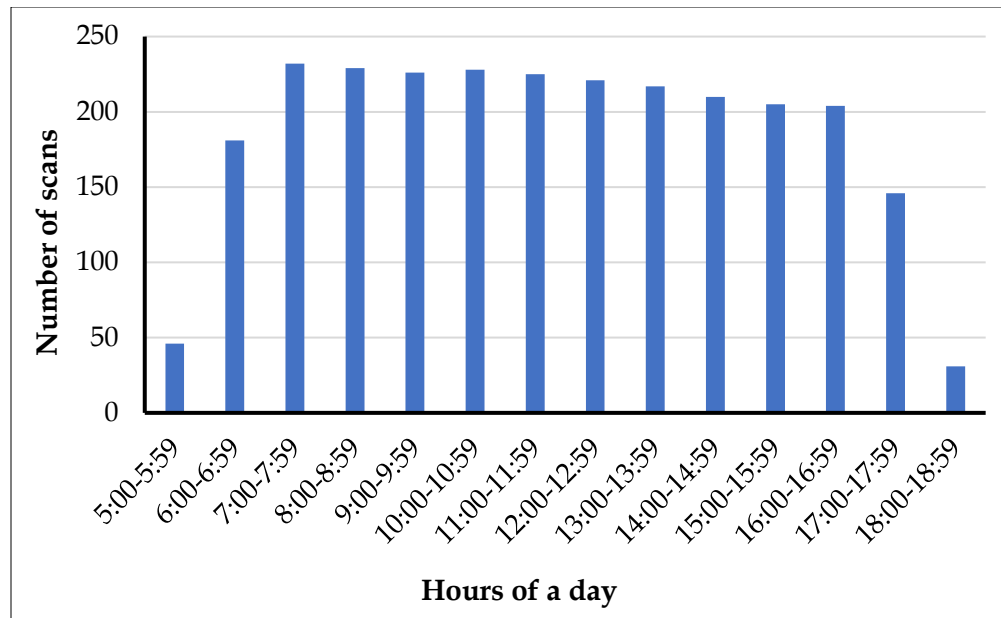


Figure 2. 7. Total number of scan samples collected for each hour of the day throughout the study period.

Scan data were collected to create activity budgets and to compare the behaviour of the study group with the other baboon groups from other populations (Chapter 3) and to compare activity budgets within the baboon group across the different persecution time periods (Chapter 6).

### **Focal animal sampling**

I conducted 10-minute continuous focal animal samples (Altmann 1974) to collect detailed behavioural data. The focal duration (10-minute) was the best possible option to maximise the data without losing animals which was determined based on the pilot study. This duration also allows two focal samples to be collected between consecutive scans. As the sex of juveniles is difficult to identify, my focal animals were only adult and sub-adult baboons. Data were collected personally from individually identified baboons from an average distance of 5 to 10 meters. Where possible, I collected two focal samples in between the 30-minute scan samples, recording both continuous (behavioural states) and instantaneous (behavioural events) data from the focal subjects. I recorded every social interaction (grooming, aggression, affiliation, playing, interspecies interaction) where the focal subject was involved (both initiated by the focal subject or by another individual towards the subject) along with the identity of the social partner. I also

recorded feeding (including identity of food consumed), self-directed behaviours and vigilance behaviours of the focal animal (detailed ethogram in Table 2.4).

I collected data using the CyberTracker (<https://www.cybertracker.org/>) programme. I set up my application on a personal computer following the ethogram described in the Table 2.4 and installed the application on an easily portable tablet (Samsung Galaxy Tab A6).

Table 2. 4. Ethogram for data collection during focal animal sampling

Category	Sub-category	Description
Date		Date of data collection
Time		Time of each behaviour started in a focal
Focal ID number		Serial of focals in a day
Individual ID		Individual identity of adult and sub-adult aged baboons
<b>Activity</b>		
Feeding		See Table 2.3
Grooming		See Table 2.3
Affiliation	Anogenital inspection	Investigate hindquarters of other individual with mouth or hands
	Embrace	Short duration of physical contact
	Social mount	Mounting other individuals' hindquarters for non-sexual context
	Penis grab	Touch or stroke penis of another individual
	Present (sexual)	Present hindquarters for copulation
	Teeth chattering	Rapid movement of teeth (often make sound) signifying desire for social contact
Aggression	Attack	Physically assaulting to other individual with mouth/teeth
	Fight	Both individuals assaulting each other
	Chase	Running after another individual, wahoo vocalisations may involve

	Lunge	An aggressive movement towards another individual
	Displace	Take over another individual's position
Interspecies interactions		Any type of interactions, including affiliation, aggression with human, dog, cow, mongoose, birds, and other species
Playing	Playing with object	Manipulating any object, such as stick, stone, tree trunk or others
	Wrestling	At least two individuals rolling around, often involving biting and chasing in playful manner
	Mock biting	Soft biting or mouthing to another individual
Displacement activities or SDBs	Scratching	Repeated movements of the hands or foot during which the finger/fingernails or toes/toenails are drawn across the fur or skin at least three times.
	Self-grooming	Picking through and/or slowly brushing aside fur with hands and/or mouth for at least five seconds. Self-groom included picking at wounds.
	Yawning	Performer looks directly at the conspecifics (a threat meaning) frequently repeated and the teeth clearly displayed. Besides a threat function, yawning may arise due to the anticipation of food (Anderson and Wunderlich 1988) and can also be triggered by conspecifics, i.e. contagious yawning (Gallup 2022).
	Body shaking	Subject performs a tremble of their entire body (shaking movement of the body similar to that displayed activity by wet dog)

Vigilance	Routine	Stationary or actively scanning the group and/or surrounding environments through observable head and eye movements
	Induced	Actively scanning as a reaction to unpredictable stimuli from the surrounding environment and/or from the group
Other behaviours		The behaviours other than these above mentioned recorded as others. These were resting, moving, mating etc.
<b>Others</b>		
Distance from the partner		Estimated distance to the partner while social interactions occur (at 1 metre intervals for 0-10m)
Location of the activity	Ground, Near ground, Lower canopy, Mid canopy and Upper canopy	See Table 2.3

There was substantial variation in daylength across the months and seasons (Figure 2.8). To avoid over-sampling at particular times of day I divided the day into four equal time blocks: early morning, late morning, early afternoon and late afternoon. The duration of each time block varied from 2 hours 40 minutes to 3 hours 24 minutes (Table 2.5) to account for variation in daylength.

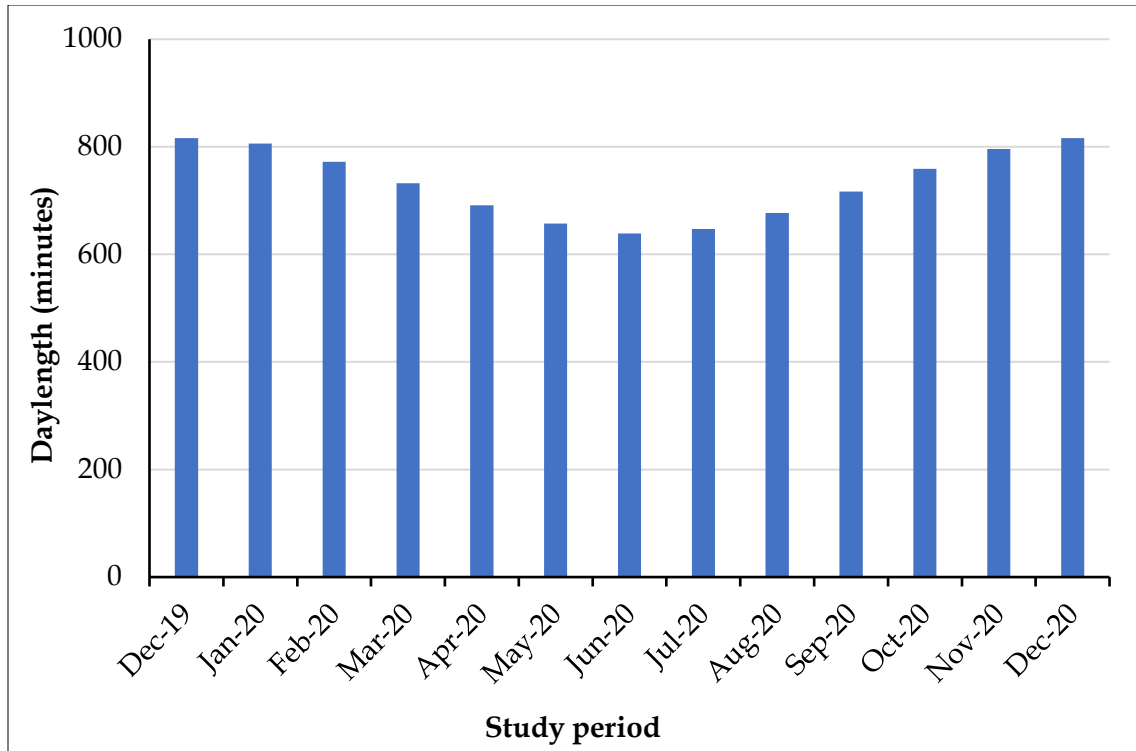


Figure 2. 8. Daylength variation in the study site across the study periods. Data were obtained from Alldays weather station (<https://www.worldweatheronline.com/alldays-weather-history/limpopo/za.aspx>).

There was no predetermined schedule for focal animal selection due to the difficulty of finding specific individuals, as the group sometimes dispersed in dense vegetation. Hence, I collected focal data in an opportunistic manner using the following rules for maintaining independence of sampling: 1) No more than one sample per individual in a time block per day; 2) following a focal on an individual from one age-sex class, the subsequent focal was conducted on an individual from a different class; 3) all individuals were sampled in a single time block before collecting repeat samples on any individual. I followed these sampling rules wherever possible. In some instances where the group was very spread out, or some members were on an inaccessible property, I relaxed the rules to continue data collection. If I had spare time after sampling all individuals in a time block, then I continued sampling the individuals who were missed in the previous time blocks or previous day.

Table 2. 5. Time blocks in each month for focal animal sampling. For data collection I allotted time blocks according to the daylength of the baboon follow day.

Months	Early morning	Late morning	Early afternoon	Late Afternoon	Duration in each block
December 19	5:09 – 8:32	8:33 – 11:56	11:57 – 15:20	15:21 – 18:45	3h 24m
January 20	5:28 – 8:49	8:50 – 12:11	12:12 – 15:33	15:34 – 18:54	3h 20m
February 20	5:49 – 9:02	9:03 – 12:15	12:16 – 15:38	15:39 – 18:42	3h 03m
March 20	6:04 – 9:07	9:08 – 12:10	12:11 – 15:13	15:14 – 18:16	2h 58m
April 20	6:16 – 9:08	9:09 – 12:01	12:02 – 14:54	14:55 – 17:47	2h 52m
May 20	6:29 – 9:13	9:14 – 11:58	11:59 – 14:43	14:44 – 17:27	2h 42m
June 20	6:42 – 9:21	9:22 – 12:01	12:02 – 14:41	14:42 – 17:22	2h 40m
July 20	6:44 – 9:25	9:26 – 12:07	12:08 – 14:49	14:50 – 17:32	2h 42m
August 20	6:28 – 9:16	9:17 – 12:06	12:07 – 14:55	14:56 – 17:45	2h 49m
September 20	5:58 – 8:57	8:58 – 11:57	11:58 – 14:57	14:58 – 17:56	2h 58m
October 20	5:27 – 8:36	8:37 – 11:46	11:47 – 14:56	14:57 – 18:07	3h 10m
November 20	5:08 – 8:27	8:28 – 11:46	11:47 – 15:05	15:06 – 18:25	3h 19m
December 20	5:09 – 8:32	8:33 – 11:56	11:57 – 15:20	15:21 – 18:45	3h 24m

Most of the time the samples were completed successfully but, occasionally, due to the inaccessible and dense vegetation, the focal animal moved out of sight. I terminated a focal sample if the focal animal was out of sight for more than a minute within the sampling time. After losing sight of an animal, if I found the focal within a minute, I continued data collection and the focal was considered successful. Unsuccessful focals, around 10% of focal samples in a follow day, were discarded. I did not include them in any analysis because incomplete focals may affect the measured rate of a behaviour. I also terminated focal observations when the focal subject appeared distressed by being followed (i.e. directing threats or fear calls towards me, conspicuously watching me, or moving in a manner that deliberately placed obstacles between themselves and me). When focal samples were terminated, I sampled that individual at a later point in the same time block.



Table 2. 6. Focal animal samples collected in the individuals across the study period. \*died in June, \*\*died in October 2020

Individual identity	Dec-19	Jan	Feb	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec-20	Total
Hound	17	24	38	37	28	38	40	39	45	58	39	10	<b>413</b>
Clubto	9	22	37	37	25	44	41	36	45	50	40	14	<b>400</b>
Eggo	12	19	30	35	29	42	46	36	46	56	39	13	<b>403</b>
Zane*	14	26	35	37	24	17	0	0	0	0	0	0	<b>153</b>
Leah**	14	23	31	36	27	42	43	35	47	31	0	0	<b>329</b>
Ruby	14	21	33	35	25	39	44	39	47	58	37	10	<b>402</b>
Fiona	3	17	36	37	24	39	48	39	48	56	39	20	<b>406</b>
Pamela	15	18	36	34	23	37	46	36	43	55	46	14	<b>403</b>
Soshi	8	9	14	26	20	35	39	35	45	55	44	17	<b>347</b>
Jamie	12	19	31	32	24	38	45	38	46	54	41	14	<b>394</b>
Hannah	0	0	0	0	0	2	17	2	1	32	35	8	<b>97</b>
Rosie	0	0	0	0	0	0	8	10	1	8	28	8	<b>63</b>
<b>Total</b>	<b>118</b>	<b>198</b>	<b>321</b>	<b>346</b>	<b>249</b>	<b>373</b>	<b>417</b>	<b>345</b>	<b>414</b>	<b>513</b>	<b>388</b>	<b>128</b>	<b>3810</b>

A total of 3810 focal animal samples were collected giving 635 hours of direct observations across 121 days. I conducted focal samples on 12 individuals with a mean number of focal samples per individual of 318 (SD=  $\pm 132$ ) and the mean number of focal samples per month was 346 (SD=  $\pm 90.5$ ). As for scan sampling there were fewer focal samples collected in December 2019 and in January, March and May 2020, and none in April 2020. After the human persecution event (Chapter 6), I tried to maximize data collection; hence there were slightly more focals in September and October (Table 2.6).

Focal data were collected for determining baboon diet, food selection and seasonal variation in diet composition, detailed feeding behaviours (Chapter 3), anxiety related behaviours (Chapter 4) and social interactions among the group members (Chapter 6).

### **Ad libitum sampling**

Ad libitum sampling was used to record rare (but important for my study) behavioural events that were not captured in the scan or focal sampling. Aggressive interactions (that were not recorded in other methods), displacement behaviours and interspecies interactions were recorded. The displacement and aggressive behaviours were used to determine a dominance hierarchy of the individuals in Chapters 4 and 5. I obtained 2142 behavioural events through this sampling technique.

### **2.4.3 GPS data collection**

I used a Garmin 64S to record GPS coordinates. GPS points were collected at an estimated centre point of the group every 30 minutes prior to each scan sample. The centre of the group was estimated based on the individuals' locations at that time. Visibility both inside and outside of the dump was good. All individuals can be seen when they were in the dump, and most of the time almost all individuals can also be seen when they are outside of the dump. In the early morning of each follow day I located the baboons at their sleeping site and started to record GPS points, continuing until they returned back to their sleeping site at the end of the day. The GPS points were downloaded and saved as a GPX file which was then converted to Excel readable tab delimited TXT file format using DNR GPS software for further analysis.

The GPS points were used determining home range area, core area, daily travel length and the travel speed of the baboon group (Chapters 3 and 6). I collected 2676 GPS points ( $243 \pm 58$  per month) throughout the study period.

### **2.4.4 Phenological data collection/ natural food availability assessment**

Phenological data were collected through plot sampling in the home range area. The "estimated" ranging area was determined during the pilot study (conducted in September and October 2019) and by consulting with the field assistants who were habituating the baboon group. Ten plots (50m x 10m), distributed throughout the baboons' home range area, were demarcated for natural food availability assessment (Figure 2.9). I aimed to cover around one percent of the "estimated" home range area which is sufficiently good for phenological survey in primatological study

contexts where the habitat is relatively homogenous as it was in the study troop's home range (Ganesh and Davidar 2005, Paoli et al. 2006, Marshall et al. 2014).

I measured the diameter at breast height (DBH, 1.3 metres from the ground) of every tree in the plots using a measuring tape. A sloping or angled tree was measured at a right angle along the centre of the tree's axis. In case of split trunk trees, if the fork was below 1.3 metre from the ground then each trunk was considered a separate tree, and if the fork was on the 1.3 metre mark, I measured diameter just below the bump where the tree split.

The trees with a diameter of 10 cm or more within the plots were selected for the phenological survey. The trees were then numbered and marked according to plot (Figure 2.10). I identified the marked trees by following a reference field guide, "Field Guide to Trees of Southern Africa" (van Wyk and van Wyk 2013).

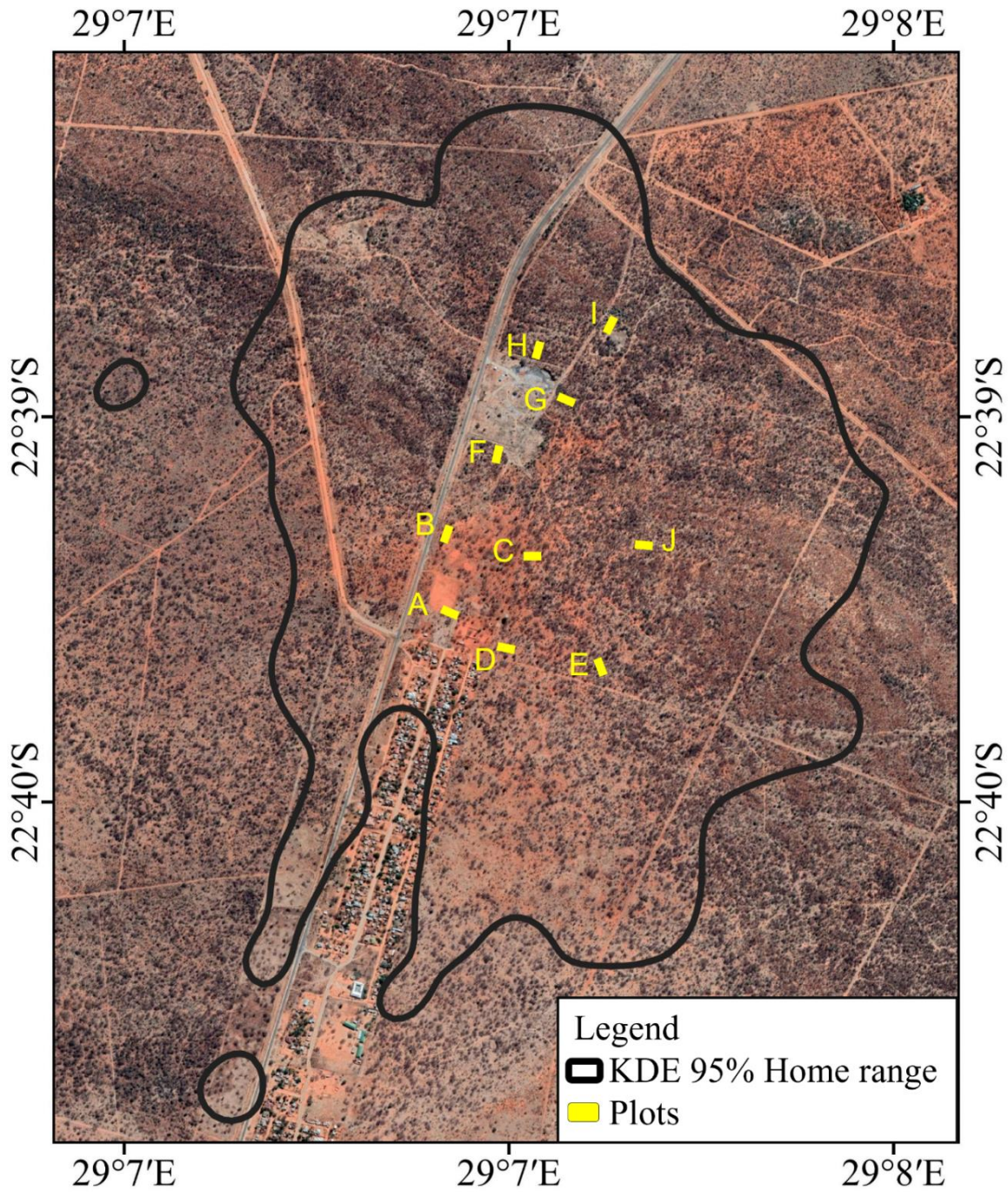


Figure 2. 9. Location of the ten plots distributed in the baboons' home range area.





Figure 2. 10. Plot name and number markings of the trees within the plot. The red letters denote which plot this tree belongs and white numbers meaning the tree number within this plot.

Table 2. 7. Name of plots and number of trees within this plot used in phenological survey.

Plot name	Number of trees (that have $\geq$ 10 cm in diameter)
A	11
B	8
C	12
D	7
E	7
F	14
G	21
H	16
I	16
J	9
<b>Total</b>	<b>121</b>

A total of 121 trees representing 14 plant species within 10 plots were used for surveying (Table 2.7 and 2.8). Plot surveys were conducted once a month, preferably around the same date in the last week of every month. I noted presence/absence or estimated percentage of leaves, fruits and/or seeds for each tree. I considered only leaves and fruits/or seeds, as these comprise a large portion of the baboons' diet.

Table 2. 8. Name and number of trees that were considered for the phenological survey (alphabetic order).

Sl no	English name	Scientific/Italic name	Number
1	Common corkwood	<i>Commiphora pyracanthoides</i>	8
2	False marula	<i>Lannea schweinfurthii</i>	5
3	Knob thorn	<i>Acacia nigrescens</i>	7
4	Marula	<i>Sclerocarya birrea</i>	6
5	Narrow-pod robust thorn	<i>Acacia robusta</i>	1
6	Purplepod clusterleaf	<i>Terminalia prunioides</i>	2
7	Red bushwillo	<i>Combretum apiculatum</i>	2
8	Rough-leaved corkwood	<i>Commiphora edulis</i>	29
9	Shepherd's tree	<i>Boscia albitrunca</i>	14
10	Sjambokpod	<i>Cassia abbreviata</i>	3
11	Stink shepherd's tree	<i>Boscia foetida</i>	3
12	Stink wood	<i>Ocotea bullata</i>	2
13	Vervet-leaved corkwood	<i>Commiphora mollis</i>	33
14	Worm-bark false-thorn	<i>Albizia anthelmintica</i>	6
	<b>Total</b>		<b>121</b>

The phenological survey was conducted for the purpose of determining monthly natural food availability index that was used in Chapters 3, 4 and 5.



### 2.4.5 Dump food availability assessment, count of dumped bags and time spent in the dump

The study baboon group spent considerable time in the garbage dump and consumed human leftovers from the rubbish at the site (Figure 2.11). People dumped rubbish in black plastic polybags or direct from bins; if the baboons were present at that time, they usually opened the bags and searched for food immediately after dumping.



Figure 2. 11. Baboon foraging in the dump (top left); an infant licking ice-cream box (top right); a baboon eating porridge (bottom left) and a baboon found a bun from rubbish bag (bottom right).

Dump food availability was assessed in the garbage dump site every 15 days (referred to as an assessment block). Unlike natural foods, dump foods are short-lived, and degrade quickly since mostly these were kitchen and table leftovers. In addition, volume of dumping fluctuated between weekdays and weekends. Considering these factors, more frequent sampling was needed to estimate dump food availability. Consequently, I decided to assess availability of dump foods in every 15 days, as twice as natural foods. On dump food assessment days, I reached the site before people started dumping. During the day, I counted the number of dumped bags and selected approximately every third bag for further inspection. For each sampled bag, all food items were taken out and weighed using a digital weighing machine. I classified dump foods into ten broad categories: 1) animal derived foods (raw or cooked meat, sausages etc.), 2) bread, 3) chips/fried potatoes, 4) cooked foods (porridge, noodles, pasta, rice etc.), 5) leftover fruits, 6) leftover vegetables, 7) milk or milk products, 8) sauces, 9) juice or any soft drinks, 10) dry foods including biscuits, dry cakes, rusks, pasta, uncooked rice and flour. Any food item that did not fall into these categories, or could not be identified, was recorded as unidentified. I noted the name and weight of each food category found in the bag. A preliminary study showed twenty bags comprised an overview of almost all human food items that were left in the dump (Figure 2.12) with new items asymptoting at this point. Twenty bags were thus inspected each assessment day; if this number was not reached, then the remaining number of bags were assessed in the next day.

For calculating dump food availability in an assessment block, I added up the weight (grams) of all food categories in that block. A total of 287 kg dump foods were found throughout the 20 assessment blocks and the mean available dump foods per assessment block was 14.56 kg (SD=  $\pm 6.77$ , Table 2.10).



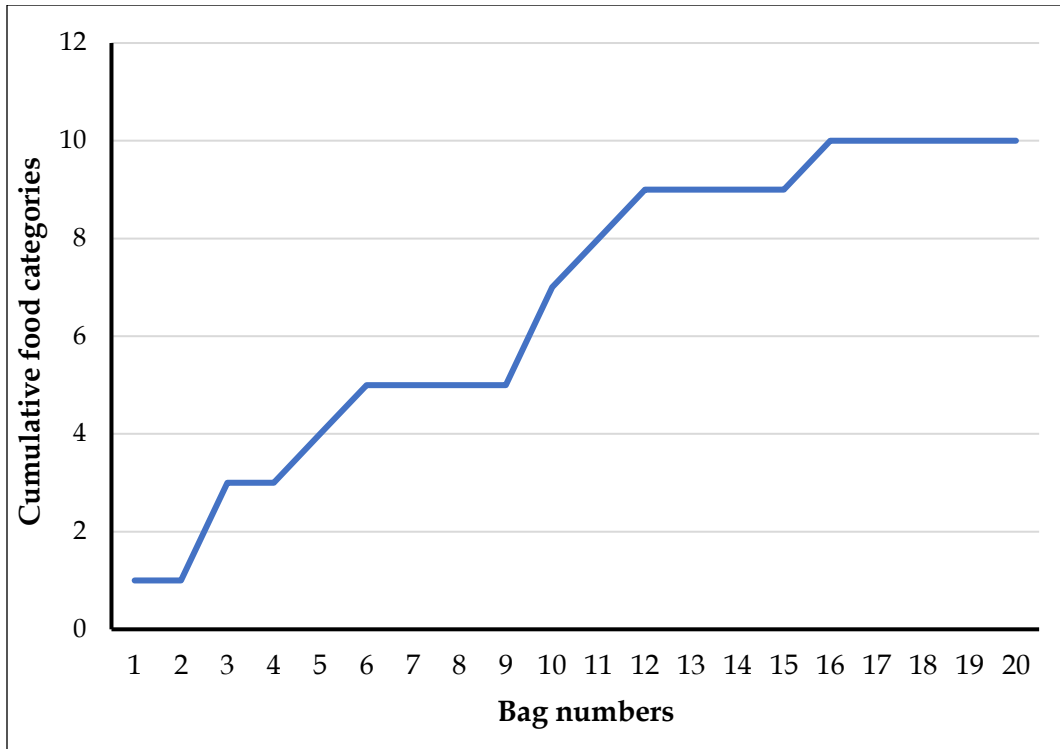


Figure 2. 12. Number of bags inspected, and cumulative food categories present in those bags.

I also collected the total number of bags that were dumped at the site each day. To do this I designed a data collection form (Table 2.9) that was kept at the landfill site office. The security guards at the site filled in the form on my behalf. I instructed the security guards about the purpose of the study and how to fill out the form. I also made sure that they agreed to fill the form voluntarily and there was no remuneration provided. I followed the same procedure for newly appointed guards. Depending on the situation and size of the dumping vehicle, the guards either asked dumpers about the bag numbers and its contents inside, or physically counted the number of bags while dumping. In the case of big dumping trucks, especially from the municipality and army camp, where it was not possible to count specific bag numbers, an estimated bag number was recorded.

Table 2. 9. Data collection form used for collecting number of dumped bags and food bags.

Date	Time	Number of total bags	Number of food waste bags (if any)	Content in the food waste bags	Type of other wastes (if any)	Signature of the writer

There were some limitations of this data collection. Firstly, security guards were changed regularly, and it took time to meet with new guards, as I was busy with other data collection. Usually, it took between 2 and 7 days to meet newly appointed guards and discuss my project. As a result, there were some days when the form was not filled out when new guards started, and also when the guards were busy with their regular work and could not fill out the form. In the case of big dumping trucks there may have been over or underestimates of the number of bags recorded.

Table 2. 10. Categories and weight (in grams) of dump foods in each assessment block. DFA= Dump Food Availability Assessment

	Dec 19	Jan 20		Feb 20		Mar 20		May 20	Jun 20		Jul 20		Aug 20		Sep 20		Oct 20		Nov 20	
Food categories	DFA 1	DFA 2	DFA 3	DFA 4	DFA 5	DFA 6	DFA 7	DFA 8	DFA 9	DFA 10	DFA 11	DFA 12	DFA 13	DFA 14	DFA 15	DFA 16	DFA 17	DFA 18	DFA 19	DFA 20
Bread	473		1534	1982	2032	803	1133	601	445	2088		1919	2308	1024	1444	810	2942	1396	1706	2152
Chips	73	160							400	30		50	179							
Cooked food	1315		920	66	1667	1257	179	3471	6254	3046	5651	5080	5124	3416	2804	2960	3718	4466	2667	2758
Leftover fruits	5450		10023	228	1223	152		531	981	4362	183	2226	3757	2099	5885	937	1060	5417	5216	7311
Leftover vegetables	1606	1381	11080	2757	590	2675	27	2128	3598	8540	3095	5176	8195	11281	3409	4621	1958	8708	8476	9445
Milk/ milk product	150		751	207	4040	2700	20	1159	84	607	190	255	1132	20	2260	400	663	22	1247	
Sauces	220	120			260	1050	50	200		73			165	96	12	5525	845			173
Soft drinks/juice	250		837	300	142	100				100	435		76	210	890	25	620	379		149
Dry foods/biscuits		10	52	988	733	28	42	124	412	2421		1409	1918	613	244	110	119		783	1868
Animal derived food							48	160	751	198	419	415	600	632	514	32	1065	78	103	374
Unidentified	260																			

I recorded the daily time spent in the dump (in minutes) by the baboon group on each follow day by recording the time in and time out on a daily basis. To get time in, I recorded the time when at least half of the troop had crossed the fence line. Similarly, time out was recorded when at least half of the troop crossed the fence line exiting the dump. For multiple dump sessions in a day, time spent in the dump was the sum of time in all sessions for that day.

The data on the dump food availability and dumped bags were collected to know how the availability of dump foods affects overall feeding behaviour. The time spent in the dump was collected for the purpose of determining how food availability affects the time spent in the dump. These data were used in Chapters 3, 4 and 5.

#### **2.4.6 Faecal sample collection, storage and transportation**

I collected faecal samples from adult, sub-adult and adolescent baboons on every follow day. My aim was to collect at least one sample per individual per week. I attempted to collect all samples roughly at the same time of the day (in the morning), although this was not always possible. Previous studies on olive baboons showed there was no circadian variation in hormonal measurements (Higham et al. 2009a), hence I continued to collect samples ad libitum throughout the day. Nearly two thirds of the samples (62%) were collected by midday.

Fresh, uncontaminated faecal samples were collected just after defecation. Each sample was homogenized by hand (using sterile rubber gloves), and seeds, grasses, gravels etc. were removed. Approximately 5 g (wet weight) faeces was taken into a screwcap tube (Azlon HDPE Wide Neck Round Bottles, Staffordshire, UK) and the tube closed tightly. The tube was then labelled with identification (sample number, individual identity with reproductive status, date and time of collection etc.), wrapped with parafilm and kept in cool bag with frozen gel packs while in the field. On return to the camp each day the samples were transferred to a freezer and stored at -20 °C until transport to the laboratory.

A total of 415 faecal samples were collected throughout the study period. The mean ( $\pm$  sd) number of samples collected per week was  $9.88 \pm 2.77$  (range: 5 to 20). The mean ( $\pm$  sd) number of samples collected per individual was  $34.58 \pm 10.15$  (range: 14 to 46; Table 2.11).

Individual females were recorded as pregnant once she stopped sexual swelling, usually confirmed approximately after two months of conception by the change of their para-callosal skin colour from black to pink (Altmann 1973). The first day of last swelling deturgescence (d-date) was taken as the conception day (Beehner et al. 2006). For individuals pregnant before the start of data collection, their pregnancy period was calculated as the six months prior to the date of birth (Beehner et al. 2006). Individuals were considered as lactating females until their baby reached one year old. If any individual started cycling during lactation, I recorded her reproductive status as cycling. Similarly, if an individual became pregnant while still lactating, I recorded her reproductive status as pregnant. The number of samples collected from each individual and each reproductive class are in Table 2.11.

Table 2. 11. Faecal samples collected from the individuals during the study period. AM= Adult male, AF= Adult female, SAM= Sub-adult male, AdoF= Adolescent female, NA= Not applicable.

Identity	Age-sex	Cycling	Pregnant	Lactating	NA	Total
Hound	AM				46	46
Clubto	AM				40	40
Eggo	AF	2	28	11		41
Zane	AF			14		14
Leah	AF	21	7	6		34
Ruby	AF	3	19	19		41
Fiona	AF	12	4	24		40
Pamela	AF	22	16	4		42
Soshi	AF		8	26		34
Jamie	SAM				40	40
Hannah	AdoF	24				24
Rosie	AdoF	9	10			19
<b>Total</b>		<b>93</b>	<b>92</b>	<b>104</b>	<b>126</b>	<b>415</b>

Weekly sampling is considered sufficient to represent overall physiological condition (Hodges and Heistermann 2003), and this is commonly practised in endocrinological studies of baboons (Crockford et al. 2008, Wittig et al. 2008, MacLarnon et al. 2015). I adopted weekly sampling for this study and collected roughly equal numbers of faecal samples for all individuals and age-sex classes (except adolescent females).

The samples were transported to the Behavioural Ecology and Physiology laboratory (category 2 laboratory), Durham University, UK, under the import licence issued for Prof Ann MacLarnon by UK's Department of Environment, Food and Rural Affairs (Authorisation number- ITIMP21.1172, Appendix 1).

#### **2.4.7 Environmental data collection**

I collected climatic and weather data (min temp, max temp, average temp, humidity, wind, cloud, rainfall, average daylength) for each day from Alldays weather station (<https://www.worldweatheronline.com/alldays-weather-history/limpopo/za.aspx>).

### **2.5 Data preparation and analysis**

Assumptions of all statistical methods were assessed prior to running analysis, and the relevant data for the analysis were prepared accordingly. Data preparation and analysis including models and statistics are described in detail within the chapters where they have been used.

### **2.6 Ethics and research permission**

The Animal Welfare Ethical Review Board (AWERB) of Durham university, UK approved this project (Reference number: ANTH-2019-05-13T13:11:53-xxxv76, Appendix 2). Throughout the study I gave the utmost consideration to any potential negative consequences to the baboons and followed the guidelines provided by the University's ethical review committees. To conduct field work, a research visa was obtained from the Republic of South Africa.

## Chapter 3. Activity, diet and ranging patterns of dump feeding chacma baboons

### 3.1 Introduction

Many non-human primates (hereafter primates) display remarkable dietary flexibility in response to habitat variation and seasonally fluctuating food resources, including the ability to incorporate human-derived foods into their diet (Grueter et al. 2013, Lewis and O’Riain 2017, Khatun et al. 2018). Variations in habitat and food source often elicit changes in primates’ activity budgets and ranging patterns (Lewis and O’Riain 2017). In natural habitats, availability of foods and their distribution may vary (Riley 2007a), and primates regulate their activities according to local seasonal changes in food availability (Ménard and Vallet 1997, Riley 2007a). For example, a wild feeding chacma baboon (*Papio ursinus*) group in Cape Peninsula, South Africa, allocated more time feeding and moving during a time of food scarcity than when food was available (Lewis and O’Riain 2017). Similarly, seasonality of rainfall and temperature affects activity budgets; for example, reduced feeding and moving was associated with high temperature for chacma baboons in De Hoop, South Africa (Hill et al. 2003) and with high rainfall in Cape Peninsula, South Africa (Van Doorn et al. 2010).

In anthropogenic environments, seasonality in food availability may be reduced due to the presence of human foods (El Alami and Chait 2012). In many areas, primates become accustomed to living closer to humans (Sha et al. 2009, Hoffman and O’Riain 2011) where they can access a variety of human foods, either directly or indirectly through provisioning. Direct access includes foraging on cultivated crops and fruits (McKinney 2011, Warren et al. 2011) and even garbage disposal sites or rubbish bins (Altmann and Muruthi 1988, Eley et al. 1989, Muruthi et al. 1991), while provisioning occurs by tourists, pilgrims, worshippers and animal lovers (Boug et al. 1994, Kamal et al. 1997, Ram et al. 2003, Sha and Hanya 2013, McKinney et al. 2015, Maréchal et al.

2016a, Ilham et al. 2018). In some places, for some species, human foods are an essential part of their daily diet (Altmann and Muruthi 1988, Saj et al. 1999, Fuentes et al. 2011, El Alami et al. 2012, Schurr et al. 2012). Human foods tend to be energy rich, palatable, easily digestible, spatiotemporally predictable and sometimes readily available in greater amounts than natural foods (Muruthi et al. 1991, Saj et al. 1999, Ilham et al. 2018). The inclusion of human foods may have a significant impact on activity budgets and ranging patterns (Altmann and Muruthi 1988). Access to human food increases the energy intake per unit of food such that animals can meet their metabolic demands quickly (Saj et al. 1999). This increased foraging efficiency may release time for other activities (Saj et al. 1999); primates with access to any form of human foods may spend significantly less time feeding and moving and more time in resting and socializing (olive baboon, *P. anubis* (Eley et al. 1989, Warren et al. 2011); yellow baboon, *P. cynocephalus* (Altmann and Muruthi 1988, Muruthi et al. 1991); Guinea baboon, *P. papio* (Strum 2010); hamadryas baboon, *P. hamadryas* (Boug et al. 1994); chacma baboon (Hoffman 2011); vervet monkeys, *Chlorocebus pygerythrus* (Saj et al. 1999)) than their naturally foraging counterparts.

Increasing human populations, urbanization and other human modifications of the landscape may negatively affect resource availability of the residing wildlife populations (McKinney 2006, Campbell-Smith et al. 2011, Stone et al. 2015). On the other hand, garbage sites, where human discard their daily kitchen and household wastes, become a potential source of foods for animals living in that habitat (Flint et al. 2016). As a result, garbage feeding is common in human-modified landscapes among numerous mammalian taxa, such as raccoons (Totton et al. 2002, Totton et al. 2004), bears (Lewis et al. 2015, Teampanpong 2021), foxes (Reshamwala et al. 2018), mongooses (Gilchrist and Otali 2002, Otali and Gilchrist 2004, Flint et al. 2016), elephants (Liyanage et al. 2021), and other carnivores and ruminants (Meyer et al. 2003, Katlam et al. 2018). Nevertheless, despite the increasing co-occurrences of primates and humans across many countries (Humble and Hill 2016), the study of garbage feeding by primates has received relatively little attention.

The costs and benefits of feeding from garbage dumps might be different compared to other anthropogenic food sources. Crop foraging reflects a trade-off between the rewards of energetic foods and the risk of deterrence which might result in injury or even death (Fehlmann et al. 2017, Schweitzer et al. 2017). Similarly, tourist provisioning requires primates to adjust their daily feeding times depending on the timing of tourist visits (Boug et al. 1994). Compared to these



human food sources, dump foraging could be more rewarding, possibly because of low or risk-free access to the garbage dumps and the opportunity of taking foraging decisions independently, although foraging decisions may need to account for the presence of other primate groups at the resource. Moreover, foods at rubbish dumps are usually abundant, spatially and temporally predictable and renewed on a daily basis (Oro et al. 2013).

Taking advantage of foraging in dumps could produce significant benefits to baboon populations. Despite its potential importance, however, research on dump feeding baboons is limited to a small number of studies on yellow baboons (Altmann and Muruthi 1988, Muruthi et al. 1991, Altmann et al. 1993) and olive baboons (Eley et al. 1989) which have investigated the impacts in relation to activity budgets (Altmann and Muruthi 1988, Eley et al. 1989), dominance rank (Altmann and Muruthi 1988), reproductive condition (Muruthi et al. 1991), energy intake and nutrition (Eley et al. 1989, Muruthi et al. 1991), body size and condition (Eley et al. 1989, Altmann et al. 1993), and parasitism (Eley et al. 1989) in comparison to wild feeding baboons. There is little information on age-sex differences in behaviour and the ranging patterns associated with this foraging strategy. Moreover, there is no information about diet composition, especially the types of food baboons consumed on garbage dumps. Further research is needed therefore to better understand the behavioural responses to feeding on these anthropogenic food sources. The present study addresses this need by investigating the effects of foraging on dump foods on chacma baboon behaviour and ranging patterns.

Baboons are opportunistic, omnivorous, generalist feeders that appear to optimize their diet by selecting from a wide variety of available foods in their environment (Norton et al. 1987). Natural baboon diets primarily consist of plant matter such as fruits or seeds, leaves, bulbs, shoots, roots, buds, bark etc. (Sithaldeen 2019). There are records of baboons feeding on animal derived foods such as invertebrates, small vertebrates, seashore life, fungi and other subterranean and/or marine foods when these are abundant in their home ranges (Lewis and O'Riain 2017). The number of plant species and plant parts eaten by baboons often varies seasonally due to the seasonal effects of food productivity (Norton et al. 1987, Hill et al. 2003, Van Doorn et al. 2010). In contrast, provisioned foods are often available almost all the year at different study sites (Kamal et al. 1997, Ilham et al. 2018), because tourists or local people feed primates daily for pleasure or religious purposes (Ilham et al. 2017). Nevertheless, temporal variation in the

availability of human foods and in deterrence activities may affect baboons' behaviour. Provisioned foods may not be available all day because the source (people who offer foods) and the amount of provisioning may vary at different times of day (Ram et al. 2003) as well as seasonally. Tourist provisioning of hamadryas baboons in Saudi Arabia (Boug et al. 1994), and of long-tailed macaques, *Macaca fascicularis* in Indonesia (Ilham et al. 2018), was greatest in the evening. Similarly, due to the deterrent activities of farmers or guards, a crop foraging olive baboon group in Kenya was also most active feeding on crops in the evening (Strum 2010). Both circadian and seasonal variation in provisioning and in natural foods may thus determine when baboons access the site.

Variability in feeding behaviour may depend on an individual's body size and dominance rank. For instance, young animals spend more time feeding and require more energy per unit of body mass than adults (Post et al. 1980, Muruthi et al. 1991, Jaman and Huffman 2011). High ranking baboons generally have longer feeding bout durations and were less likely to be interrupted than lower ranking baboons (Post et al. 1980) and could monopolize food patches until they reached satiety (Altmann and Muruthi 1988). In Japanese macaques (*M. fuscata*), high ranking adult individuals may acquire most of their energy from provisioned foods while low ranking individuals forage more on natural foods available in their home ranges (Soumah and Yokota 1991). Age and dominance effects may thus have important impacts for baboons feeding on garbage dumps.

Spatial and temporal variation in food resources are considered the main predictors of primates' space use and home range size (Hoffman and O'Riain 2012b, Pebsworth et al. 2012). The proportion of natural versus human modified habitat that animals exploit can have a large effect on ranging behaviours with home range and daily travel length generally increasing with the percent of time spent using natural habitat (Hoffman and O'Riain 2012b). Since natural foods are usually widely dispersed, unpredictably available, and grow in finite patches which are distributed heterogeneously, primates may travel long distances to meet their nutritional requirements (Ganas and Robbins 2005). In contrast, human foods have relatively homogenous distribution in space and time. Reliance on these foods has been shown to result in shorter daily travel length and smaller home range sizes in yellow baboons (Altmann and Muruthi 1988), chacma baboons (Hoffman and O'Riain 2012b), olive baboons (Strum 2010), pig-tailed macaques,

*M. leonina* (José-Domínguez et al. 2015), vervet monkeys (Saj et al. 1999). Dump feeding is thus likely to have significant implications for ranging behaviours compared to naturally foraging baboon groups.

The study focuses on a chacma baboon group living near to a garbage dump in Alldays, South Africa (hereafter Alldays Dump Group). The site is where residents of Alldays can dump their domestic waste and no deterrence methods were used to hinder baboons from entering beyond a fence encircling the dump boundary that they could easily cross. The risk-free access to the dump, in conjunction with the possibility of getting high quality human foods on a daily basis, provided an opportunity to examine intragroup variability in feeding behaviour, potential drivers of the time spent in the dump, the effects of all these factors on range use patterns by the group, and the extent to which activity and range use by this baboon group vary compared with other baboon populations. From the above context, I have developed a series of hypotheses and predictions to test (Table 3.1):

Table 3. 1. Hypotheses and predictions for this chapter

Hypothesis	Predictions
1. Access to foraging on dump foods will impact on the time budgets and ranging behaviour of baboons because dump foods are high in energy and require less processing time.	Compared to naturally foraging chacma baboon groups, the Alldays Dump Group will: <ol style="list-style-type: none"> <li>a. spend less time feeding and moving and more time resting and grooming;</li> <li>b. occupy a smaller home range area and have shorter daily travel lengths.</li> <li>c. The activity budgets and ranging behaviours of the Alldays Dump Group will be similar to those of other anthropogenic foraging baboons.</li> </ol>
2. Baboons' dietary diversity and feeding time will vary according to seasonal changes in food availability.	<ol style="list-style-type: none"> <li>a. Seasonal variation in natural dietary diversity will be greater than seasonal variation in the diversity of dump foods.</li> <li>b. Baboons will spend an increased proportion of time feeding on natural foods when these are more available.</li> </ol>

3. Access to the dump foods depends on the age/size of baboons, because size and social status may affect access to good quality foods.	a. Smaller, younger baboons will spend more time feeding on natural foods than dump foods, while larger-bodied adults will spend more time feeding on dump compared to natural foods.
4. Since dump foods are high in energy, dump food availability will have a significant impact on baboon ranging and the use of the dump for foraging.	a. Time spent in the dump will be positively related to dump food availability. b. Baboons will spend an increased proportion of time in the dump when natural foods are limited.
5. Baboons' ranging behaviour is influenced by the spatial and temporal variability of food resources in their home range.	a. Monthly ranging area, core area and daily travel length will decrease in response to increasing natural food availability.

## 3.2 Methods

### 3.2.1 Data collection

For a detailed description of the data collection methods see Chapter 2.

### 3.2.2 Literature search protocol and baboons' socioecological data collection

To compare the activity budgets and ranging behaviours of the Alldays Dump Group with other baboon populations, I searched relevant literature published on baboons (*Papio* sp.). I made a comprehensive search in Web of Science, Google Scholar, PubMed and ResearchGate using the search words 'baboon', '*Papio*', 'natural feeding', 'crop-foraging', 'garbage-feeding', 'provisioning baboon', 'activity budgets', 'ranging' and combinations of these. I scanned titles of the search results and selected those relevant for this study. I read abstracts of these initial papers and retained papers meeting any one of the following criterion- i) it focused on at least one group of naturally foraging chacma baboons, or ii) it focused on a group of any baboon species that was crop-foraging, provisioned, garbage feeding or displayed any other kind of anthropogenic

foraging. I made two sets of papers, one for each criterion mentioned above. I also used the bibliographic section of the selected papers to find further literature missing from the initial searches based on search words. From this selection, I excluded papers based on only one season due to limited data. This selection protocol resulted in 30 research items, of which 21 were peer-reviewed journal articles, seven PhD theses and two masters' theses.

Each research item was carefully read, and relevant data were extracted to compare the activity and ranging behaviours of baboon populations across Africa. I use the terms 'literature', and 'paper' interchangeably; however, I make a distinction between these words and 'study'. For example, when a paper deals with multiple baboon groups, I treated each group as an individual study for the convenience of data handling and presentation. In some cases, the ecology (i.e. food habit, habitat etc.) of baboon groups is different, so it's more appropriate to treat them separately. If groupwise data were not available in a paper, I treated that paper as a single study. Therefore, one 'paper' may have one or several 'studies'. From the selected papers or theses, a total of 29 studies are tabulated here. The feeding habit of a group was considered as natural, unless otherwise described in the paper. In some previous literature, the term socializing was used, which represents mostly grooming. I used grooming, and for comparison, I recorded socializing data from previous papers as grooming, unless these were mentioned separately.

### **3.2.3 Data preparation**

*Proportion of activity* (e.g., feeding, grooming, moving, resting and others) for each individual was estimated from scan data. I divided the number of records of each category of behaviour per each hour of observation (e.g., 5:00-5:59, 6:00- 6:59, 7:00-7:59, ... 18:00-18:59) by the total number of behavioural records of the respective hour (Back et al. 2019).

*Feeding rate* was determined from focal samples. Feeding rate was calculated by dividing total feeding time (in seconds) by the total observation time (in minutes) for each sample. Similarly, feeding time on any food item was divided by the total observation time yielding feeding rate per minute on that food item.

*Leaves and fruits availability index* was calculated based on the percentage of the crown area covered by leaves and fruits. I ranked trees on a 5-point scale where a score of 0 related to no leaves and 1, 2, 3 and 4 reflecting 1-25%, 26-50%, 51-75% and 76-100% leaves, respectively

(Sengupta et al. 2015). The Leaf Availability Index (LAI) for a month was then estimated based on the following formula (Johnson et al. 2015, Sengupta et al. 2015):

$$LAI = \sum_{k=1}^n D_k B_k P_{km}$$

Where  $D_k$  is the density of a particular species  $k$  in the home range area,  $B_k$  is the mean DBH (Diameter at Breast Height) of species  $k$  (cm),  $P_{km}$  is the phenology score of leaves for species  $k$  in a given month  $m$ , and  $n$  is the number of plants considered in the study.

Similarly, the monthly Fruit Availability Index (FAI) was calculated:

$$FAI = \sum_{k=1}^n D_k B_k P_{km}$$

Where  $D_k$  is the density of a particular species  $k$  in the home range area,  $B_k$  is the mean DBH of species  $k$  (cm),  $P_{km}$  is the phenology score of fruits for species  $k$  in a given month  $m$ , and  $n$  is the number of plants considered in the study.

Monthly leaves and fruits availability index during the study period are shown in Figure 3.1.

*Daily time spent in the dump* (in minutes) was the duration the baboon group stayed in the dump on a follow day. I noted time in and time out when at least half of the troop members had crossed in and crossed out the dump fence line, respectively. For multiple dump sessions in a day, time spent in the dump was the sum of time in all sessions for that day.

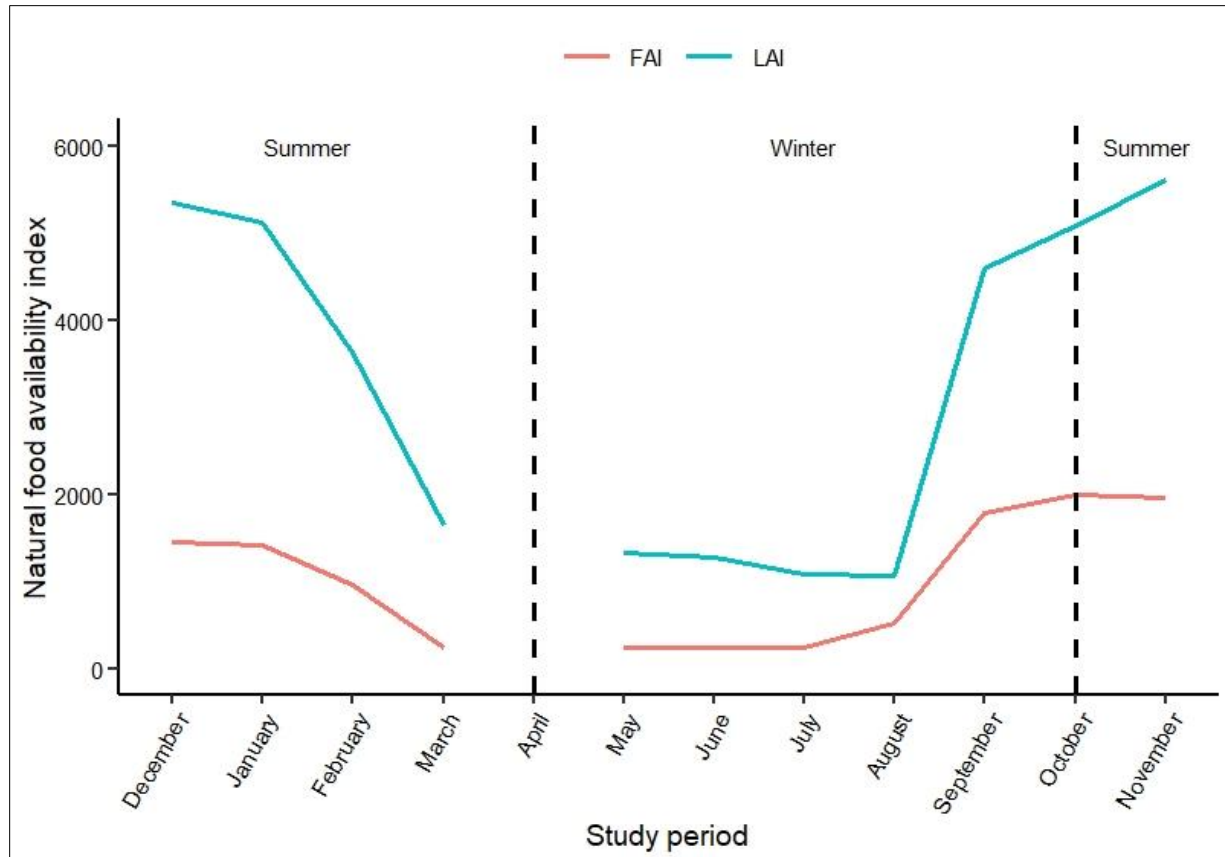


Figure 3. 1. Monthly leaves and fruits availability index in the natural habitat within the Alldays Dump Group's home range area. LAI= leaf availability index, FAI= fruit availability index. Months are ordered according to the starting time of the study. The dashed lines in the plot indicate the transition between the seasons.

*Dump food availability per block* (in kg) was calculated by summing weights of all food categories in 20 bags for each 15-day assessment block. In the case of block 2, only seven bags were assessed due to heavy rain limiting dump use. Similarly, in block 7, 20 bags could not be assessed due to the covid lockdown restrictions. In these cases, the amount of available foods in these blocks was estimated through multiplying the amount of food I got per assessed bag by 20.

*Availability of dump foods per day* in an assessment block was estimated through mean number of bags per day and mean amount of foods per bag. The estimation was calculated by using following formulas.

$$\text{Mean number of bags per day} = \frac{\text{total dumped bags}}{\text{number of days of data per block}}$$

$$\text{Mean foods per bag} = \frac{\text{dump food availability per block}}{20 (\text{number of bags assessed on each phenology day})}$$

$$\text{Availability of dump foods per day} = \text{Mean number of bags per day} \times \text{Mean foods per bag}$$

I had no data on dumped bags for the assessment blocks 1, 8 and 9. In these cases, mean number of bags per day was estimated by averaging the values for the two adjacent assessment blocks. There was a sharp increase in mean dumped bags per day in dump phenology block 6, because nearly 300 bags were dumped, mostly by the Army, over the 2 days, although this may not reflect the general pattern at this time (Figure 3.2).

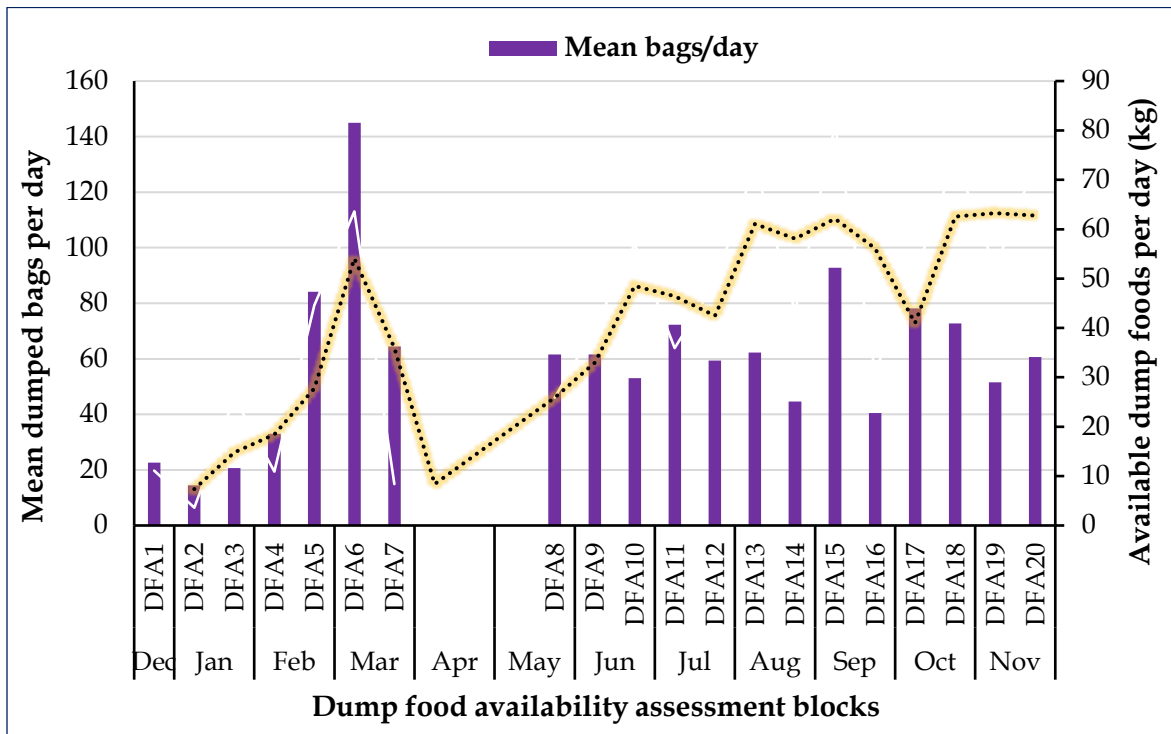


Figure 3. 2. Mean dumped bags per day and mean available dump foods per day (dotted line) in each 15-day dump food availability assessment block. DFA= Dump food availability assessment

Monthly home range and core area of the baboon group was estimated through Kernel Density Estimation using the reproducible home ranges (“rhr”) R package (Signer and Balkenhol 2015). Kernel density relies on non-parametric algorithms to estimate the probability density function



from a set of Cartesian points (Silverman 2018). In the case of home range use, kernel density refers to the estimation of the probability of occurrence within the study area based on the GPS coordinates taken on the centre point of the group. Only GPS coordinates that were collected at a fixed time interval (30 min) were used in this analysis to ensure that the utilization distribution was proportional to the amount of time spent in each location. The reference bandwidth technique was used with the 95 % contour as the home range boundary, which excluded some outlying data points (Howell and Chapman 1997). Core area was defined as the 50% isopleth (Worton 1989, Cimino and Lovari 2003). The location data were projected to Universal Transverse Mercator (UTM) map coordinates using zone 36 S (for South Africa) and WGS-84 ellipsoid. Seasonal home ranges and core areas were calculated based on the respective GPS points collected in these seasons.

*Daily travel lengths* were determined based on distance between consecutive GPS locations (points taken every 30 minutes) from successful follow days using the great-circle equation. Great-circle equation measures the shortest distance between two points on the surface of a sphere (Anonymous 2003). Successful follow days were defined as days on which the animals were followed from sleeping site to sleeping site without losing audio-visual contact for a continuous period greater than one hour. Among the 123 possible follow days, I was able to complete 108 successful follow days. The GPS location data were imported into ArcGIS as XY data for analysis. Using a data management tool (points to line) I made a line feature that was re-projected to the Universal Transverse Mercator (UTM) map coordinates using zone 36 S (for South Africa) and WGS-84 ellipsoid in the projected coordinate system. Using calculate geometry function of ArcGIS I then calculated the daily travel length of each successful follow day.

### **3.2.4 Data analysis and model fitting**

I performed one sample t-tests to compare activity budgets and ranging behaviours between the Alldays Dump Group and other naturally foraging chacma baboons, as well as between the Alldays Dump Group and other anthropogenic foraging baboon groups.

I used Shannon-Wiener Diversity Index (SWDI) to calculate dietary diversity of natural and dump food items. I calculated this index monthly by using time spent feeding on each food item in each month based on the formula (Wilson and Bossert 1971):

$$SWDI = - \sum_{i=1}^s p_i \times \ln(p_i)$$

Where,  $p_i$  = proportion of time spent feeding on food item  $i$ , calculated through time spent feeding in a month on food item  $i$  divided by total time spent feeding on all food items in that month;  $s$  = number of total food items;  $\ln$  = natural log. Higher index value in a month means the diet is more diverse in that month.

I used non-parametric Wilcoxon rank sum tests to explore the seasonal variation in consumption of each natural and dump food item, as the distribution of time spent feeding on each food item was not normal (Shapiro-Wilk normality test,  $p < 0.05$ ). I also used Wilcoxon rank sum test to examine the feeding rate on different food types across age-sex classes.

I used a Generalized Linear Mixed Model (GLMM) to explore the effect of predictor variables on the time spent in the dump. I used daily time spent in the dump as a response variable and the number of dumped bags in last two days, dump food availability per day, dump food availability in 15-day blocks, monthly fruit availability index and day length as predictor variables. I included dump food availability assessment block and month as the random effects in the model.

I performed Wilcoxon rank sum test to examine the seasonal variation in home range use, core area and daily travel length of the Alldays Dump Group.

Three GLMMs were used to see which ecological and/or environmental variables explain home range size, core area and daily travel length of the baboon troop. Monthly fruit availability index, dump food availability in 15-day blocks, rainfall and temperature were the continuous fixed effects and dump food availability assessment block was used as random effects for the model for ranging and core area. Instead of dump food availability in 15-day blocks I used dump food availability per day in the model for daily travel length. I also added humidity, cloud cover and daylength as fixed effect and month as random effect for this model.

Before running GLMMs, co-linearity between all effects was checked using variance inflation factors, VIF (Field et al. 2012), with a cut-off criterion multicollinearity efficiency value  $>10$  for including variables inside the same model (Myers and Myers 1990). The model fitting was

performed by using “lme4” and “lmerTest” packages in R with the “CAR” package was used to check the multicollinearity.

All statistical analyses were completed using R (Version 4.0.4, R development core team). All tests were two tailed with a 5% level for significance ( $p < 0.05$ ). For the data visualization I used “ggplot2” with the “cowplot” and “gridExtra” packages in R.

### 3.3 Results

#### 3.3.1 Activity budgets and comparison with other baboon populations

The activity budget of the Alldays Dump Group was dominated by resting ( $33.1 \pm \text{SD } 9.79\%$ ) and moving ( $31.3 \pm \text{SD } 9.21\%$ ), followed by feeding ( $18.1 \pm \text{SD } 6.11\%$ ), grooming ( $10.3 \pm \text{SD } 5.39\%$ ), and other behaviours ( $7.09 \pm \text{SD } 7.06\%$ ). Time budgets varied by age-sex classes (Appendix 3).

I found 18 studies in the literature on naturally foraging chacma baboons and 11 studies on anthropogenic foraging baboons in Africa. Their activity budgets and ranging patterns are presented in Table 3.2 and 3.3, respectively. Naturally foraging chacma baboon groups spent on average almost half of their total activity feeding (46.5%, range: 28-62%,  $n= 13$  groups), followed by moving 24.3% (12-38%,  $n= 13$  groups), resting 17.8% (9-28%,  $n= 13$  groups) and grooming 10.2% (5-22%,  $n= 13$  groups; Table 3.2). Comparison with the Alldays Dump Group showed it spent significantly less time feeding ( $t = 8.95$ ,  $df = 12$ ,  $p < 0.001$ ) and more time resting ( $t = -10.39$ ,  $df = 12$ ,  $p < 0.001$ ) and moving ( $t = -3.02$ ,  $df = 12$ ,  $p = 0.010$ ). There was no significant difference observed in grooming activity ( $t = -0.09$ ,  $df = 10$ ,  $p = 0.930$ ; Figure 3.3).

Mean foraging time of other anthropogenic foraging baboon populations was 27.8% (range: 20-39%,  $n= 9$  groups), resting 31.1% (21-44%,  $n= 9$  groups), moving 22.7% (16-31%,  $n= 8$  groups) and grooming 14.3% (4-27%,  $n= 8$  groups; Table 3.3). Alldays Dump Group spent significantly less time feeding ( $t = 4.11$ ,  $df = 8$ ,  $p = 0.003$ ) and more time moving ( $t = -5.76$ ,  $df = 7$ ,  $p < 0.001$ ) in comparison to other anthropogenic foraging baboon populations, but there were no significant differences observed in resting ( $t = -0.68$ ,  $df = 8$ ,  $p = 0.513$ ) and grooming ( $t = 1.31$ ,  $df = 7$ ,  $p = 0.232$ ; Figure 3.3).

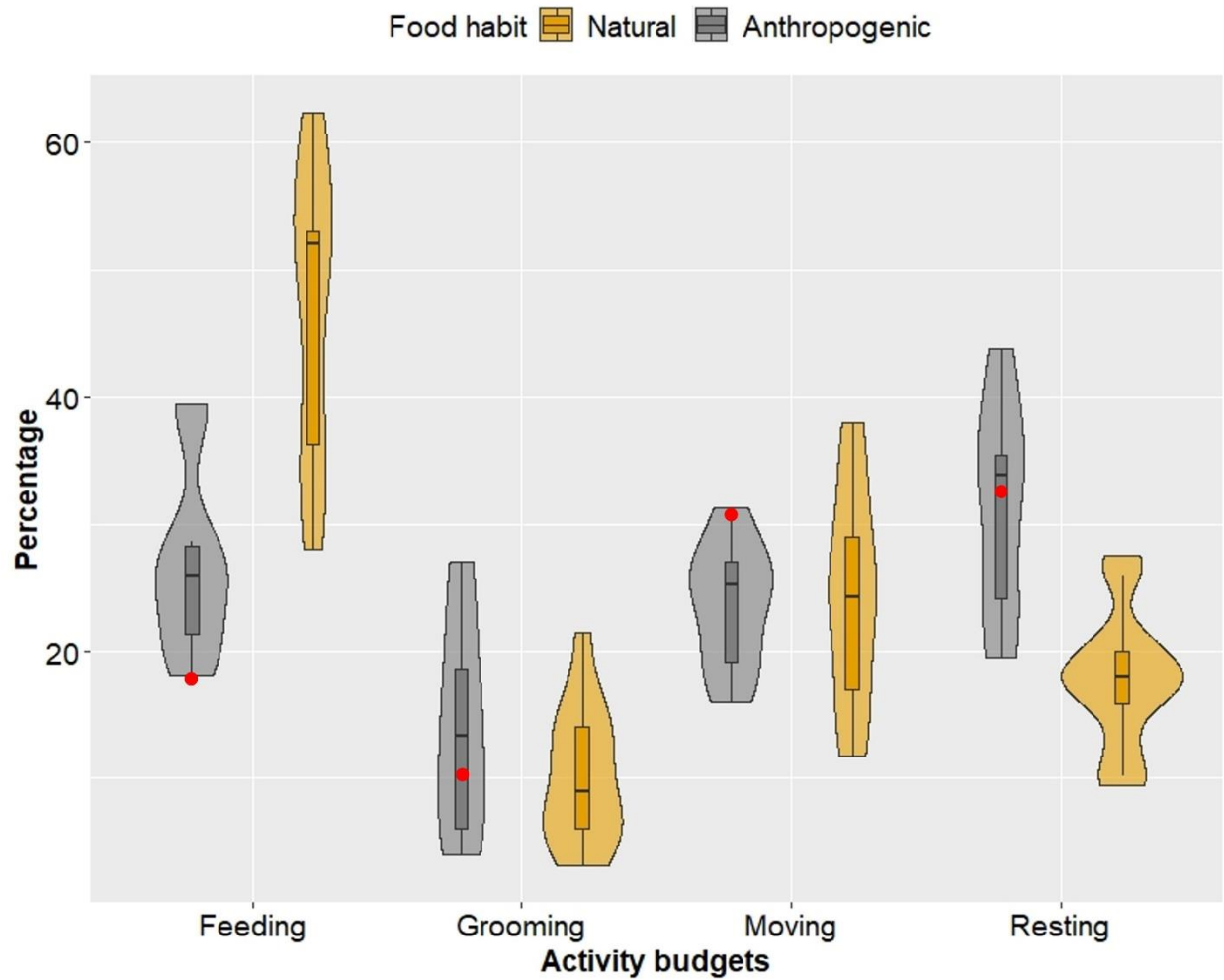


Figure 3. 3. Violin plot comparing activity budgets between naturally foraging chacma baboons and anthropogenic foraging baboon populations across the Africa. Boxes inside the violin represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values; outliers are removed. Red dot in each anthropogenic box represents the Alldays Dump Group.

Table 3. 2. Activity budgets and ranging behaviours naturally foraging chacma baboon populations across Africa. In case of multiple groups in a single study site the group name is in parenthesis. F= Feeding (%), R= Resting (%), M= Moving (%), G= Grooming (%), HR= Home Range (km<sup>2</sup>), DTL= Daily Travel Length (km), SA= South Africa.

Study site (group name), Country	Group size	F	R	M	G	HR	DTL	References
Cape Peninsula (O troop), SA	85	34	26	29	11	37	7.9	(Davidge 1978a, b)
Cape Peninsula (Kanonkop), SA	56	52 <sup>#</sup>	9.4 <sup>#</sup>	33.3 <sup>#</sup>	5.3 <sup>#</sup>	45.3	5.93	(Hoffman 2011, Lewis and O'Riain 2017)
De Hoop (Vlei troop), SA	40-44	36.3	15.9	35.7	15.9	18.76		(Hill 1999)
De Hoop (Small troop), SA	17-21	58.03	12.8	14.9	14.3	12.36		(Hill 1999)
Drakensberg (High), SA	9	53	17	24	6	18.9	4.3	(Whiten et al. 1987)
Drakensberg (Low), SA	14	53	18	22	7	10.0	3.8	(Whiten et al. 1987)
Mkuzi game reserve (Flash's), SA	28	28	27.5	26.5	14	4.72	3.63	(Gaynor 1994)
Mkuzi game reserve (Darth's), SA	43	37	19	25.5	13	6.88	3.86	(Gaynor 1994)
Mkuzi game reserve (Mtshopi), SA	71	32	17	38	9	11.76	6.04	(Gaynor 1994)
Blyde Canyon (Bourke's Luck), SA	18	62.3	10.2	24.3	3.2	10.35	3.37	(Marais et al. 2006)
Hemel-en-Aarde Valley, SA	21	48.47	18.23	11.78	21.5			(Ellwanger 2020)

Study site (group name), Country	Group size	F	R	M	G	HR	DTL	References
Honnet (RB troop), SA	57-60					23.31	10.46	(Stoltz and Saayman 1970)
Wildcliff, SA	115					11.98 (5.30- 20.58)	3.6- 6.5	(Pebsworth et al. 2012)
Drakensberg (London), SA	42					14.96		(Henzi et al. 2011)
Drakensberg (Driekop), SA	40					14.13		(Henzi et al. 2011)
Suikerbosrand, SA*	38 (18-70)					26.7 (13.7- 57.2)	1.64- 2.91	(Segal 2008, Slater et al. 2018)
Tsaobis (J troop), Namibia	57	58	20	14	5	12.25	5.7-6	(King 2008)
Tsaobis (L troop), Namibia	32	52	21	17	7	26.75	6-6.2	(King 2008)

# The values based on the percentage of daily activities in a single season; \*the result from multiple study groups

Table 3. 3. Activity budgets and ranging behaviours of anthropogenic foraging baboon populations across Africa. In case of multiple groups in a single study site the group name is in parenthesis. Abbreviations are as same as Table 3.2

Study site (group name), Country	Taxon/ Species name	Group size	Type of human foods	% of human food	F	R	M	G	HR	DTL	References
Amboseli (Lodge), Kenya	<i>P. cynocephalus</i>	38-56	Garbage dump	38	23.7	43.8	19.2	13.3	< 4	4	(Altmann and Muruthi 1988, Bronikowski and Altmann 1996)
Gilgil (Wabaya), Kenya	<i>P. anubis</i>	36	Garbage and crop foraging	29.2-58	28.6	23.5	27.2	5.6	4.5-8.75		(Eley et al. 1989, Strum 2010)
Gashaka (G troop), Nigeria	<i>P. anubis</i>	19.3	Crop foraging		26.7	34.5	25.2	4	1.4	3.1	(Warren 2003, Higham 2006)
Bole Valley, Ethiopia	<i>P. anubis</i>	19	Crop foraging		20.5	35.4	25.4	15.9		1.2	(Nagel 1973, Dunbar 1992)
Al Hada, Saudi Arabia	<i>P. hamadryas</i>	220	Tourist provisioning	58-97	20	41	27	6			(Boug et al. 1994)
Cape Peninsula (Plauteau Road), SA	<i>P. ursinus</i>	33	Garbage and crop foraging		37-41	16-23			9.05	4.85	(Van Doorn et al. 2010, Hoffman and O'Riain 2012b)

Study site (group name), Country	Taxon/ Species name	Group size	Type of human foods	% of human food	F	R	M	G	HR	DTL	References
Cape Peninsula (RH troop), SA	<i>P. ursinus</i>	16	Garbage and human handouts, shops, kitchens		27.3	35.3	18.7	18.6	1.5	1.80	(Hoffman 2011, Kaplan et al. 2011, Hoffman and O’Riain 2012b)
Cape Peninsula (Tokai), SA	<i>P. ursinus</i>	115	Crop foraging		39.4	20.6	16.0	24.2	9.50	2.93	(Hoffman and O’Riain 2011)
Cape Peninsula (MT1 troop), SA	<i>P. ursinus</i>	65	Garbage and crop foraging		25.1	26.0	22.7	27.0	2.72		(Dubay 2018)
Suikerbosrand (Kraal), SA	<i>P. ursinus</i>	88	Crop foraging						22.38	4.5	(Anderson 1981)
Alldays, SA	<i>P. ursinus</i>	18-25	Garbage dump	45	18.1	33.1	31.3	10.3	2.95	3.4	this study



### 3.3.2 Natural food plants and items consumed by Alldays Dump Group

Alldays Dump Group consumed plant parts from at least 23 species (including eight trees, 15 shrubs and some unidentified forbs and herbs) that constituted 55% of their annual diet (Table 3.4), based on feeding time in habitat outside of the dump area. Among them, one species (papaya, *Carica papaya*) was cultivated by Alldays residents. Among the natural food items, more than two thirds of their diet came from fruits and seeds (69%), followed by grasses (12%), and leaves (9%). They also consumed very small amounts of bark, flowers, sap and roots from some plants (Figure 3.4 and Table 3.4). Occasionally they fed on fungi (but not during focal observations).

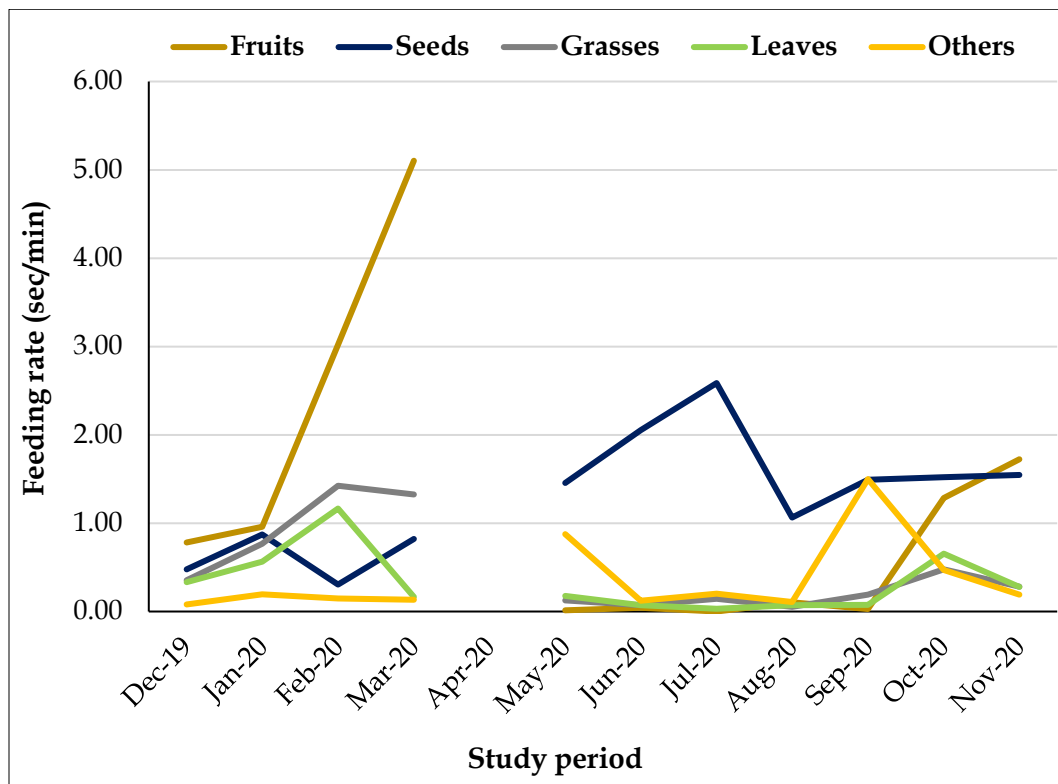


Figure 3. 4. Monthly variation in the feeding rate of natural food items. Top four consumed items are presented here, all other items are presented in 'others' category.

Fruit consumption started from early October when plants started fruiting and peaked in March. Similarly, leaf and grass consumption started in early October and continued throughout the summer months. In contrast, seeds from various plants were the only natural foods available in the winter months. Seed consumption was highest in July and lowest in February (Figure 3.4).

Table 3. 4. Natural and anthropogenic foods for the Alldays Dump Group with the average feeding rate per minute and the percentage of specific food items in their annual diet. Items are listed in alphabetic order. \* plant species cultivated by Alldays residents, br= bark, fr= fruit, bd= bud, lf= leaf, se= seed, fl= flower, sa= sap, gr= grass, hr= herb, pi= pith, rt= root, inv= invertebrate, inv coc= invertebrate cocoon, inv lar= invertebrate larva.

Food plants and items in natural habitat					
Name of plants	Plant	Parts eaten	Average	Average	
English name	Scientific name	type	feeding	percentage	
			rate per	of diet	
			minute		
Baobab	<i>Adansonia digitata</i>	Tree	br, fr,	0.024	0.35
Common corkwood	<i>Commiphora pyracanthoides</i>	Shrub	bd, fr, lf, se	0.183	2.71
Copperstem corkwood	<i>Commiphora harveyi</i>	Tree	br, fr, lf	0.002	0.04
Flame thorn	<i>Acacia ataxacantha</i>	Shrub	lf	0.000	0.01
Glossy-leaved corkwood	<i>Commiphora schimperi</i>	Shrub	bd, fr, lf, se	0.042	0.62
Knob thorn	<i>Acacia nigrescens</i>	Tree	fr, lf, se	0.034	0.50
Mallow raisin	<i>Grewia villosa</i>	Shrub	bd, fl, fr, lf, se	0.027	0.40
Marula	<i>Sclerocarya birrea</i>	Tree	bd, fl, fr, lf, se, sa	1.186	17.54
Papaya*	<i>Carica papaya</i>	Shrub	fr	0.008	0.11
Poison-grub corkwood	<i>Commiphora africana</i>	Shrub	fr	0.011	0.16
Purple-pod clusterleaf	<i>Terminalia prunioides</i>	Shrub	fl, fr, lf, se	0.011	0.17
Red bushwillo	<i>Combretum apiculatum</i>	Tree	br, bd, fr, lf, se	0.018	0.27
Rough-leaved corkwood	<i>Commiphora edulis</i>	Shrub	bd, fr, lf	0.008	0.11
Sandpaper raisin	<i>Grewia flavescens</i>	Shrub	bd, se	0.168	2.48
Shepherd's tree	<i>Boscia albitrunca</i>	Tree	fl, fr, se	0.411	6.08

## Ch. 3- Activity, diet and ranging patterns

Sicklebush	<i>Dichrostachys cinerea</i>	Shrub	br, lf, se	0.019	0.28
Small clusterleaf	<i>Terminalia randii</i>	Shrub	se	0.000	0.01
Sweet thorn	<i>Acacia karroo</i>	Shrub	lf	0.004	0.06
Velvet raisin	<i>Grewia flava</i>	Shrub	br, fl, fr, lf, se	0.086	1.27
Velvet-leaved corkwood	<i>Commiphora mollis</i>	Tree	bd, fr, lf, se	0.028	0.42
White raisin	<i>Grewia bicolor</i>	Shrub	bd, lf, se	0.069	1.02
Worm-bark false-thorn	<i>Albizia anthelmintica</i>	Shrub	lf	0.007	0.10
Zig-zag clusterleaf	<i>Terminalia stuhlmannii</i>	Tree	bd, lf	0.003	0.05
Unidentified plants (mostly grasses)		Forbs, Herbs	br, bd, fl, fr, gr, hr, lf, pi, rt, se	1.372	20.30
<b>Prey animals</b>					
Birds			cheek	0.001	0.01
Grasshopper			inv	0.000	0.01
Locust			inv	0.004	0.06
Moth			inv	0.003	0.04
Others			inv coc, inv lar	0.006	0.09
<i>Subtotal</i>				3.736	55.26
<b>Food items in the Alldays dump</b>					
Animal derived foods				0.009	0.13
Biscuit or other dry foods				0.139	2.06
Bread				0.380	5.61
Chips				0.023	0.33
Cooked food				0.295	4.36
Juice or any soft drinks				0.056	0.83
Leftover fruits				0.691	10.23
Leftover vegetables				0.484	7.15

Milk or milk product	0.210	3.11
Sauces	0.071	1.04
Unidentified	0.667	8.82
<i>Subtotal</i>	3.024	44.74
<b>Total</b>	<b>6.760</b>	<b>100.00</b>

### 3.3.3 Dump foods consumed by the Alldays Dump Group

Alldays Dump Group fed both on the natural foods available in their home ranges and on dump foods. Dump foods constituted 45% of their annual diet based on the feeding time (Table 3.4). Among the dump food items, leftover fruits and vegetables constituted 39%, followed by bread (13%), cooked food (10%), milk or milk products (7%) and others (Table 3.4). Various dump food items were consumed all year. Feeding rate of all dump items went up in January and declined until March, rising again from June to September, Figure 3.5).

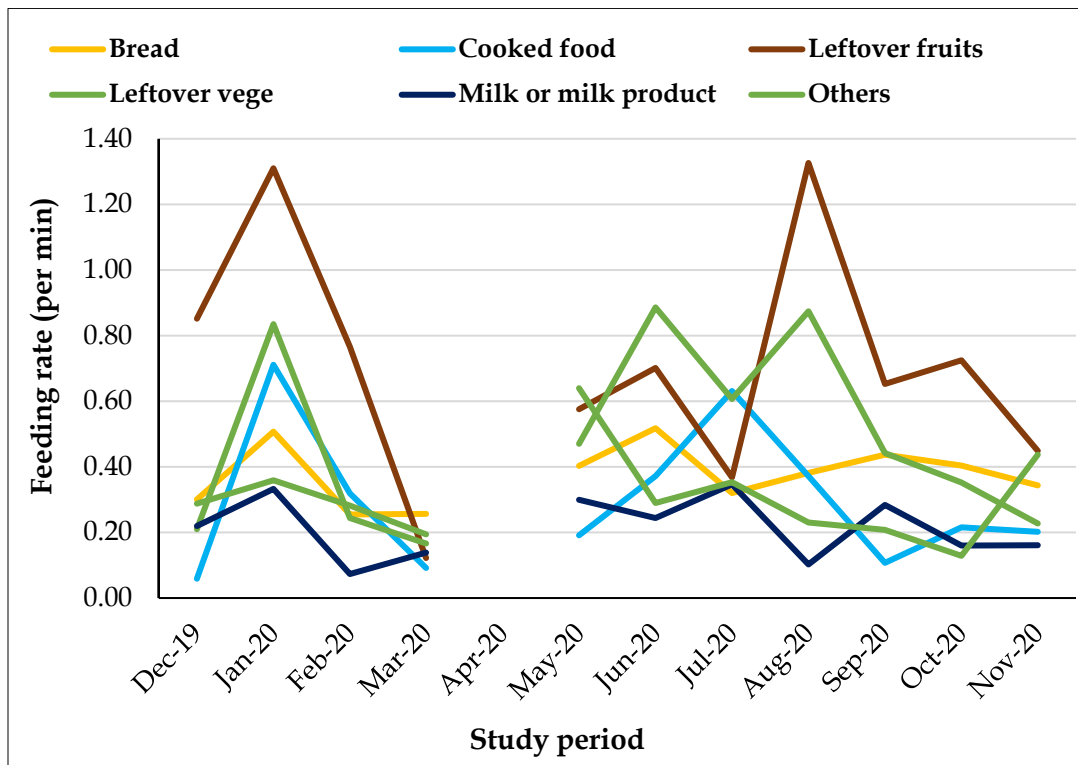


Figure 3. 5. Monthly variation in the feeding rate of different dump food items. Top five consumed items are presented here, other items are presented in the 'others' category.

Shannon-Wiener Diversity Index (SWDI) showed that there was substantial variation in the diversity of natural foods consumption across the study period. Dietary diversity of natural foods was higher in summer months compared to winter (Figure 3.6). In contrast, there was no variation in dietary diversity of dump foods, although greater diversity observed in dump foods than natural foods throughout the study period.

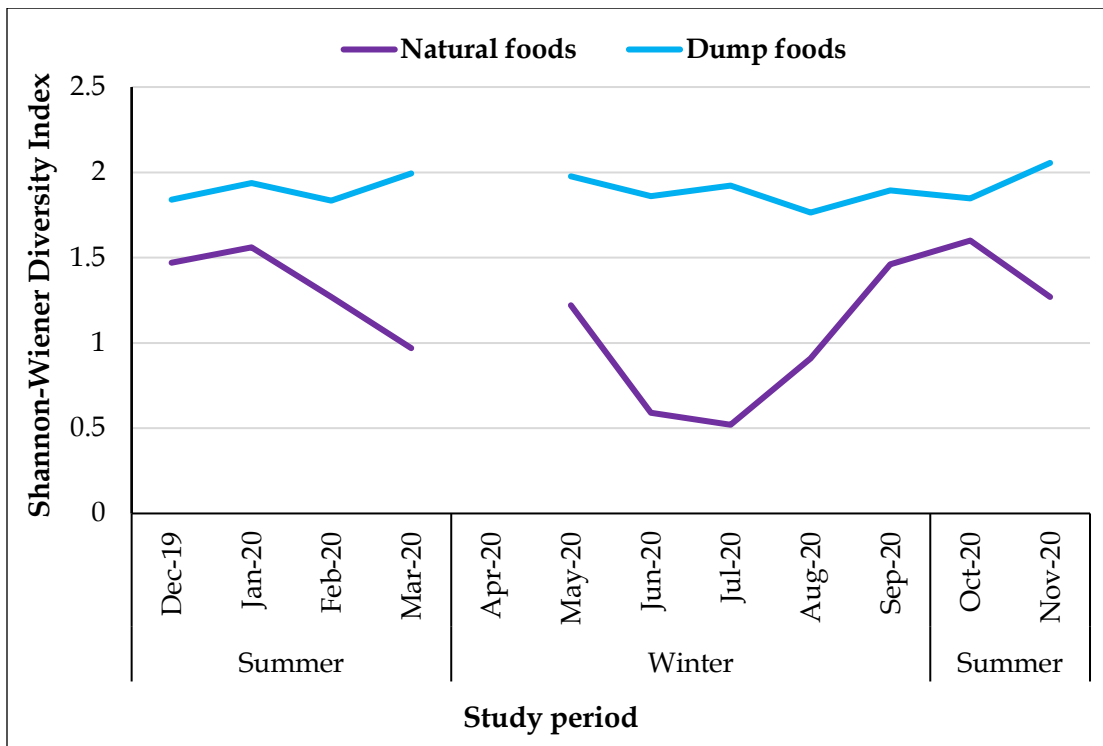


Figure 3. 6. Monthly variations in dietary diversity in natural and dump foods.

### 3.3.4 Seasonal and age-sex differences in diet composition

Alldays Dump Group’s diet showed significant seasonal differences in most of the natural food items (Table 3.5). Leaves, fruits, grasses were ingested more in summer than winter, while seeds and bark were eaten more in winter than summer. Of the dump foods only consumption of cooked foods, leftover vegetables and milk products differed between seasons (Table 3.5).

Table 3. 5. Diet composition of the Alldays Dump Group across seasons. IQR= interquartile range; statistically significant p-values appear in bold text.

Diet composition	Feeding rate per minute				Wilcoxon rank sum test	
	Summer		Winter		W	p
Natural foods	Median	IQR	Median	IQR		
Leaves	0.32	0.63	0.00	0.11	2969	<b>&lt;0.001</b>
Fruits	1.34	2.58	0.00	0.00	3277	<b>&lt;0.001</b>
Seeds	0.44	1.07	1.27	2.00	1218	<b>0.001</b>
Grasses	0.44	0.74	0.04	0.18	2976	<b>&lt;0.001</b>
Flowers	0.00	0.00	0.00	0.00	1942	0.364
Barks	0.00	0.00	0.00	0.00	1593	<b>0.042</b>
Buds	0.00	0.00	0.00	0.00	2029	0.071
Others	0.02	0.13	0.05	0.16	1646.5	0.335
<b>Dump foods</b>						
Animal derived foods	0.00	0.00	0.00	0.00	1789.5	0.512
Biscuit or dry foods	0.00	0.18	0.00	0.12	1949	0.461
Bread	0.13	0.41	0.15	0.41	1648.5	0.352
Chips	0.00	0.00	0.00	0.00	1698	0.255
Cooked foods	0.00	0.29	0.17	0.59	1422	<b>0.028</b>
Juice or soft drinks	0.00	0.02	0.00	0.08	1538	0.078
Leftover fruits	0.16	0.85	0.25	0.89	1535.5	0.130
Leftover vegetables	0.14	0.48	0.47	0.81	1184	<b>&lt;0.001</b>
Milk or milk product	0.06	0.23	0.17	0.37	1410.5	<b>0.028</b>
Sauces	0.00	0.08	0.00	0.10	1607.5	0.195
Unidentified	0.22	0.53	0.76	0.92	936	<b>&lt;0.001</b>

In winter, there were significant differences between natural and dump food consumption rates across all age-sex classes except adolescent females, while in summer there were no significant differences in consumption of different food types across all age and sex classes (Table 3.6).

Table 3. 6. Variations in feeding rate on different food types in a season across age-sex classes. Statistically significant p-values appear in bold text.

Age-sex classes	Median feeding rate per minute							
	Wilcoxon rank				Wilcoxon rank			
	Winter		sum test		Summer		sum test	
	Dump	Natural	W	p	Dump	Natural	W	p
Adult male	6.60	2.11	2061.5	<b>&lt;0.001</b>	4.36	2.49	2009.5	0.855
Adult female	7.08	2.63	2577	<b>&lt;0.001</b>	3.09	3.71	1978.5	0.742
Sub-adult male	10.95	1.06	2304	<b>&lt;0.001</b>	2.50	3.31	1913	0.965
Adolescent female	5.50	0.43	1639	0.069	0.19	6.05	1742	0.068

All baboons, regardless of age-sex class, spent more time feeding on dump foods than natural foods. Adults of both sexes and sub-adult males showed significant differences in mean feeding rate between dump and natural foods, while no differences were observed in adolescent females (Table 3.7).

Table 3. 7. Differences in feeding rate between food types across age-sex classes. IQR= interquartile range; statistically significant p-values appear in bold text.

Age-sex class	Feeding rate per minute				Wilcoxon rank sum test	
	Dump foods		Natural foods		W	p
	Median	IQR	Median	IQR		
Adult male	4.97	7.59	2.29	5.54	8220.5	<b>0.016</b>
Adult female	5.43	6.12	2.87	4.69	9203.5	<b>&lt;0.001</b>
Sub-adult male	6.90	14.40	2.21	7.49	8476	<b>0.003</b>
Adolescent female	0.38	13.63	4.89	8.91	931	0.311

### 3.3.5 Factors determining daily time spent in the dump

Alldays Dump Group regularly visited the dump to forage and did not visit on only five out of 123 follow days. Average daily time spent in the dump was 180 minutes and ranged from 17 to 381 minutes per day. The baboons spent significantly more time in the dump when the number of recently dumped bags was higher and dump foods were more available compared to fewer dumped bags and less dump foods. Daylength was also significant predictor of daily time spent in the dump, with more time in the dump when daylength was shorter (Table 3.8, Figure 3.7A, B, C). Natural fruits availability and daily dump food availability did not have a significant effect on the time spent in the dump (Table 3.8).

Table 3. 8. GLMM for the daily time spent in the dump (n= 3810). Statistically significant p-values appear in bold text.

Predictor variables	Estimate	SE	t value	p value
Intercept	760.940	163.673	4.649	<b>&lt;0.001</b>
Number of recently dumped bags	0.150	0.014	10.507	<b>&lt;0.001</b>
Dump food availability per block	6.096	2.692	2.265	<b>0.036</b>
Availability dump foods per day	-1.070	0.746	-1.434	0.170
Monthly fruit availability index	0.025	0.029	0.876	0.386
Daylength	-0.912	0.242	-3.758	<b>&lt;0.001</b>



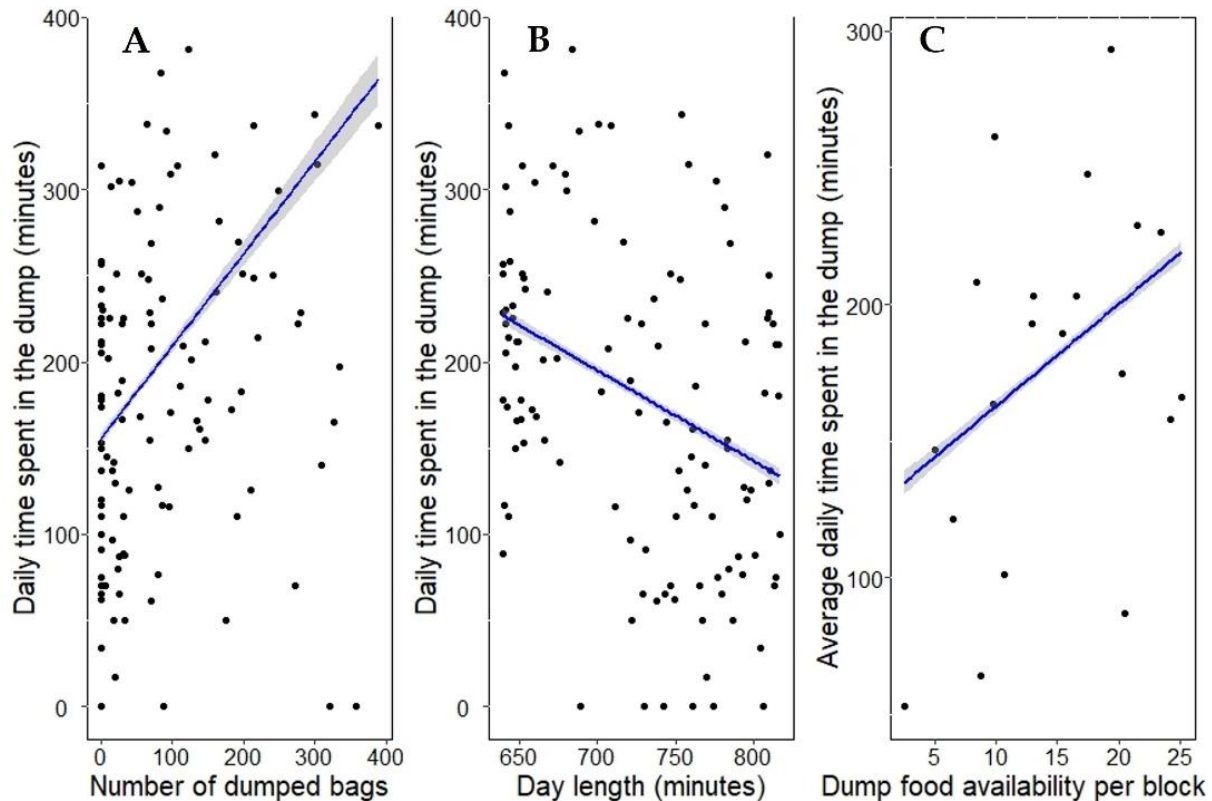


Figure 3. 7. Time spent in the dump as a function of the total number of dumped bags that day (A), daylength (B) and dump food availability per 15-day blocks (C). Blue lines indicate the direction of relationships defined by the linear model and the shaded area represents upper and lower limits at 95% confidence interval.

### 3.3.6 Ranging behaviours

Alldays Dump Group's total home range and core area over the course of the study were 2.95 km<sup>2</sup> and 0.24 km<sup>2</sup> (n= 2676 GPS locations), respectively. Two areas, corresponding to the dump and the water tower- sleeping site were very heavily utilized compared to the rest of the home range (Figure 3.8).

Alldays Dump Group's home range area in summer was 3.89 km<sup>2</sup> (n= 1429 GPS locations) and in winter 1.63 km<sup>2</sup> (n= 1247 GPS locations). The home range area varied significantly between summer and winter (Wilcoxon rank sum test:  $W= 30$ ,  $p= 0.004$ ). Similarly, the core area in summer was 0.38 km<sup>2</sup> and in winter 0.18 km<sup>2</sup> (n= 1429, 1247, respectively), with this difference also significant ( $W= 29.5$ ,  $p= 0.010$ ; Figure 3.9).

Daily travel distances ranged from 1.89 to 7.4 km with a mean ( $\pm$  sd) daily travel distance of  $3.4 \pm 1.28$  km ( $n= 108$  days). The daily travel length varied significantly between summer ( $3.85 \pm 1.39$  km,  $n= 53$  days) and winter ( $3.04 \pm 1.04$  km,  $n= 55$  days; Wilcoxon rank sum test:  $W= 1938$ ,  $p= 0.003$ ).

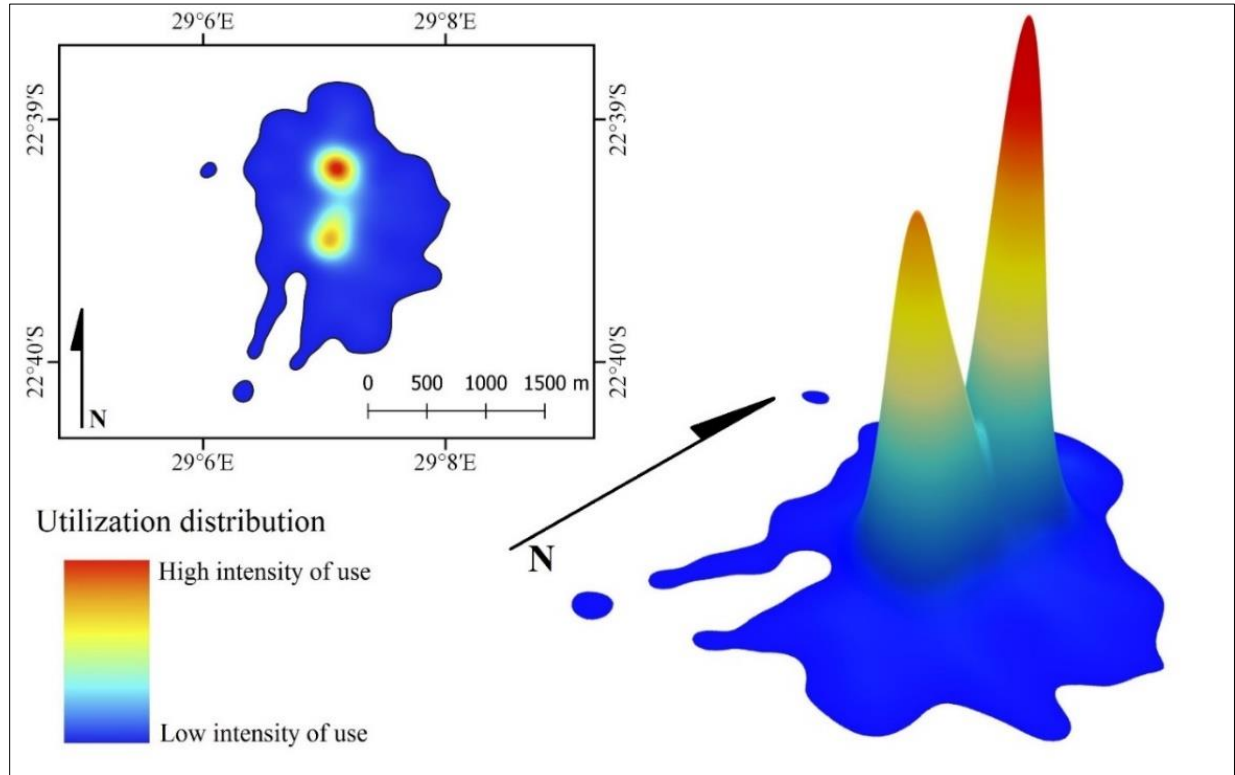


Figure 3. 8. Home range area of the Alldays Dump Group as obtained through kernel density estimation. Peaks and colour coding of the utilization distribution are proportional to the intensity of space use. The taller peak denotes the dump, while the shorter one denotes the water tower.

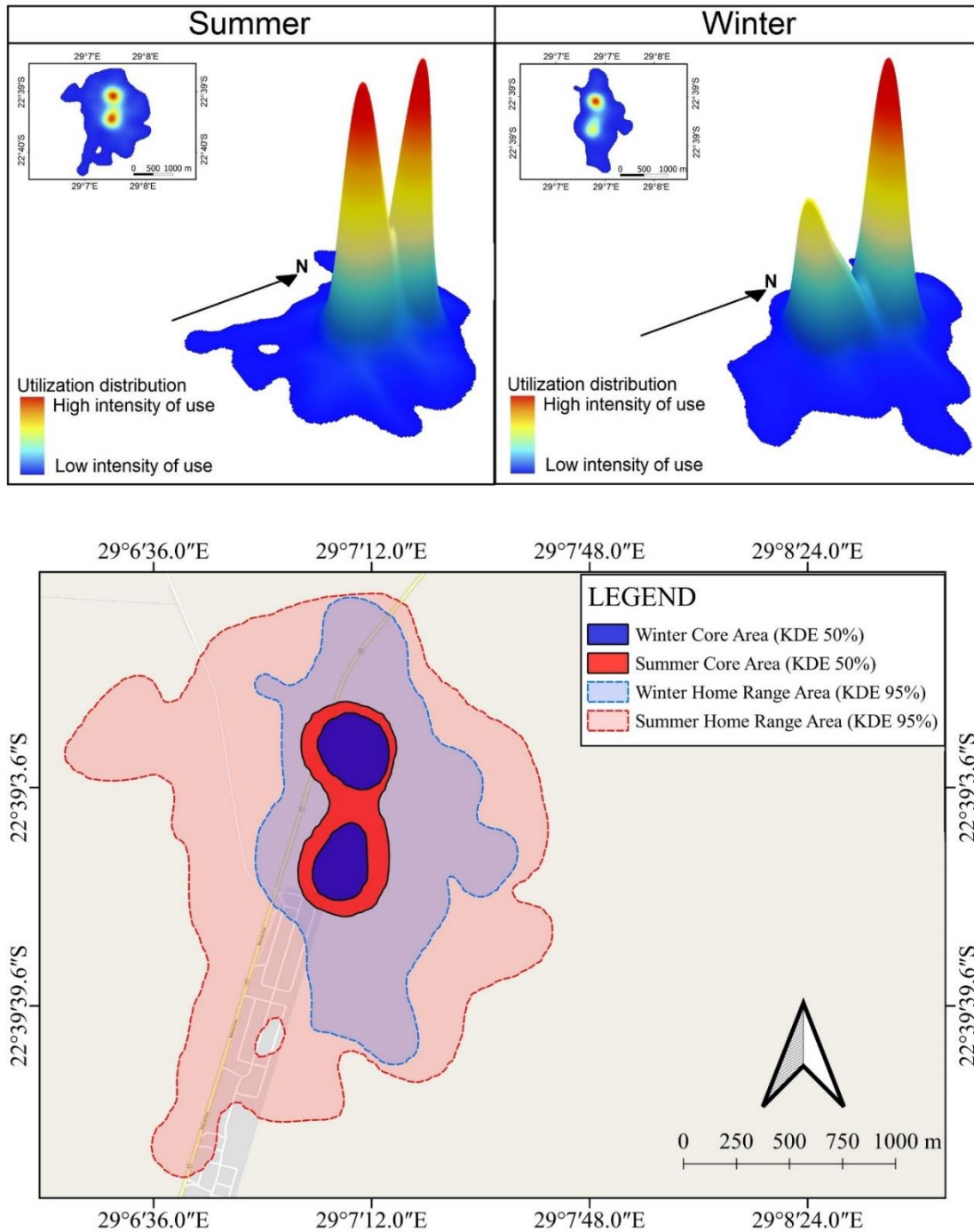


Figure 3. 9. Seasonal home range and core area of the Alldays Dump Group in three-dimensional panel (top). Peaks and colour coding of the utilization distribution are proportional to the intensity of space use. The taller peaks denote the dump, while the shorter peaks denote the water tower. Seasonal home range and core area of the Alldays Dump Group in two-dimensional panel (bottom).

Alldays Dump Group occupied a smaller home range area and had shorter daily travel length compared with naturally foraging chacma baboon groups (home range,  $t = 5.73$ ,  $df = 16$ ,  $p < 0.001$ ; daily travel length,  $t = 3.36$ ,  $df = 13$ ,  $p = 0.005$ ; Figure 3.10). They showed similar ranging measures to other anthropogenic foraging baboons (home range,  $t = 1.59$ ,  $df = 7$ ,  $p = 0.155$ , daily travel length,  $t = -0.39$ ,  $df = 6$ ,  $p = 0.706$ ; Figure 3.10, Table 3.2, 3.3).

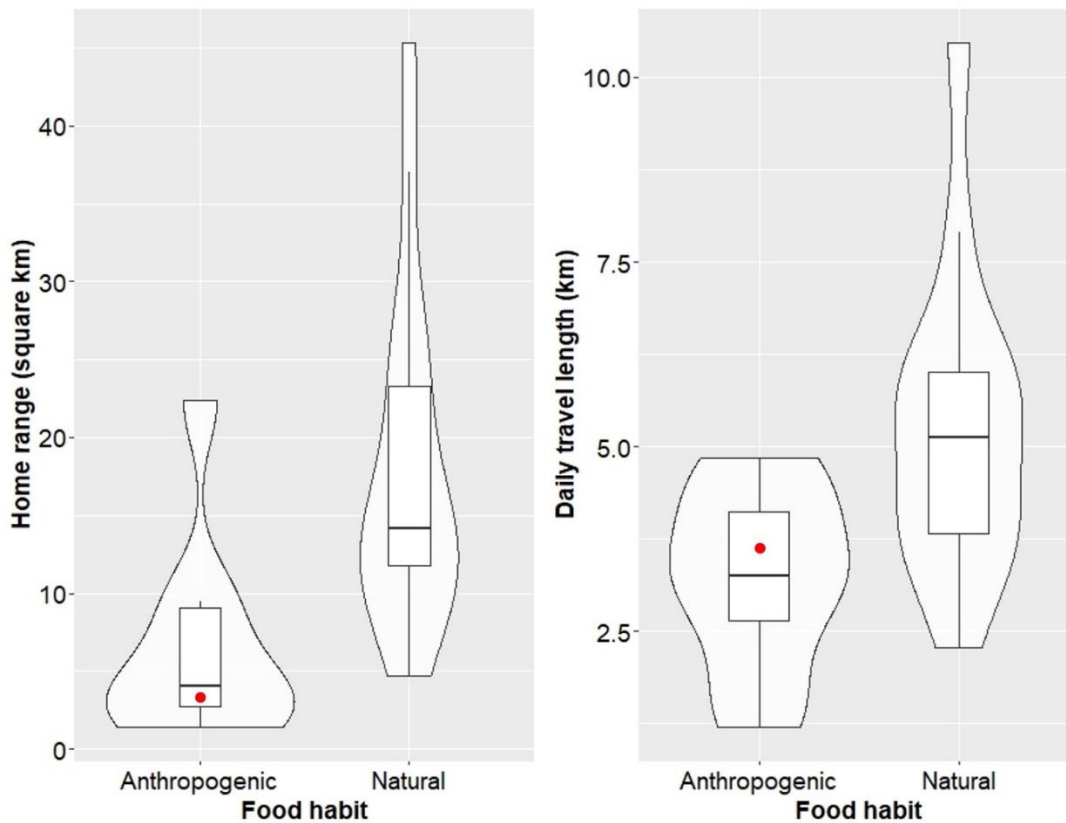


Figure 3. 10. Violin plot comparing ranging behaviours between naturally foraging chacma baboons and anthropogenic foraging baboon populations across Africa. Boxes inside the violin represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values; outliers are removed. Red dot in each anthropogenic box represents the Alldays Dump Group.

Monthly ranging and core area significantly decreased when monthly natural food availability increased (Table 3.9). Ranging area also significantly decreased with increasing temperature, whereas core area unaffected by temperature. Dump food availability and rainfall did not have any effect on baboons ranging and core area.

The model for daily travel length showed that daily dump food availability, daylength and cloud cover had a significant effect on daily travel length. Daily travel length increased when daily dump foods were available, daylength was longer and cloud cover increased. Natural food availability, rainfall, temperature, humidity did not have any effect on daily travel length (Table 3.9).

Table 3. 9. GLMM for home range, core area (n= 3810 in both cases) and daily travel length (n= 3594). Significant p-values appear in bold text.

<b>Home range area</b>	<b>Estimate</b>	<b>SE</b>	<b>t value</b>	<b>p value</b>
Intercept	160.600	45.56	3.53	<b>0.002</b>
Monthly fruit availability index	-0.048	0.001	-29.24	<b>&lt;0.001</b>
Dump food availability per block	1.700	2.848	0.60	0.558
Rainfall	-0.017	0.091	-0.19	0.848
Temperature	-0.025	0.011	-2.09	<b>0.036</b>
<b>Core area</b>				
Intercept	30.380	9.578	3.17	<b>0.005</b>
Monthly fruit availability index	-0.011	0.0001	-91.58	<b>&lt;0.001</b>
Dump food availability per block	0.377	0.599	0.629	0.537
Rainfall	-0.0006	0.007	-0.09	0.928
Temperature	-0.0009	0.0009	-1.01	0.314
<b>Daily travel length</b>				
Intercept	-4.118	2.172	-1.896	0.059
Monthly fruit availability index	-0.0002	0.0003	-0.430	0.670
Available dump foods per day	0.022	0.009	2.463	<b>0.026</b>
Rainfall	-0.026	0.020	-1.256	0.209
Temperature	-0.007	0.006	-1.092	0.275
Humidity	-0.002	0.001	-1.287	0.198
Cloud cover	0.006	0.0007	8.576	<b>&lt;0.001</b>
Daylength	0.009	0.003	2.964	<b>0.003</b>

### 3.4 Discussion

Activity patterns of the Alldays Dump Group greatly differed from both naturally foraging chacma baboons and the anthropogenic foraging baboon populations. The natural diet of the Alldays Dump Group came from at least 23 plant species, with consumption varying seasonally. The baboon group divided their feeding time almost equally between natural and dump foods (55% and 45%, respectively) and spent an average of three hours per day in the dump. Regardless of age and sex, all baboons consumed more dump foods than natural foods, with higher feeding rates in younger baboons than adults. The group's total home range area and average daily travel length were smaller and shorter, respectively, compared to naturally foraging chacma baboon groups elsewhere. These results indicate that access to dump foods had significant impacts on the study groups' activity budgets, dietary diversity and ranging patterns.

#### 3.4.1 Activity budgets

Feeding time of the Alldays Dump Group was approximately 40% and 65% of the average feeding time of naturally foraging chacma baboons and anthropogenic foraging baboon groups, respectively. This result suggests that dump foods were nutritionally richer and/or required less processing, satisfying individuals demands with less time investment. Feeding time of rhesus macaques (*M. mulatta*) groups at various sites with different degrees of provisioning was negatively related to the amount of provisioning they received (Seth and Seth 1986). This suggests that reduced feeding time by the Alldays Dump Group was likely because of the higher inclusion of human foods in their diet. Unlike natural foods, and even some human food sources e.g. crops, direct human provisioning, the dump foods were spatially clumped and predictable, allowing baboons to fulfil their nutritional demands with less foraging cost (Altmann and Muruthi 1988). Resting time was almost double that of naturally foraging chacma baboons, and similar to other anthropogenic foraging baboons. Higher resting time is influenced by the quality and distribution of food sources (Saj et al. 1999). This pattern of feeding and resting behaviour is also observed in other primate taxa that have access to human foods e.g. rhesus macaques (Malik 1986, Jaman and Huffman 2013), Barbary macaques, *M. syloanus* (Unwin and Smith 2010), and vervet monkeys (Saj et al. 1999).

Patterns for time spent moving and grooming contrasted with the predictions. The higher moving time by the Alldays Dump Group compared to both naturally and anthropogenic foraging

baboons could be explained by frequent human interference. It was observed that within the baboons' ranging area, humans frequently moved through a narrow trail as a shortcut path to collect firewood and for other purposes, and would often harass or pose a threat to the baboons. The trail was by the water tower, connecting a nearby village and the dump. In addition, local children often chased baboons, used catapults and threw stones and similar objects as a part of their play, and once it happened, the group became restless and moved on for quite a long time. Another possible reason could be they travelled more slowly than baboons elsewhere, and so took more time to cover the distances they travelled; a garbage feeding group of yellow baboons in Kenya travelled at a slower pace than natural feeding groups (Altmann and Muruthi 1988). Increased moving time reflects decreased proximity between members of the troop, which means fewer opportunities for grooming. In addition, being a smaller group size, there were possibly few benefits to additional time spent on social activity.

### **3.4.2 Dietary diversity, seasonal and age-sex differences**

Natural foods in the diet of the Alldays Dump Group were less diverse and contained fewer plant species (23 species) compared to wild feeding baboon populations: 68 species in Wildcliff, South Africa (Pebsworth 2020); 76 species in Hemel-en-Aarde Valley, South Africa (Ellwanger 2020); 76 species in Laikipia, Kenya (Barton 1989); 84 species in Comoe, Ivory Coast (Kunz and Linsenmair 2008); 180 species in Mikumi, Tanzania (Norton et al. 1987). The presence and easy access to the dump foods in their home range area is likely to account for this, which supports previous findings that dietary diversity in primates is greatly influenced by the presence of human foods (Altmann and Muruthi 1988, El Alami et al. 2012). The result is also comparable with other primate populations living in anthropogenic habitats; for example, chacma baboons in human-modified habitat in the Drakensberg, South Africa, consumed 35 plant species (Henzi et al. 2011). Garbage and crop foraging olive baboons in Budongo, Uganda, consumed plant parts from 51 plant species (Okecha and Newton-Fisher 2006). A tourist provisioned hamadryas baboon group in Al Hada, Saudi Arabia, consumed 39 plant species (Boug et al. 1994). Semi-provisioned Barbary macaques in Morocco consumed fewer plant species than the diet of wild feeding populations (21 vs 34 species, respectively; El Alami et al. 2012). The utilization of fewer plant species compared to other baboons and primate populations elsewhere suggests the higher levels of dependency on the easily accessible dump resources by the Alldays Dump Group.

Monthly dietary diversity and consumption of natural foods by the Alldays Dump Group tended to be higher in summer, whereas in winter, when there was very little available to eat in the natural habitat, food diversity was lowest suggesting that dietary diversity was most influenced by the natural food availability (Post 1982). Unexpectedly, there was low dietary diversity in February and March, towards the end of the summer season, reflecting the intensive utilization of a couple of food items, Marula fruits and grasses, which together made up 85% of the diet at that time (fruits alone constituted 67%), reflecting their higher relative abundance at that time (Post 1982, Schreier 2010, Henzi et al. 2011). Interestingly, even though natural foods were available in summer, feeding rates on natural and dump foods did not differ, suggesting that they probably followed an energy/nutrient maximizing strategy. Similar energy maximizing strategies were observed in red-ruffed lemurs, *Varecia rubra* (Vasey 2005) and green monkeys, *Cercopithecus sabaues* (Harrison 1985). It was expected that adults would eat more dump food than younger baboons (Seth and Seth 1986, Altmann and Muruthi 1988, Foerster and Monfort 2010), but, regardless of body size and social status, all baboons consumed more dump foods than natural foods. Most likely the availability and easier accessibility of dump foods which also required minimal handling and processing time, coupled with the relatively small group size, were the underlying reasons for this.

### **3.4.3 Daily time spent in the dump**

The number of recently dumped bags was an important predictor for daily time spent in the dump. Dumping of more bags means the baboons spend more time exploring new bags, and, on average, more dumped bags meant that the dump had more resources. As expected, the study group's time spent in the dump was positively correlated with dump food availability. The results are similar to those for tourist provisioning primates, where visiting and feeding at the provisioning sites is associated with the number of visitors and amount of provisioned foods (hamadryas baboons (Boug et al. 1994), long-tailed macaques (Ilham et al. 2018), Barbary macaques (O'Leary and Fa 1993)). It was also observed that the baboons usually entered the dump early and stayed a long time, especially in winter when natural foods were limited. The baboons possibly adopted a "wait and see" approach; probably daily time spent in the dump was longer at that time. Similar strategies have been observed in a semi-provisioned chacma baboons in Cape Peninsula, South Africa, where the baboons waited at a potential provisioning site during the time of low natural food availability (Van Doorn et al. 2010).



#### **3.4.4 Ranging patterns**

Alldays Dump Group ranged over a comparatively smaller area and travelled shorter distances compared to naturally foraging chacma baboon populations elsewhere. Two factors, namely available food sources and suitable sleeping sites nearby may account for this. Their favoured sleeping site, the water tower, was located within 500 metres of the dump. The group used this same sleeping site until human persecution events occurred nearly at the end of the study period (Chapter 6). Easy access to water, good protection from rain and being close to the dump made the water tower a suitable place for sleeping. Frequent use of the same sleeping site, close to the source of human foods, was also observed in other anthropogenic foraging baboons (Altmann and Muruthi 1988, Strum 2010).

Unlike a crop farm or other human properties, the dump was not closely managed, and no deterrent methods were used against baboons. So, the baboons could consume foods there until they meet their foraging demands. Consequently, the group was able to satisfy their nutritional requirements within a small ranging area, resulting in short daily travel distances and small home ranges. Similar patterns of ranging behaviours were observed in the other primates incorporating anthropogenic foods into their diet (baboons (Anderson 1981, Altmann and Muruthi 1988, Warren 2003, Higham 2006, Strum 2010, Van Doorn et al. 2010, Hoffman and O'Riain 2011, Hoffman and O'Riain 2012b); vervet monkeys (Saj et al. 1999)).

Alldays Dump Group's monthly home range and core area were determined by the natural food availability. Their home range and core area decreased when natural foods were available, as expected. When natural foods were available, the baboons likely did not need to travel so much to locate them, and as a result, they could meet their foraging demands within a smaller area. This pattern is also observed in a chacma baboon group living in a seasonal habitat (Hoffman and O'Riain 2011). Daily travel length for the study group was determined by the availability of dump foods, and travel length increased when dump foods were available. This may be because when dump foods were more available, they reached satiety quickly, which left time for travelling further to seek out diverse and preferred food items.

## **Conclusion**

Overall, the activity budget of the Alldays Dump Group was different from the typical patterns of activity observed in other anthropogenic foraging baboons. The lower feeding time by the Alldays Dump Group compared to both naturally foraging chacma and anthropogenic foraging baboon groups elsewhere strongly suggests that access to the dump foods provides benefits compared to other human food sources. This result also suggests that dump feeding is potentially a particularly extreme form of anthropogenic feeding. The utilization of fewer plant species compared to other baboon populations and the higher dietary diversity on dump foods throughout the study suggests their dependency and preference on dump foods. Visiting the dump multiple times in a day and spending longer time in the dump did not always indicate that baboons were feeding more on human foods; rather it meant limited availability of natural foods around. The availability of anthropogenic foods greatly influence ranging patterns of a primate population. The study results indicate that dumps are likely to be a much more important interface between primates and human foods that should be given much greater precedence in future work.

## Chapter 4. Effects of the dump food consumption on behavioural anxiety in chacma baboons

### 4.1 Introduction

Anxiety is a physiological state, triggered by stimuli that cause negative emotional reactions (Coleman and Pierre 2014). Anxiety may have effects on psychological well-being, physical fitness and reproduction (Reamer et al. 2010). Thus, studying anxiety has important implications for welfare and management practices in captive and free-ranging primates. The study of anxiety and anxious behaviours in primates has increased in the past several decades, but there is still much we do not know and need to explore about correlates, causes, and mechanisms that modulate anxiety. Anxiety in primates has been studied in relation to interactions with tourists (Maréchal et al. 2016), group density (Pearson et al. 2015), social correlates (Castles et al. 1999, Reamer et al. 2010, Ellis et al. 2011), and physiological stress measures (Higham et al. 2009a). Little is known about whether the availability of resources, particularly human foods, have effects on animals' anxiety levels. Understanding the factors that link food resources with primates' anxiety, and investigating how animals respond behaviourally, are therefore important.

The commonest approach for measuring anxiety levels non-invasively is quantifying animals' displacement activities (Higham et al. 2009a, Ellis et al. 2011, Maréchal et al. 2016a). Displacement activities, which are motor responses and consist mostly of movements focused on one's own body (Troisi 2002), can provide an index of animals' anxiety levels (Maestriperi et al. 1992). In primates, these displacement activities include self-directed behaviours (SDBs) such as self-touching, self-grooming, scratching, body shaking and yawning (Maestriperi et al. 1992, Troisi 2002). There is evidence that primates' SDBs are more frequent in stressful situations (Maestriperi et al. 1992). For example, when a dominant individual was in close proximity, increased rates of SDBs were observed in olive baboons (*Papio anubis*) in Gilgil, Kenya (Castles et al. 1999), and

captive long-tailed macaques (*Macaca fascicularis*) in Rome, Italy (Troisi and Schino 1987). Mothers of rhesus macaques (*M. mulata*) showed higher rates of SDBs when their infants moved away from them (Maestriperi 1993). Agonistic interactions between individuals for key resources such as food and mates can also lead to a rise in SDBs, which is reported to occur frequently during or immediately after agonistic behaviours (Maestriperi et al. 1992, Castles and Whiten 1998, Troisi 2002). SDBs can thus provide an index of animals' anxiety levels.

However, measuring SDBs only may not truly represent anxiety levels. One of the components of SDBs is used for self-cleaning and personal hygiene purposes, particularly if animals live in highly ectoparasite loaded habitats, this component may contribute larger proportion of overall SDBs (Castles et al. 1999). Vigilance is also used to indicate anxiety levels in primates (Coleman and Pierre 2014). The duration of vigilance increased in wild chimpanzees (*Pan troglodytes*) when there was potential for receiving threats from conspecifics (Kutsukake 2007), while mothers of rhesus macaques increased vigilance when there was a chance of harassment of their infants by other group members (Maestriperi 1993). Combining measures of cause (e.g. aggression) and effects (e.g. SDBs and vigilance) could be an effective integrated approach for assessing overall anxiety levels.

Little is known about whether human food consumption induces or reduces primates' anxiety levels. The Alldays Dump Group of chacma baboons depended on dump foods, spending a considerable amount of time at the Alldays garbage dump for foraging (Chapter 3). Dump foods tend to be energy rich, easily digestible, spatiotemporally predictable and sometimes readily available in greater amounts than natural foods (Muruthi et al. 1991, Saj et al. 1999, Ilham et al. 2018). These qualities of dump foods might reduce baboons' anxiety levels. The benefits of getting high quality foods may also mask other social and ecological factors that could influence baboons' anxiety such as competition with other groups at the dump. Nevertheless, these factors may be important in determining anxiety levels in the baboons. Here, I examine the relationship between dump-related and ecological variables known or suspected to affect anxiety in primates to determine their impact on the garbage-foraging baboons:

**Habitat** may be an important factor determining anxiety levels due its impact on food resource abundance and distribution. Dump foods at Alldays were clumped in distribution and present all year, while the abundance and distribution of natural foods fluctuated seasonally (Chapter 3).

Primates with access to high quality, concentrated and predictable food resources show increased group densities (Saj et al. 1999, Hoffman and O’Riain 2012b) that can increase aggressive interactions (Judge and de Waal 1993) and intragroup feeding competition which might elevate anxiety levels. Primates also increase vigilance when they have clumped or temporally predictable foods resources (Unwin and Smith 2010).

*Feeding time and food availability.* Feeding time among wild animals commonly varies seasonally, decreasing in months when foods are available (Masi et al. 2009). The Alldays Dump Group foraged at the Alldays dump on a daily basis, so, the availability of dump foods may be the main predictor of their anxiety, increasing when dump foods decrease. Number of dumped bags was the key factor for availability of dump foods (Chapter 3). The high number of dumped bags possibly benefits the baboons through supplying food, although there may be a cost associated with accessing it. It is also evident that the availability of concentrated food resources causes social tension among the group members (Altmann and Muruthi 1988, Jaman and Huffman 2013). Concomitantly, vigilance also increases to monitor conspecifics (Unwin and Smith 2010). In addition, high numbers of dumped bags do not always reflect high levels of available dump food, but rather it may encourage baboons to stay for a longer time to explore all bags.

*Individuals’ dominance rank.* High ranking dominant baboons enjoy priority access to high quality foods (Kaplan et al. 2011), monopolize food patches and threaten low ranking baboons (Altmann and Muruthi 1988) when the foods are concentrated and predictable.

*External stimuli* such as proximity to humans and other predators might be stressful particularly because they are unpredictable and uncontrollable (Crockford et al. 2008, McLennan et al. 2019). Similarly, proximity to other groups might influence social instability and physiological stress levels through immigration and emigration of dominant individuals between groups (Crockford et al. 2008). Intergroup feeding competition might also increase when two groups use the same food resources. Exposure to these social and anthropogenic stressors might increase anxiety levels in the baboons.

*Nearest neighbours.* Proximity to another individual may act as a social stressor because it increases the likelihood of aggression (Judge and de Waal 1993, Crockford et al. 2008). Wild

chimpanzees in Mahale, Tanzania, increased the duration of vigilance when the number of nearest neighbours increased (Kutsukake 2007).

From the above context, I have developed a series of hypotheses and predictions to test (Table 4.1):

Table 4. 1. Hypotheses and predictions for this chapter

Hypothesis	Predictions
1. Baboons' anxiety levels will vary based on the quality and distribution of food resources.	a) Baboons will show higher rates of SDBs, aggression and vigilance when they are in the dump compared to the natural habitat due to the clumped, high value resources in the dump.
2. Availability of dump resources will affect anxiety levels of the baboons due to feeding competition.	a) Overall rates of SDBs, aggression and vigilance will increase with increasing feeding time in the dump; b) When dump foods are more available, baboons will exhibit lower levels of SDBs, and higher levels of aggression and vigilance.
3. Individuals' dominance status affects anxiety levels because this affects access to the resources.	a) Low ranking baboons will have higher rates of SDBs, aggression and vigilance than high ranking baboons.
4. The presence of external stimuli or stressors will induce anxiety in the baboons.	a) Baboons will show higher rates of SDBs, aggression and vigilance when they encounter social and anthropogenic stressors.
5. Near neighbours influence baboons' anxiety levels, because of the increased likelihood of agonistic interactions when near neighbours are present.	a) Rates of SDBs and vigilance will increase with increasing numbers of near individuals.

## 4.2 Methods

### 4.2.1 Data collection

For a description of the general data collection methods see Chapter 2.

### 4.2.2 Definitions of variables and data preparation

Scratching and self-grooming are the dominant SDBs, though their mode of actions and purposes are different. The definitions of each category are described in the behavioural ethogram in Chapter 2 (Table 2.4). In this chapter, I use only scratching and self-grooming to represent SDBs; these together constituted nearly 94% of all SDBs. As these behaviours are functionally different, I analyse them separately as response variables.

Aggressive interactions include attacking, fighting, chasing (including vocal chasing), lunging and displacing another individual of the group or other group or any other animals. The definitions of each category are described in the behavioural ethogram (Chapter 2, Table 2.4).

I categorised vigilance into routine and induced following the definitions described by Blanchard & Fritz (2007). Routine vigilance concerns an animal's visual scanning and monitoring of other individuals and the surrounding environment during normal activities when no threatening stimuli are present. In contrast, induced vigilance is the active response to a stimulus. I analyse induced and routine vigilance separately.

*Rates of scratching, self-grooming, aggression, and vigilance* were calculated for each focal sample by dividing the total time (seconds) spent on an activity by the total observation time (minutes), yielding a rate in seconds per minute.

*Habitat* was categorised as dump and natural. The dump is fenced with a barbed metal fence line (Chapter 2, Figure 2.3). Activities performed inside the fence line were recorded as dump habitat and outside of the fence line as natural habitat.

*Feeding rate* was the unit for analysing feeding behaviour of the baboon group. Feeding rate per minute was calculated against each focal samples through dividing total feeding time (seconds) by the total observation time (minutes). Monthly feeding rate was calculated by averaging across the samples in that month (Figure 4.1).

*Fruit availability index (FAI)* was the measure of abundance of natural foods, calculated monthly based on the percentage of the crown area covered by fruits (details in Chapter 3, section 3.2.3).

*Mean number of dumped bags per day* was calculated in every dump food assessment block through the total number of dumped bags divided by the number of days of data in that block (details in Chapter 3, section 3.2.4).

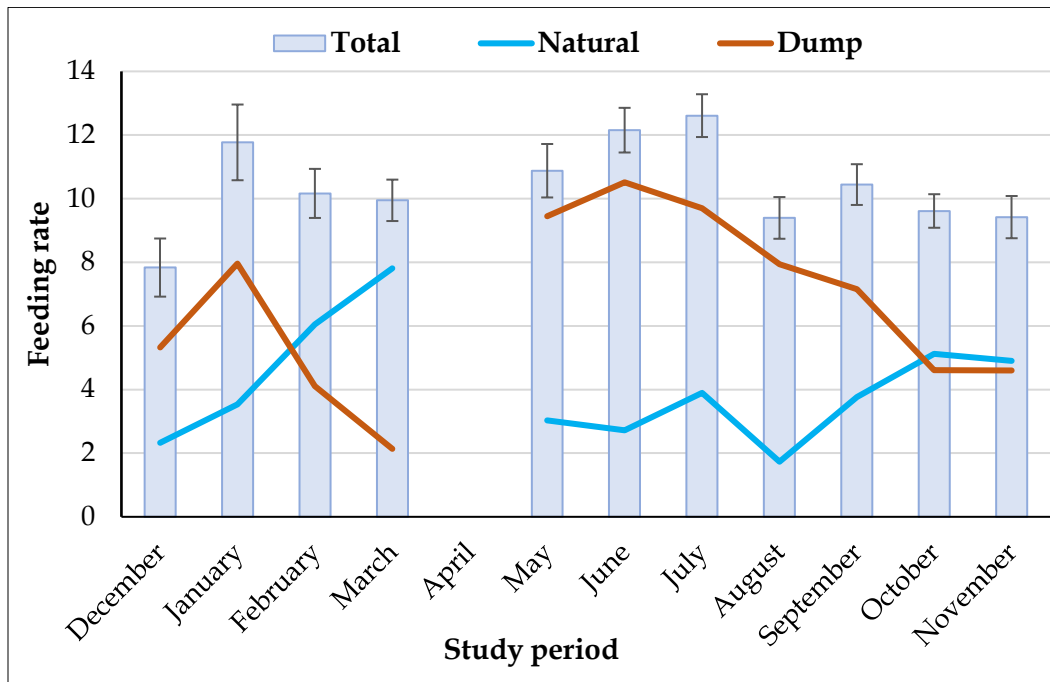


Figure 4. 1. Mean monthly feeding rate per minute across the study period for total feeding and dump and natural feeding separately (standard errors added only for total feeding).

*Availability of dump foods per day* was an estimate of the amount of dump foods arriving in a day, calculated through multiplying mean number of bags per day and the mean amount of foods per bag (details in Chapter 3, section 3.2.4).

*Daily time spent in the dump* (in minutes) was the duration the baboon group stayed in the dump on a follow day (details in Chapter 3, section 3.2.3).

*Individual dominance rank* was calculated through a David score (Gammell et al. 2003). Higher David's scores indicate more dominant individuals. Aggressive interactions and patterns of supplants were extracted from scan, focal and ad-libitum observations. Supplants were recorded



when one individual moved to within a metre of another individual who then moved away. The proportion of wins by individual  $a$  in their interactions with another individual  $b$  ( $P_{ab}$ ) is the number of times that  $a$  defeats  $b$  ( $a_{ab}$ ) divided by the total number of interactions between  $a$  and  $b$  ( $n_{ab}$ ), i.e.  $P_{ab} = a_{ab}/n_{ab}$ . The proportion of losses by  $a$  in interactions with  $b$ , is  $P_{ba} = 1 - P_{ab}$ . If there is no interaction between  $a$  and  $b$  in a certain month then  $n_{ab} = 0$ ,  $P_{ab} = 0$  and  $P_{ba} = 0$  (Gammell et al. 2003). Finally, David's score for each member was calculated by using the "compete" package of R with an individual's rank based on this score (Table 4.2).

Table 4. 2. David's score and individual dominance rank based on this score throughout the study period. The rank is ordered in each age-sex class.

Individual Identity	Age and sex class	David's Score	Dominance Rank
Hound	Adult male	59.2	1
Clubto	Adult male	35.8	2
Leah	Adult female	26.5	1
Eggo	Adult female	17.8	2
Ruby	Adult female	4.6	3
Soshi	Adult female	-10.2	4
Pamela	Adult female	-18.9	5
Zane	Adult female	-29.8	6
Fiona	Adult female	-46.8	7
Jamie	Sub-adult male	30.9	1
Rosie	Adolescent female	-32.5	1
Hannah	Adolescent female	-36.5	2

*Stressors.* During the study period I identified some factors, such as presence of humans (adults and children) nearby, presence of other groups, dogs barking nearby and burning in the landfill site that could potentially cause anxiety to the baboons. I categorised the stressors into three types: social stressor (presence of other groups), anthropogenic stressor (presence of humans and/or dogs barking nearby) and event stressor (burning in the landfill site). I considered the focal animal to be experiencing a social stressor if other group members were present within a radius of

around five metres. I also noted when humans were present within five metres radius of the group or focal animal.

*Engaged behaviours* were those that require visual and physical attention at the same time. Grooming another individual, self-grooming, digging, searching substrate (e.g., leaf litter, wafting grass, rock rolling, fanning dirt), and playing were considered engaged behaviours.

*Daylength* (in minutes) is the period of time from sunrise to sunset and is a measure of when baboons could be active (Chapter 2, section 2.4.2, Figure 2.8).

*Time block.* For focal samples I divided a follow day into four equal time blocks (early morning, late morning, early afternoon and late afternoon), calculated through dividing daylength of a follow day by four (Chapter 2, Table 2.5).

*Number of near neighbours* was recorded for each behavioural observation during scan sampling. The individuals who were within three metres were considered as near neighbours of an individual.

### **4.2.3 Data analysis**

I used Generalized Linear Mixed Models (GLMMs) to assess the effects of dump and other variables on anxiety levels of the baboon group. I created broader models where I included all possible variables as predictors. I ran one model for aggression, two separate models for scratching and self-grooming, and two separate models for the two different vigilance types, induced and routine, along with a combined model for vigilance behaviour.

For the GLMMs for scratching, self-grooming and aggression, I fitted rate of scratching, self-grooming or aggression as the response variable, respectively, with feeding rate, available dump foods per day, number of dumped bags per day, daily time spent in the dump, monthly fruit availability index, dominance rank, and daylength as continuous fixed effects. Habitat, stress factors and the time block of a day were the categorical fixed effects with month and individual identity as random effects.

I included rate of vigilance as the response variable in the vigilance models, with rate of engaged behaviour as a fixed effect along with all other fixed effects used in the models for scratching,

self-grooming and aggression. Like other models, I used month and individual identity as random effects. In every model the sample size was 3810.

Co-linearity between all effects was checked using variance inflation factors, VIF (Field et al. 2012), with a cut-off criterion multicollinearity efficiency value  $>10$  for including variables inside the same model (Myers and Myers 1990). The model fitting was performed by using “lme4” and “lmer” packages of R-language and the “CAR” package was used to check the multicollinearity.

I performed Pearson correlation tests to examine whether the number of nearby neighbours is related to increase SDBs and vigilance.

All statistical analyses were completed using R (Version 4.0.4, R development core team). All tests were two tailed with a 5% level for significance ( $p < 0.05$ ).

## **4.3 Results**

The mean ( $\pm$  sd) rate of SDBs of the baboon troop was 1.92 ( $\pm 3.04$ ) seconds per minute, with aggressive interactions 0.5 ( $\pm 1.89$ ) seconds per minute, and vigilance 1.18 ( $\pm 3.86$ ) seconds per minute (Table 4.3). Aggression given was higher than received. Scratching and self-grooming were the most dominant SDBs, and baboons spent almost double the time in routine vigilance compared to induced vigilance. Adult males gave more aggression, had higher vigilance and lower SDBs than other age-sex classes (Table 4.3).

### **4.3.1 Rate of scratching**

Rate of scratching was significantly predicted by habitat, feeding rate, availability of dump foods per day and number of dumped bags per day (Table 4.4, Figure 4.2). Scratching increased when baboons were in the dump, when feeding rate decreased and when dump foods were less available. However, scratching increased with an increasing number of dumped bags. The baboons scratched significantly less when they encountered social and event stressors, and more scratching was observed in early morning. Daily time spent in the dump, natural food availability, dominance rank and daylength did not have any significant impact on scratching behaviour of the baboon group (Table 4.4).

Table 4. 3. Average rates (seconds per minute) of aggression, SDBs and vigilance of the baboon group. AM= Adult male, SAM= Sub-adult male, AF= Adult female, AdoF= Adolescent female. n= 3810 focal observations.

Age-sex class	Individual Identity	Aggression rate		SDBs rate				Vigilance rate	
		given	received	scratching	self-grooming	body shaking	yawing	induced	routine
AM	Hound	0.95	0.17	0.72	0.51	0.07	0.27	0.39	1.14
AM	Clubto	0.38	0.31	0.88	0.81	0.04	0.14	0.56	1.05
SAM	Jamie	0.41	0.13	1.12	0.84	0.04	0.13	0.37	0.80
AF	Eggo	0.22	0.09	0.93	1.04	0.02	0.03	0.48	0.51
AF	Leah	0.23	0.11	0.58	0.59	0.05	0.01	0.49	1.38
AF	Pamela	0.14	0.10	0.83	0.86	0.02	0.01	0.31	0.59
AF	Ruby	0.15	0.11	1.01	0.79	0.03	0.02	0.26	0.50
AF	Soshi	0.28	0.15	0.89	1.19	0.03	0.03	0.33	0.58
AF	Zane	0.09	0.10	0.97	1.15	0.05	0.10	0.19	0.97
AF	Fiona	0.18	0.22	0.92	1.51	0.06	0.05	0.43	0.76
AdoF	Hannah	0.23	0.53	0.87	1.14	0.03	0.00	0.25	0.36
AdoF	Rosie	0.39	1.13	0.55	0.64	0.05	0.00	0.33	0.16
<b>Overall</b>		<b>0.32</b>	<b>0.18</b>	<b>0.88</b>	<b>0.92</b>	<b>0.04</b>	<b>0.08</b>	<b>0.39</b>	<b>0.79</b>

Table 4. 4. GLMM to determine the factors explaining the rate of scratching by baboons in the Alldays Dump Group. n= 3810

Predictor variables for scratching	Estimate	SE	t value	p value
Intercept	2.569	1.033	2.486	<b>0.017</b>
Habitat <sup>1</sup> , Natural	-0.142	0.049	-2.899	<b>0.003</b>
Feeding rate	-0.010	0.001	-8.408	<b>&lt;0.001</b>
Available dump foods per day	-0.007	0.001	-5.661	<b>&lt;0.001</b>
Number of dumped bags per day	0.003	0.001	2.406	<b>0.017</b>
Daily time spent in the dump	0.00007	0.0002	0.324	0.745
Fruits availability Index	0.0003	0.0001	1.975	0.060
Dominance rank	0.005	0.015	0.362	0.724
Daylength	-0.002	0.001	-1.429	0.160
Stress factors <sup>2</sup>				
Anthropogenic	-0.159	0.177	-0.905	0.365
Event	-0.588	0.243	-2.418	<b>0.015</b>
Social	-0.153	0.050	-3.066	<b>0.002</b>
Time block of a day <sup>3</sup>				
Early morning	0.162	0.048	3.354	<b>&lt;0.001</b>
Late morning	-0.002	0.051	-0.039	0.968
Early afternoon	-0.079	0.049	-1.612	0.107

<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.

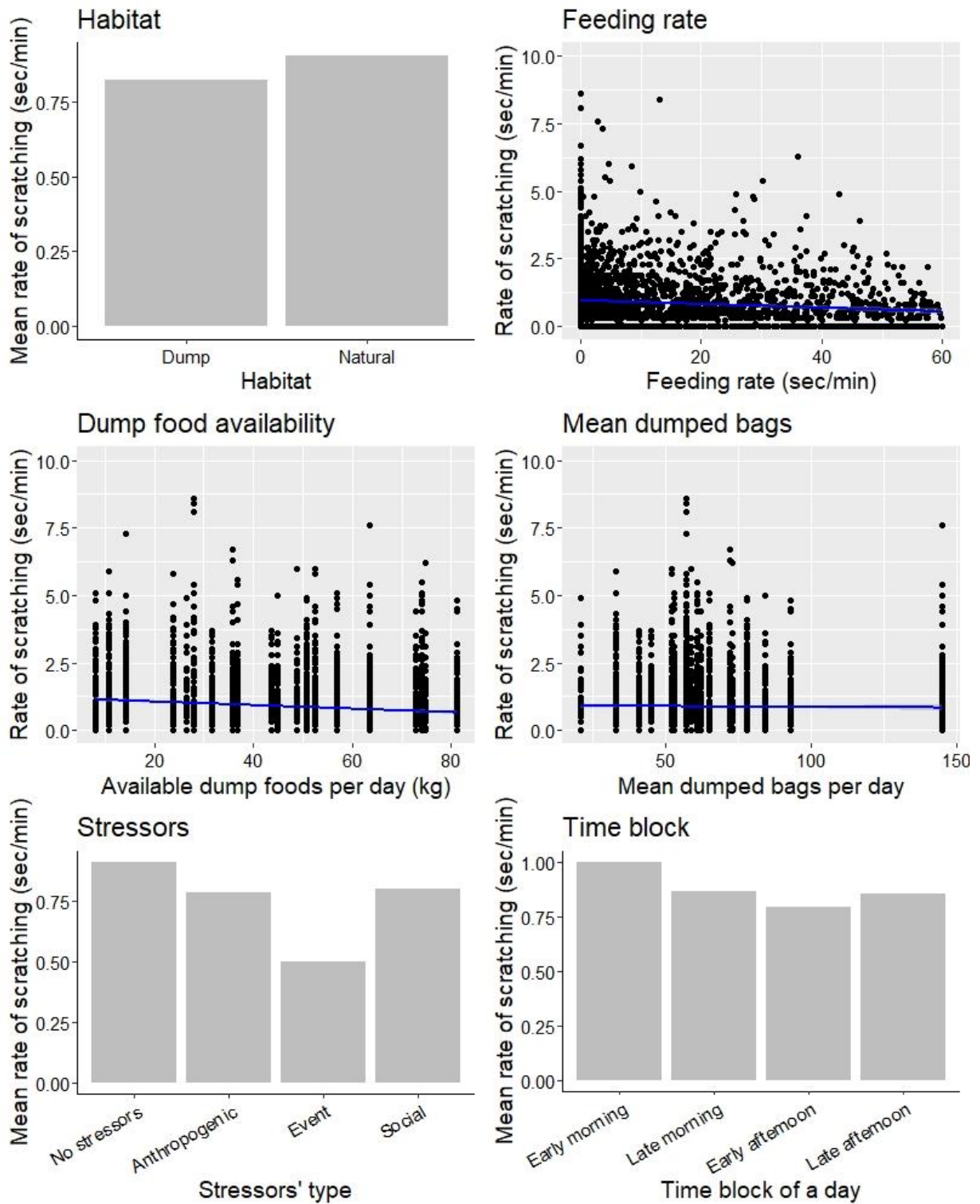


Figure 4. 2. Rate of scratching as a function of habitat, feeding rate, dump food availability, mean dumped bags, stressors and time blocks of a follow day. The blue lines in scatter plots indicate direction of relationships according to the model.

### 4.3.2 Rate of self-grooming

Rate of self-grooming was significantly predicted by feeding rate and availability of dump foods per day (Table 4.5, Figure 4.3). Self-grooming increased when feeding rate decreased and dump foods were less available. There was also more self-grooming observed early in the morning than other time blocks. Self-grooming was not predicted by habitat, stress factors, or volume of dumped bags, daily time spent in the dump, natural food availability, dominance rank or daylength (Table 4.5).

Table 4. 5. GLMM to determine the factors explaining for the rate of self-grooming by baboons in the Alldays Dump Group. n= 3810

Predictor variables for self-grooming	Estimate	SE	t value	p value
Intercept	2.405	1.735	1.386	0.182
Habitat <sup>1</sup> Natural	-0.017	0.111	-0.160	0.872
Feeding rate	-0.028	0.002	-10.321	<b>&lt;0.001</b>
Available dump foods per day	-0.008	0.002	-2.993	<b>0.003</b>
Number of dumped bags per day	0.001	0.002	0.682	0.498
Daily time spent in the dump	0.0006	0.0005	1.165	0.244
Fruits availability Index	0.0001	0.0002	0.599	0.558
Dominance rank	0.071	0.019	3.647	<b>0.004</b>
Daylength	-0.002	0.002	-0.867	0.398
Stress factors <sup>2</sup>				
Anthropogenic	-0.201	0.402	-0.501	0.616
Event	-0.610	0.553	-1.103	0.270
Social	-0.034	0.112	-0.309	0.757
Time block of a day <sup>3</sup>				
Early morning	0.251	0.110	2.284	<b>0.022</b>
Late morning	0.083	0.116	0.711	0.477
Early afternoon	-0.018	0.112	-0.166	0.868

<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.

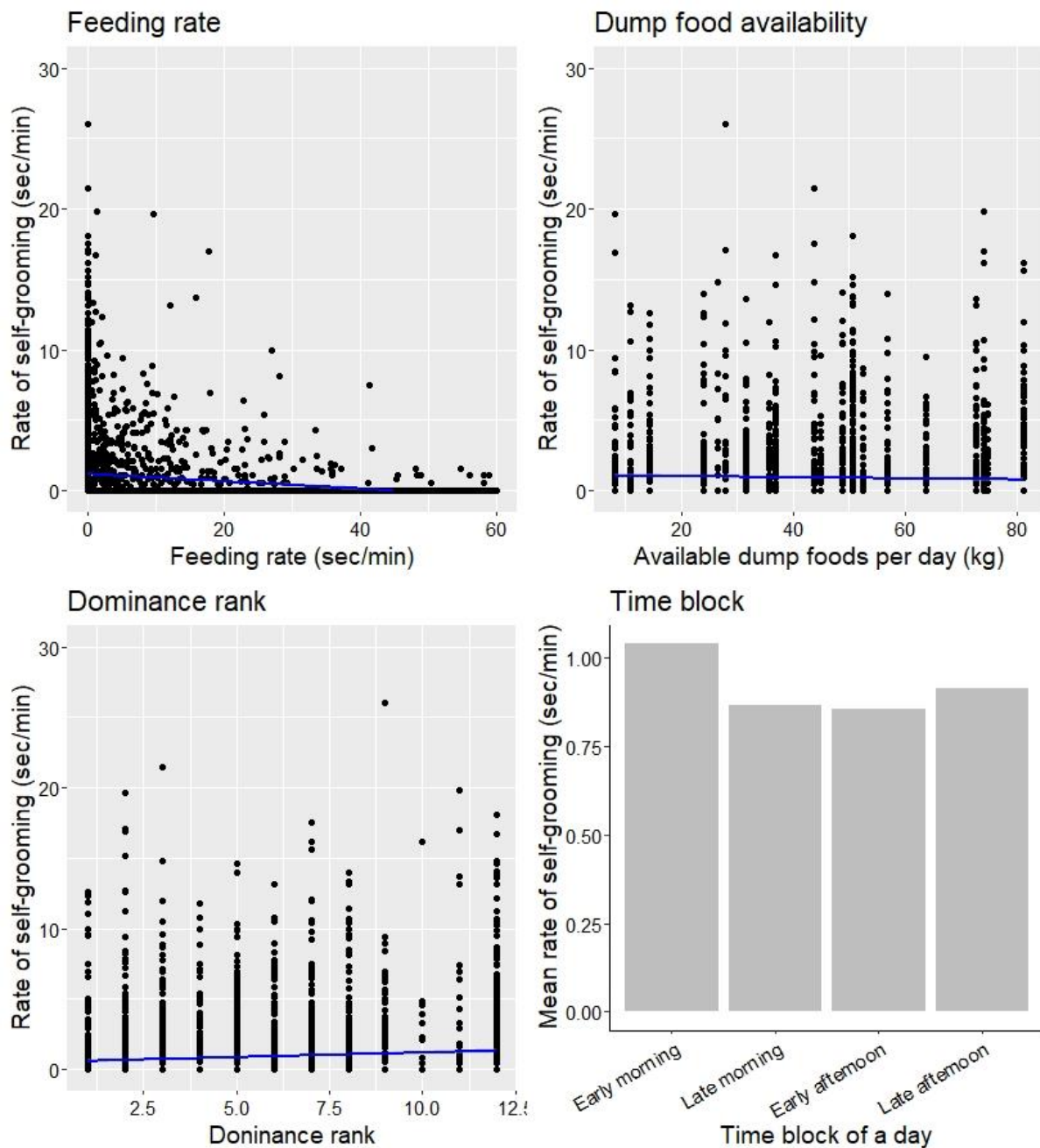


Figure 4. 3. Rate of self-grooming as a function of feeding rate, dump food availability, dominance rank and time blocks of a follow day. The blue lines in scatter plots indicate direction of relationships according to the model.

#### 4.3.3 Rate of aggression

The rate of aggression was significantly predicted by habitat, feeding rate, availability of dump foods per day and number of dumped bags per day (Table 4.6, Figure 4.4). Aggression increased when the baboons were in the dump, when feeding rate and number of dumped bags increased, but decreased when dump food availability increased. Time period of the day



also predicted aggressive interactions, with more aggression observed in the early morning than during other time period. Daily time spent in the dump, natural food availability, dominance rank, daylength and stress factors did not have any significant impact on aggression in the baboon group (Table 4.6).

Table 4. 6. GLMM to determine the factors explaining the rate of aggression by baboons in the Alldays Dump Group. n= 3810

Predictor variables for aggression	Estimate	SE	t value	p value
Intercept	-0.532	0.434	-1.225	0.245
Habitat <sup>1</sup> Natural	-0.071	0.032	-2.229	<b>0.025</b>
Feeding rate	0.002	0.0007	3.478	<b>&lt;0.001</b>
Available dump foods per day	-0.001	0.0007	-2.350	<b>0.023</b>
Number of dumped bags per day	0.001	0.0006	2.148	<b>0.041</b>
Daily time spent in the dump	0.0001	0.0001	1.179	0.238
Fruits availability Index	-0.00009	0.00005	-1.771	0.110
Dominance rank	-0.003	0.004	-0.910	0.393
Daylength	0.001	0.0006	1.583	0.143
Stress factors <sup>2</sup>				
Anthropogenic	0.090	0.115	0.782	0.434
Event	-0.112	0.158	-0.712	0.476
Social	-0.024	0.032	-0.774	0.439
Time block of a day <sup>3</sup>				
Early morning	0.098	0.031	3.116	<b>0.001</b>
Late morning	0.046	0.033	1.393	0.163
Early afternoon	0.053	0.032	1.668	0.095

<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.

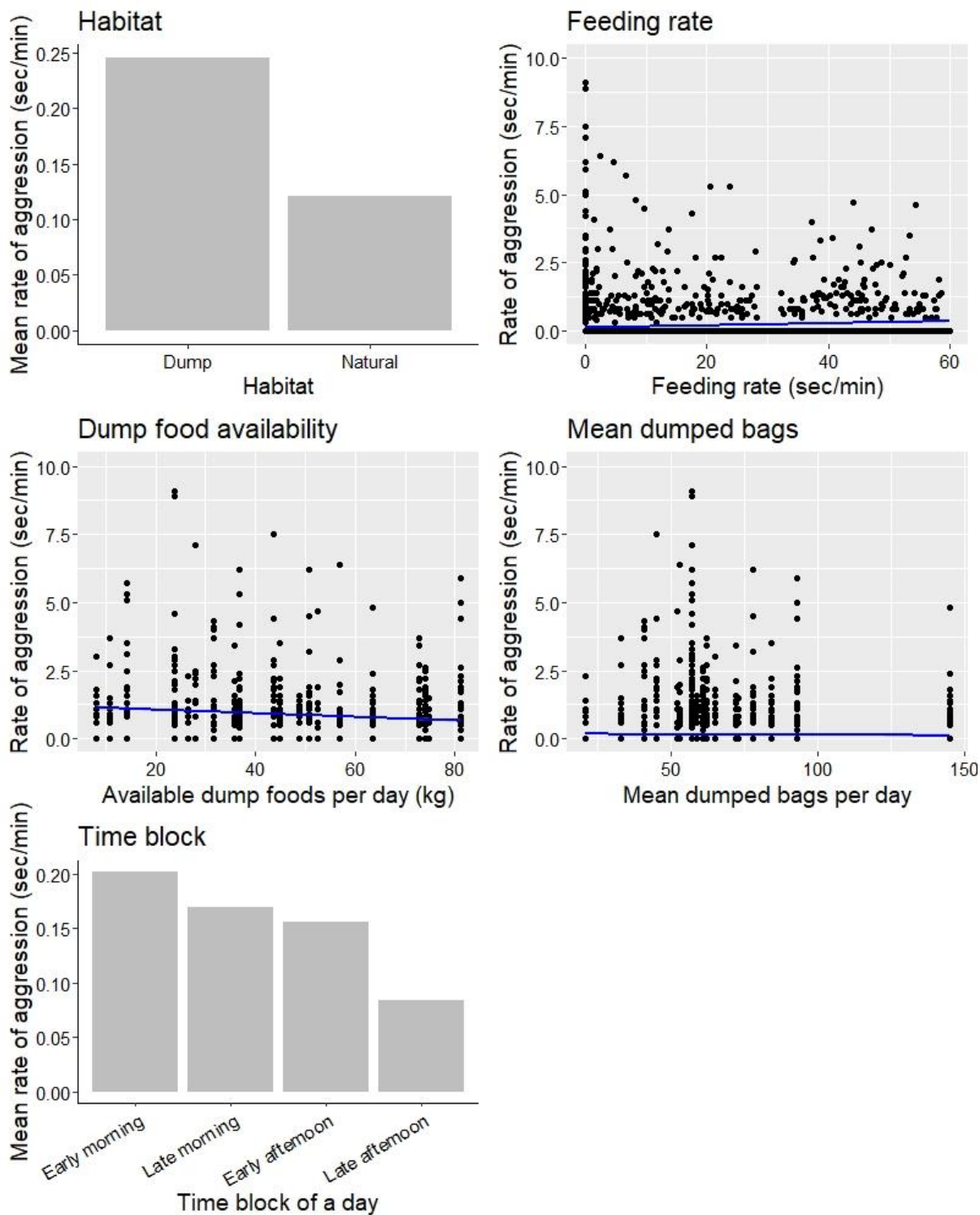


Figure 4. 4. Rate of aggression as a function of habitat, feeding rate, dump food availability, mean dumped bags and time blocks of a follow day. The blue lines in scatters plots indicate direction of relationships according to the model.

#### 4.3.4 Rate of vigilance

The rate of vigilance was significantly predicted by habitat, feeding rate, availability of dump foods per day and rate of engaged behaviour (Table 4.7, Figure 4.5). Vigilance increased when baboons were in the dump, when feeding rate increased and when dump foods were less available. Vigilance decreased when the baboons were in engaged behaviour, with more vigilance observed in the early morning than any other time period. Daily time spent in the dump, number of dumped bags, natural food availability, dominance rank, daylength and stress factors did not have any significant impact on vigilance behaviour of the baboon group (Table 4.7).

Table 4. 7. GLMM to determine the factors explaining the rate of vigilance by baboons in the Alldays Dump Group. n= 3810

Predictor variables for vigilance	Estimate	SE	t value	p value
Intercept	-1.465	3.078	-0.476	0.635
Habitat <sup>1</sup> Natural	-0.397	0.129	-3.076	<b>0.002</b>
Feeding rate	0.010	0.004	2.425	<b>0.015</b>
Available dump foods per day	-0.010	0.003	-2.634	<b>0.008</b>
Number of dumped bags per day	0.005	0.003	1.548	0.122
Daily time spent in the dump	-0.00003	0.0006	-0.018	0.985
Fruits availability Index	-0.0007	0.0004	-1.641	0.112
Dominance rank	-0.040	0.026	-1.541	0.151
Daylength	0.005	0.004	1.204	0.232
Rate of engaged behaviour	-0.021	0.003	-5.685	<b>&lt;0.001</b>
Stress factors <sup>2</sup>				
Anthropogenic	-0.497	0.465	-1.070	0.284
Event	-0.557	0.640	-0.871	0.383
Social	-0.020	0.131	-0.157	0.875
Time block of a day <sup>3</sup>				
Early morning	0.863	0.126	6.806	<b>&lt;0.001</b>
Late morning	0.179	0.134	1.337	0.181

Early afternoon	-0.030	0.129	-0.233	0.815
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<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.

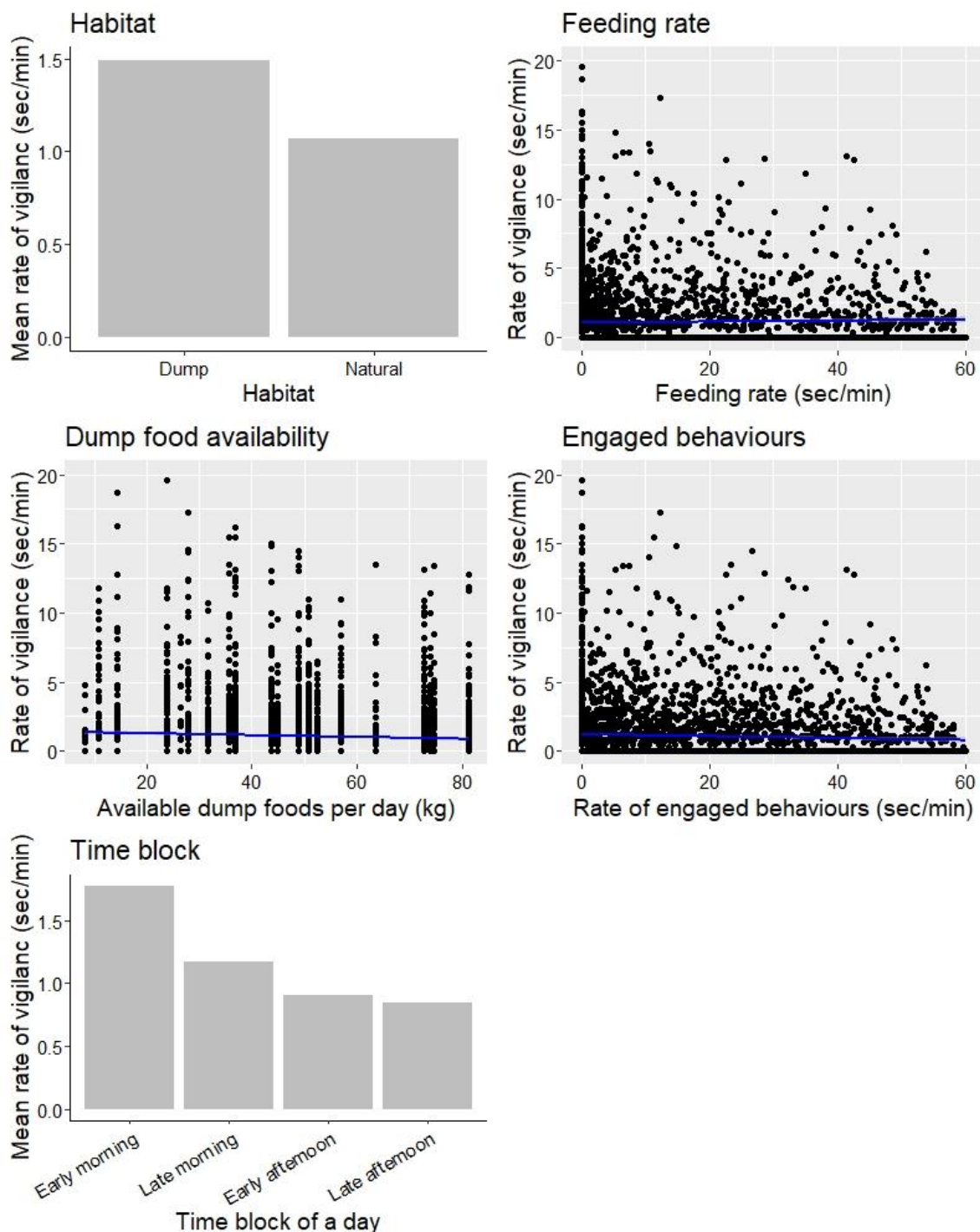


Figure 4. 5. Rate of vigilance as a function of habitat, feeding rate, dump food availability, rate of engaged behaviours and time blocks of a follow day. The blue lines in scatters plots indicate direction of relationships according to the model.

#### **4.3.5 Rate of routine vigilance**

The model for routine vigilance showed that habitat, feeding rate, availability of dump foods, volume of dumped bags and rate of engaged behaviour, and social stressors significantly affected routine vigilance (Table 4.8, Figure 4.6). Routine vigilance increased when the baboons were in the dump, when feeding rate and number of dumped bags increased, and when dump foods were less available. Routine vigilance decreased when the baboons were in engaged behaviour. The baboons showed less routine vigilance when they encountered social stressors with more vigilance observed in the early morning than at other times. Daily time spent in the dump, natural food availability, dominance rank and daylength did not have any significant impact on routine vigilance behaviour of the baboon group (Table 4.8).

#### **4.3.6 Rate of induced vigilance**

The rate of induced vigilance decreased when baboons were in engaged behaviours but increased when they encountered social stressors around (Table 4.9, Figure 4.7). Unlike routine vigilance, induced vigilance was not predicted by habitat, feeding rate, availability of dump foods, number of dumped bags and time period of a day. Daily time spent in the dump, natural food availability, dominance rank and daylength also did not affect induced vigilance (Table 4.9).

Table 4. 8. GLMM to determine the factors explaining the rate of routine vigilance by baboons in the Alldays Dump Group. n= 3810

Predictor variables for routine vigilance	Estimate	SE	t value	p value
Intercept	-2.901	2.552	-1.136	0.258
Habitat <sup>1</sup> Natural	-0.269	0.102	-2.625	<b>0.008</b>
Feeding rate	0.009	0.003	2.779	<b>0.005</b>
Available dump foods per day	-0.013	0.003	-4.427	<b>&lt;0.001</b>
Number of dumped bags per day	0.007	0.002	2.686	<b>0.007</b>
Daily time spent in the dump	-0.0002	0.0005	-0.434	0.664
Fruits availability Index	-0.0006	0.0004	-1.685	0.104
Dominance rank	-0.033	0.022	-1.523	0.157
Daylength	0.006	0.003	1.762	0.080
Rate of engaged behaviour	-0.014	0.003	-4.887	<b>&lt;0.001</b>
Stress factors <sup>2</sup>				
Anthropogenic	-0.689	0.370	-1.862	0.062
Event	-0.269	0.509	-0.528	0.597
Social	-0.219	0.105	-2.093	<b>0.036</b>
Time block of a day <sup>3</sup>				
Early morning	0.731	0.101	7.243	<b>&lt;0.001</b>
Late morning	0.143	0.107	1.342	0.179
Early afternoon	-0.119	0.103	-1.159	0.246

<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.

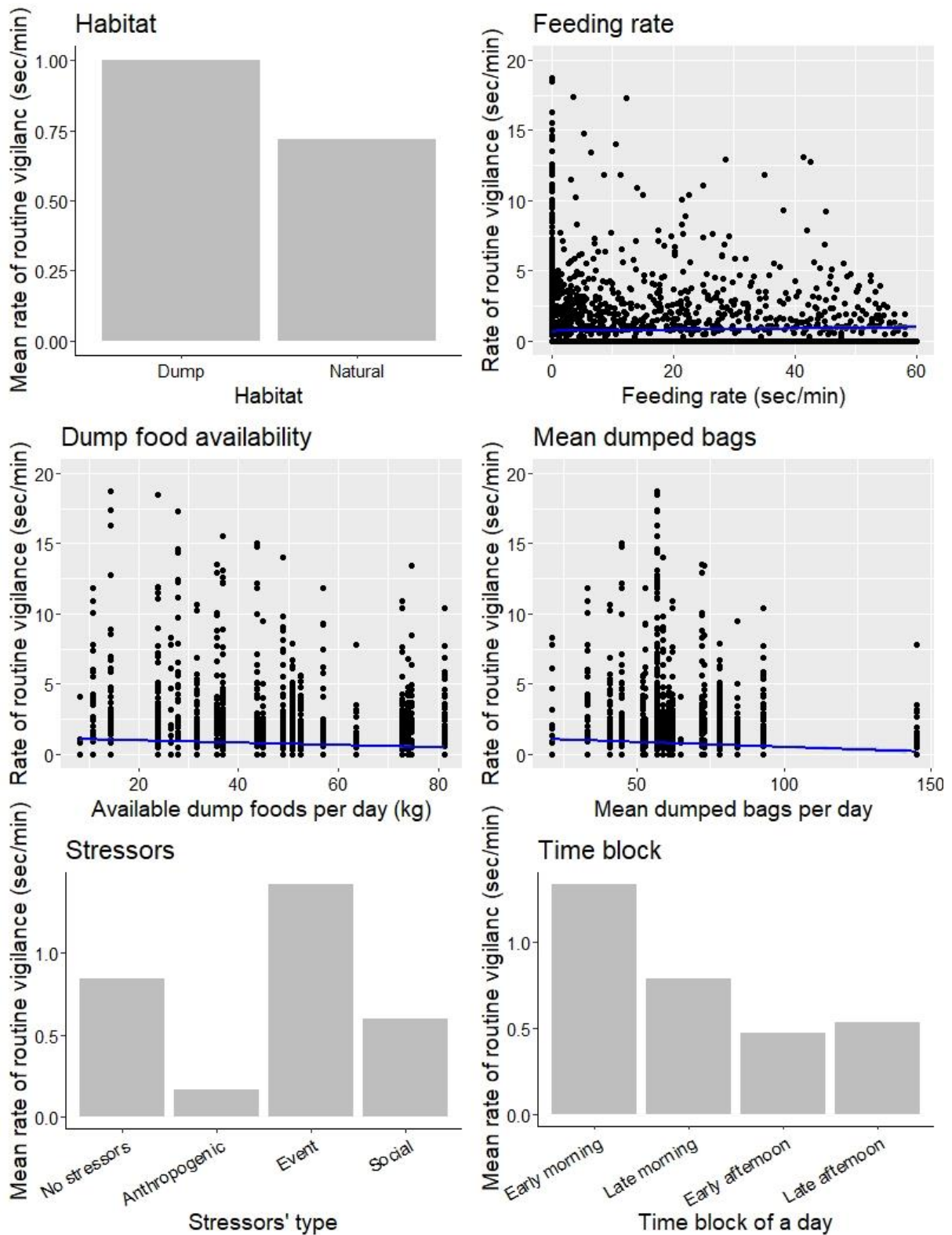


Figure 4. 6. Rate of routine vigilance as a function of habitat, feeding rate, dump food availability, mean dumped bags, stressors and time blocks of a follow day. The blue lines in scatter plots indicate direction of relationships according to the model.

Table 4. 9. GLMM to determine the factors explaining the rate of induced vigilance by baboons in the Alldays Dump Group. n= 3810

Predictor variables for induced vigilance	Estimate	SE	t value	p value
Intercept	1.252	1.172	1.068	0.305
Habitat <sup>1</sup> Natural	-0.128	0.076	-1.686	0.091
Feeding rate	0.0009	0.002	0.380	0.704
Available dump foods per day	0.001	0.001	0.910	0.367
Number of dumped bags per day	-0.001	0.001	-0.806	0.426
Daily time spent in the dump	0.0001	0.0003	0.492	0.622
Fruits availability Index	-0.0001	0.0001	-0.716	0.490
Dominance rank	-0.004	0.008	-0.524	0.610
Daylength	-0.0008	0.001	-0.501	0.625
Rate of engaged behaviour	-0.006	0.002	-3.025	<b>0.002</b>
Stress factors <sup>2</sup>				
Anthropogenic	0.214	0.274	0.783	0.433
Event	-0.242	0.377	-0.642	0.520
Social	0.190	0.076	2.478	<b>0.013</b>
Time block of a day <sup>3</sup>				
Early morning	0.133	0.075	1.781	0.074
Late morning	0.038	0.079	0.484	0.628
Early afternoon	0.084	0.076	1.103	0.270

<sup>1</sup>reference category was dump; <sup>2</sup>reference category was no stressors; <sup>3</sup>reference category was late afternoon.



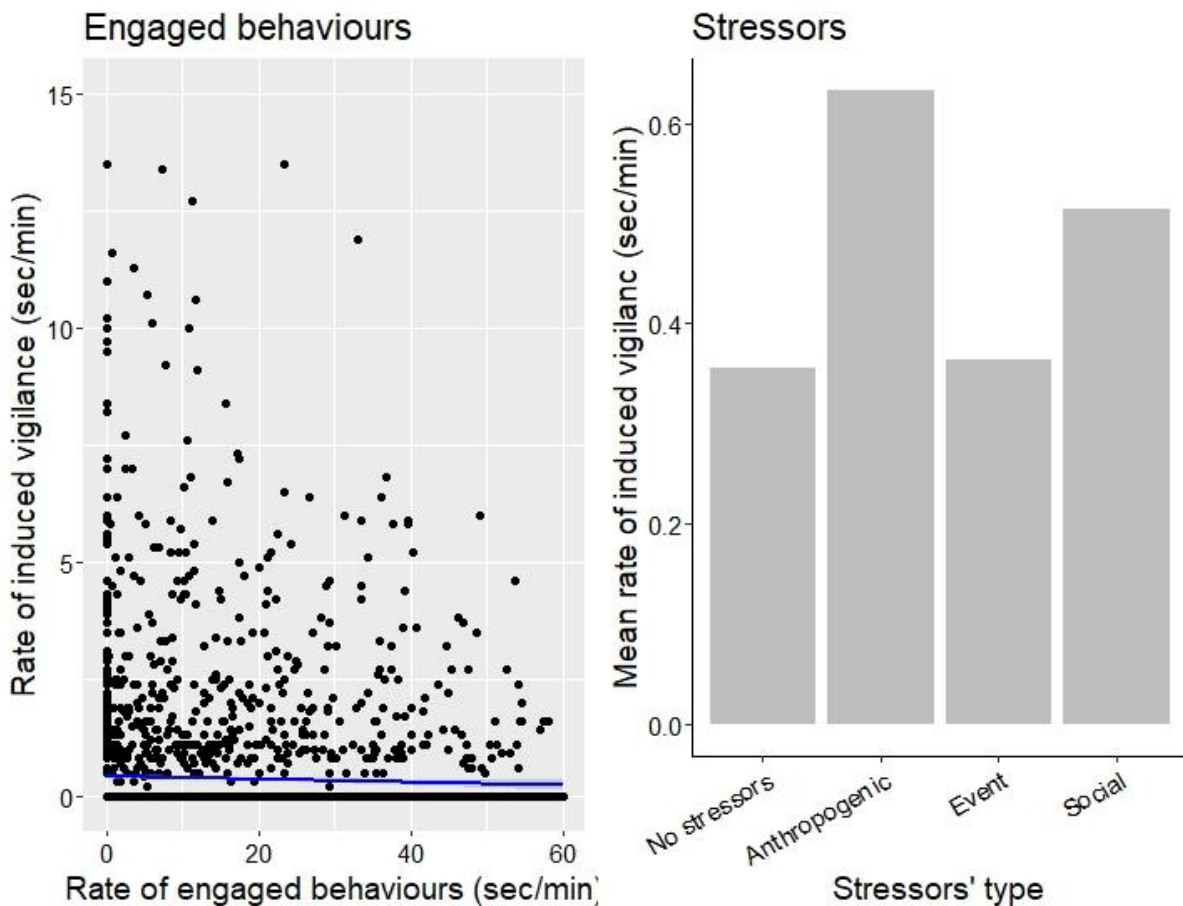


Figure 4. 7. Rate of induced vigilance as a function of engaged behaviours and stressors. The blue line in scatter plots indicate direction of relationships according to the model.

#### 4.3.7 Effects of neighbours

Out of 32000 behavioural observations collected in scan sampling, I recorded 5074 (1567 in the dump, 3507 in the natural) events of vigilance while the baboons were involved in other activities including both engaged and non-engaged behaviours. In the dump, the rate of vigilance significantly increased when individuals had more neighbours within three metres, whereas a negative relationship was observed when baboons were in natural habitat (Pearson's product-moment correlation: dump:  $r = 0.96$ ,  $t = 7.51$ ,  $df = 5$ ,  $p = <0.001$ ; natural:  $r = -0.71$ ,  $t = -2.28$ ,  $df = 5$ ,  $p = 0.071$ ; Figure 4.8). In contrast, there was a strong negative relationship found in between SDBs and number of near neighbours in both habitats (Pearson's product-moment correlation: dump:  $r = -0.89$ ,  $t = -3.38$ ,  $df = 3$ ,  $p = 0.042$ ; natural:  $r = -0.88$ ,  $t = -3.27$ ,  $df = 3$ ,  $p = 0.046$ ; Figure 4.8).

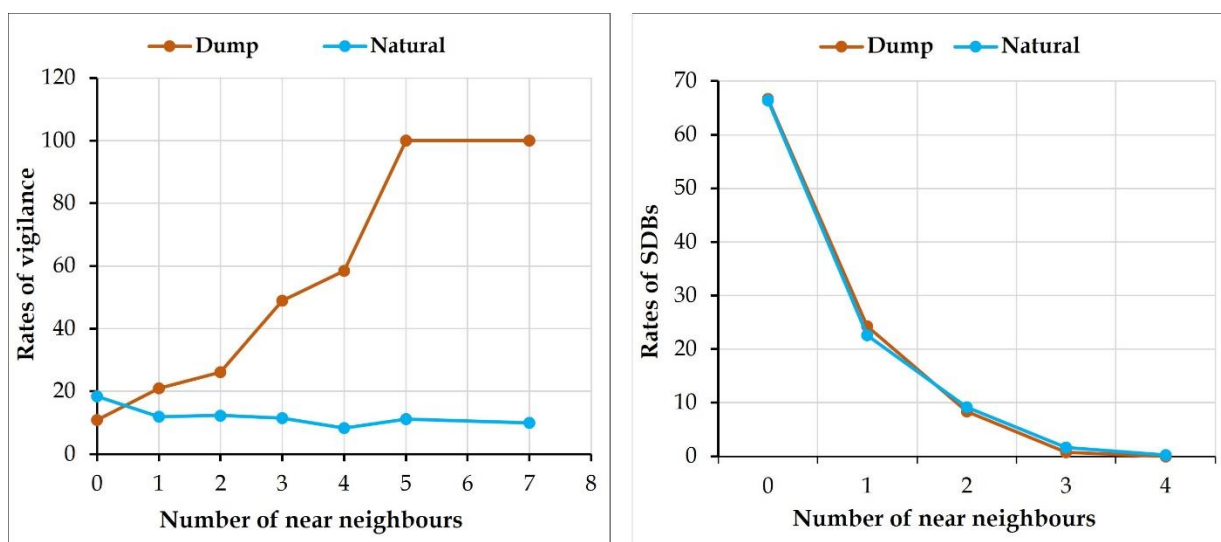


Figure 4. 8. Relationship between number of near neighbours and rates of vigilance (left) and SDBs (right).

## 4.4 Discussion

Anxiety levels of individuals in the Alldays Dump Group were influenced by the variables associated with the dump. The baboons showed greater anxiety when dump foods were less available, and when the number of dumped bags was high. Baboons' scratching and self-grooming increased when feeding rate decreased, while they had higher aggression and vigilance when feeding rate increased. Unexpectedly, the baboon group showed lower or no significant change in anxiety levels in the presence of stressors, and dominance rank did not affect anxiety measures. Vigilance was highly positively correlated with increasing number of nearest neighbours when baboons were in the dump, while there was a negative relation observed in the natural habitat. These findings provide evidence that there is a trade-off between the perceived risk and potential benefits of living in this type of anthropogenic habitat.

### 4.4.1 Food availability and feeding

Scratching, aggression and vigilance increased when baboons were in the dump compared to natural habitat. This could be explained by the different resources and their distribution. The foods in the dump are probably energetically rich, as these are basically human leftovers, as well as being concentrated in the dump. When dump foods were less available, scratching, self-grooming, aggression and vigilance all significantly increased. When dump foods were

limited, the competition for foods between individuals likely increased, resulting in agonistic interactions between conspecifics. As aggression induces anxiety, scratching and monitoring others increased in response. However, number of dumped bags has a significant effect only on scratching and aggression. The baboons tried to explore bags soon after they were dumped, and high ranked individuals attempted to monopolize food bags. Consequently, aggressive interactions between individuals and then scratching increased, which suggest that increasing bag numbers may provide more foods, but it may also induce anxiety related to having access to those foods. This result also indicates for the Alldays Dump Group that scratching was more responsive to a stimulus than self-grooming.

Previous studies have reported that members of a food enhanced primate group spent significantly more time in aggressive interactions (El Alami et al. 2012, José-Domínguez et al. 2015, Ilham et al. 2018), and did more vigilance (Unwin and Smith 2010) than their wild feeding counterparts, interpreted as due to the clumped distribution of provisioned foods. Increased SDBs among the group members followed by aggressive interactions have been observed in primates (Castles and Whiten 1998, Troisi 2002) and also in other mammals (Schino 1998). However, this study results showed monthly natural food availability did not have any effect on these behaviours, which emphasises that availability of the concentrated dump resources and competition over these resources seems to be the main driver of behavioural anxiety of the baboon group.

Both measures of SDBs increased when feeding rate decreased, possibly because of the time trade-off between these behaviours; both scratching and self-grooming require physical involvement. On the other hand, vigilance and aggression, increased with feeding rate, as predicted. Engaging in aggression while feeding provides a means of monopolizing foods and a similar result was observed in bonnet macaques (*M. radiata*), where animals exhibited more aggression during feeding (Ram et al. 2003). Similarly, the increased vigilance perhaps reflects that the baboons were searching for other feeding opportunities from the surroundings as well as collecting social information.

#### **4.4.2 Social and other stressors**

Potential stressors such as proximity to other baboon groups and burning in the dump (event stressor) had a significant impact on scratching, but not the other behavioural anxiety measures. Interestingly, however, the effect estimate was negative, meaning that dump baboons were less anxious when they encountered any of the stress factors compared to when

no stressors were present. This result is contradictory to my predictions and to previous studies (Crockford et al. 2008, McLennan et al. 2019). A possible explanation could be that the baboon group was already habituated to humans and dump workers, who collect recyclable materials in the dump. It was also observed that when workers found good items of food these were offered to the baboons, enhancing the commensal relationships (Maréchal and McKinney 2020). As a result, the baboons may have had a positive attitude towards the presence of humans in the dump. While not all interactions between the baboons and humans on the dump were positive, it appears the benefits of having humans nearby outweighed the costs of threats from them. As a result, the studied baboon group most possibly considered the presence of humans as more beneficial than harmful.

Similarly, the presence of another group nearby may also have provided benefits. The other group that used the dump was much larger than the study group (around 60 individuals, including approximately ten large adult males) and individuals were aggressive against dog attacks. In contrast the Alldays Dump Group was defensive and ran away when they were alone and chased by dogs. Proximity of the larger groups may have helped reduced the potential threats from predators.

#### **4.4.3 Number of near neighbours**

In the dump, the number of near neighbours influenced vigilance behaviours, while it had apparently no effect when baboons were in the natural habitat. Again, this may be related to the food and feeding competition in the dump. Numerous researchers have reported a negative relationship between vigilance and number of nearby neighbours or group size (Isbell and Young 1993, Caro 2005, Teichroeb and Sicotte 2012), although, there was a positive relationship found between vigilance and near neighbours, in certain circumstance (Hirsch 2002). The vigilance behaviour of Alldays Dump Group fits with the later one, suggesting that vigilance increased in the dump due to the competitive interests over the same resources. This result reinforces the evidence that vigilance is not only used to detect the threat, but also used to monitor conspecifics (Kutsukake 2007).

Rates of SDBs decreased when the number of near neighbours increased, which was opposite to my prediction. However, this result supports other studies demonstrating that there was no effect of crowding on SDBs in hamadryas baboons, *P. hamadryas* (Pearson et al. 2015) and there was no relationship between SDBs and time spent with the nearest dominant individuals in olive baboons (Ellis et al. 2011). As described above, the baboon group may be

getting benefits in the presence of previously known social and anthropogenic stressors, and the negative relationship between SDBs and the number of near neighbours suggests that having more neighbours does not increase anxiety levels in the baboons. Instead, this might be a defensive strategy of living in an anthropogenic habitat, as well as this may create an opportunity for socializing which is less stressful.

#### **4.4.4 Dominance rank and time periods**

Unexpectedly, dominance rank did not significantly affect aggression, scratching and vigilance. Most probably, the relationship between rank and priority access to dump foods was very weak. I had an impression that the resources in the dump were plentiful in relation to the group size and that all baboons ate more dump foods than natural foods (Chapter 3). Individual rank might not limit their access to resources, which was one of the reasons for increasing animals' anxiety levels in other circumstance. Another possible reason could be that a very stable and consistent dominance hierarchy existed among males and females throughout the study period. Even between the two adult males, no challenge was observed, which means that the baboons were aware of their social status, resulting in no effects of individual rank on anxiety levels.

The results revealed that the studied baboon group showed more anxiety in the early morning period compared to other time periods of a day. It was observed that most of the time the baboons foraged first at the dump, particularly during the time of natural food scarcity, and spent most of the morning at the dump. Since dump variables are mostly responsible for initiating anxiety, this could explain the increased levels in early morning.

#### **4.4.5 Induced vs routine vigilance**

In the presence of social stressors, routine vigilance decreased and induced vigilance increased, while routine vigilance was also determined by the habitat, feeding rate and food availability. Induced and routine vigilance are qualitatively different: routine vigilance is often cost-free and can be done mutually with other behaviours, while induced vigilance requires attention to react to unpredictable stimuli (Blanchard and Fritz 2007). So, induced vigilance in this study was probably directed towards anxiety, whereas routine vigilance might serve multiple purposes, such as monitoring conspecifics and locating foods. The results also revealed that the study baboons showed more routine than induced vigilance, which seems normal accounting their social stability and threats.

## **Conclusion**

Overall, the findings of this study suggest that access to anthropogenic foods can cause anxiety, such that there are not uniform benefits of these foods to animals. Intragroup competition for foods occurred amongst conspecifics due to the concentrated distribution of dump resources. Aggressive interactions and conspecific monitoring between individuals increased when in the dump, and as a result, baboons were more anxious in the dump compared to when they were in natural habitats. Contrary to previous studies, dominance had no significant effect on the anxiety levels of the baboon group. Similarly, the presence of another group or of humans did not induce increased anxiety, but rather the baboons gained benefits and lower levels of anxiety through the social security ensured by their presence, suggesting that the behavioural anxiety of the baboon group was primarily driven by the intragroup competition over the dump resources.

# Chapter 5. Physiological response to dump feeding in chacma baboons

## 5.1 Introduction

Assessing physiological changes in wild animals is challenging and may involve repetitive trapping and measuring parameters such as weight, energy intake, energy expenditure, and body temperature (Gesquiere et al. 2018b). The development of techniques that measure hormones in urine or faeces has provided an opportunity to quantify animals' physiological changes non-invasively (Hodges and Heistermann 2003). Glucocorticoids and thyroid hormones are useful non-invasive biomarkers involved in metabolic processes and excreted through faeces and urine (Whitten et al. 1998, Sapolsky et al. 2000, Wasser et al. 2010). Both hormones are involved in energetics; glucocorticoids release stored energy (Sapolsky et al. 2000), while thyroid hormones regulate the rate of energy use for basal metabolism (Kim 2008). Their levels vary in a variety of circumstances related to energy requirements and availability. For example, during nutritional constraints, glucocorticoid secretion increases to promote mobilization of stored energy (Sapolsky et al. 2000), while thyroid secretions decrease, related to the lowering the basal metabolic rate (BMR) to conserve energy (Hulbert and Else 2004, Cristóbal-Azkarate et al. 2016). In addition, glucocorticoid increase may be associated with psychosocial causes that potentially require energy to overcome (Engh et al. 2006b, Wittig et al. 2008, Carnegie et al. 2011), whereas thyroid hormones seem not to be associated with psychosocial causes (Ayres et al. 2012). Thus, a combined assessment of both glucocorticoid and thyroid hormone levels may provide useful understanding of primates' physiological responses to different nutritional and non-nutritional conditions.

BMR is the body's metabolic platform providing energy to perform fundamental functions, such as breathing and blood circulation. Since thyroid hormones regulate energy metabolism, measuring them can be used as an index of measuring BMR (Chastel et al. 2003, Hulbert and

Else 2004). Two major thyroid hormones are secreted from the thyroid gland: thyroxin (T4) and triiodothyronine (T3). T4 is the less potent, primary form in the blood, whereas, T3 is the biologically more active, more potent form of thyroid hormone (Wasser et al. 2010, Gesquiere et al. 2018b). Therefore, after developing non-invasive immuno-assay techniques, faecal T3 levels have been reliably used as an index for measuring BMR (Wasser et al. 2010). When food is limited, limiting available energy, T3 secretion may be downregulated as a part of energy saving strategy, and hence BMR decreases; by contrast, when food is plentiful, the opposite applies. T3, thus, indirectly responds to nutritional factors and energy balance (Eales 1988). Increased secretion of T3 was observed during higher caloric intake in captive yellow-breasted capuchins, *Sapajus xanthosternos*, in Frankfurt zoo, Germany (Schaebis et al. 2016) and in wild mantled howler monkeys, *Alouatta palliata*, in Veracruz, Mexico (Dias et al. 2017). On the other hand, during caloric restriction in yellow-breasted capuchins, T3 secretion was downregulated to conserve energy (Schaebis et al. 2016). As provisioned foods tend to be energy-rich (Muruthi et al. 1991, Saj et al. 1999), higher T3 levels in a group of Barbary macaques, *Macaca sylvanus*, in the Atlas Mountains, Morocco, are associated with provisioning (Cristóbal-Azkarate et al. 2016).

In natural habitats, physical environmental factors such as rainfall and temperature may correlate with animals' T3 levels. For example, rainfall may positively correlate with natural food availability (Coe et al. 1976), and wild female yellow baboons, *Papio cynocephalus*, in Amboseli, Kenya, had lower T3 concentrations in the dry season when natural food was reduced (Gesquiere et al. 2018b). When exposed to cold temperature, T3 levels and therefore BMR may be boosted to maintain thermal homeostasis (Silva 2011). Thus, T3 is involved in thermoregulatory functions. For example, T3 secretions in Japanese macaques, *M. fuscata* (Thompson et al. 2017), Barbary macaques (Cristóbal-Azkarate et al. 2016) and mantled howlers monkeys (Thompson et al. 2017) were negatively related to the minimum temperature.

T3 levels, and therefore BMR, may also vary with reproductive stage. Seasonally breeding male primates show elevated T3 levels during (mouse lemur, *Microcebus murinus* (Petter-Rousseaux 1984)), and additionally prior to (squirrel monkey, *Simia sciurea* (Kaack et al. 1980); Barbary macaques (Cristóbal-Azkarate et al. 2016)) the mating season, associated with highly energetically demanding mating activity in polygamous male primates (Emery Thompson and Georgiev 2014) and pre-mating resumption of testicular activity (Wagner et al. 2008). Pregnancy and lactation are highly energy-demanding reproductive states in primates (Emery



Thompson 2013). During pregnancy and lactation, females need extra energy to cover the costs of growth and development of the foetus, milk production and infant carrying (Butte and King 2005); T3 levels increase in these stages indicating an increase in BMR (Dias et al. 2017).

In primates, physiological stress responses are mediated through the activation of the Hypothalamic-Pituitary-Adrenal (HPA) axis that culminates with the secretions of cortisol, a glucocorticoid hormone (Herman et al. 2003). Glucocorticoids (GCs), a class of steroid hormone, are secreted from the adrenal glands. Their primary function involves regulating metabolism through mobilizing energy reserves and increasing glucose supply in the bloodstream (Genuth 1998, Sapolsky et al. 2000). During nutritional stress, mobilization of energy is necessary to maintain homeostasis and energy balance (Sapolsky et al. 2000) and GCs are one of the hormones that play key role in this process. GC secretions are also associated with psychological (Beehner et al. 2005, Engh et al. 2006b, a) and social stress (Bergman et al. 2005, Engh et al. 2006b, Wittig et al. 2008, Carnegie et al. 2011, Pearson et al. 2015). The association of any psychosocial factors with GC variation is thought to be related to adaptation to energy requirements. For example, during agonistic interactions elevated GC levels are related to releasing energy reserves needed to cope with the immediate energy demands for aggressive displays (Beehner et al. 2005).

GC levels have been found to be higher during periods of low food availability compared to when foods are more abundant in a range of primate species; for example wild-feeding white-faced capuchins, *Cebus capucinus* (Carnegie et al. 2011), yellow baboons (Gesquiere et al. 2011), black howler monkeys, *A. pigra* (Rangel-Negrín et al. 2014), Sykes' monkeys, *Cercopithecus mitis* (Foerster and Monfort 2010), and mandrills, *Mandrillus sphinx* (Charpentier et al. 2018). A crop foraging olive baboon, *P. anubis* group in Gashaka-Gumti National Park, Nigeria had GC levels almost half of a natural foraging group (Lodge et al. 2013). However, access to high-quality anthropogenic foods may not always result in decreased GC levels due to the psychological and social stress for animals accessing these resources. For instance, clumped and predictable anthropogenic foods are likely to increase exposure to potential psychological stressors because of increasing agonistic interactions, leading to elevated GC levels among the group members (Dettmer et al. 2014, Pearson et al. 2015). Moreover, provisioned or crop foraging primate groups usually live very close to humans. The increasing interactions with humans defending their crops may also be associated with a rise in GC levels (Behie et al. 2010). Access to anthropogenic foods thus has multiple potential impacts on physiology, both

increasing psychosocial stress due to intra and inter species conflict (Ahlering et al. 2011, Maréchal et al. 2011, Dias et al. 2017) and decreasing energetic stress due to increased foraging benefits (Rangel-Negrín et al. 2014, Rangel-Negrín et al. 2018a).

Female GC levels may vary depending on reproductive state. For example, due to higher energetic demands, pregnant and lactating females had significantly higher faecal GC levels than cycling females in chacma baboons, *P. ursinus* (Weingrill et al. 2004) and black howler monkeys (Martínez-Mota et al. 2017). However, availability of natural and provisioned foods may help to meet metabolic demands during these periods, and thus GC levels may not increase (Foerster and Monfort 2010). Female reproductive state should be taken into account in analysing variation in GC levels.

Having access to high-quality human foods, the Alldays Dump Group might gain energetic benefits, thus increasing BMR and reducing energetic stress. On the contrary, this might increase exposure to psychosocial stress, particularly since anxiety measures increased when the baboons were at the dump (Chapter 4). Here, I evaluate whether the nutritional enrichment provided by garbage dumps has an effect on BMR, measured through T3 levels, as well as whether access to human foods increases or reduces physiological stress responses, assessed through GC levels, in the baboons. In contrast with the numerous studies on GC variation, the T3 hormone concentrations of wild primates have only been studied in a few species and in baboons have been quantified only once (Gesquiere et al. 2018b). The combined measurements of GC and T3 in a single study are rare; only two studies of the same two groups of naturally and anthropogenically foraging Barbary macaques (Cristóbal-Azkarate et al. 2016, Maréchal et al. 2016b) and studies of wild foraging mantled howler monkeys (Dias et al. 2017, Rangel-Negrín et al. 2018b). I test the following hypotheses and predictions (Table 5.1) for the study group of anthropogenically foraging wild baboons.

Table 5. 1. Hypotheses and predictions for this chapter

Hypothesis	Predictions
1. Fluctuations of thyroid hormones will be related to food availability because thyroid hormones are associated with energy acquisition	a) T3 levels will be lower when natural food availability is reduced compared to when natural foods are more readily available. b) T3 levels will be positively related to dump food availability.
2. As thyroid hormones regulate BMR to maintain thermal homeostasis, fluctuations of these hormones will be related to thermoregulatory functions.	a) T3 levels will be negatively related to daily minimum temperature.
3. Thyroid hormones regulate energy metabolism; these hormones fluctuate in response to energy acquisition and expenditure behaviours.	a) T3 levels will be higher when baboons spend less time feeding, indicating greater food availability. b) T3 levels will be lower when the baboons have longer daily travel distances, indicating reduced food availability.
4. GC hormone secretion is related to nutritional stress levels, because the primary function of this hormone is to release stored energy.	a) GC levels will be higher when natural foods are limited compared to when natural foods are more readily available. b) GC levels will be negatively related to dump food availability.
5. Due to their role in energy release, GC hormone levels fluctuate in response to energy acquisition and expenditure.	a) GC levels will be lower when baboons spend less time feeding. b) GC levels will be higher when baboons have longer daily travel distances. c) GC levels will be higher when baboons are involved in more agonistic interactions.

## 5.2 Methods

### 5.2.1 Faecal sample collection, storage and transportation to the laboratory

See the Chapter 2, data collection section 2.4.6.

### 5.2.2 Preparation of samples and conducting hormone assays

The frozen faecal samples were freeze dried and then ground to faecal powder. 0.1 g of faecal powder per sample was extracted into 3 ml 80% methanol. The faecal extracts were then analysed for total T3 and GC metabolites. Total T3 levels were measured using a commercial enzyme-linked immunosorbent assay (ELISA) kit (Total T3 ELISA RUO, Ref: EIA-4569R, DRG Instruments GmbH, Germany). The T3 assay used in this study has been biologically validated for use in baboons, in relation to marked with seasonal variation in food availability in chacma baboons at Lajuma, South Africa (A.M. MacLarnon and V.S. Affleck, pers. Comm. 2021). The T3 assay was conducted following the manufacturers protocol. A wide variety of GC metabolites are excreted in primate faeces. In this study, I assayed steroid- 5 $\beta$ -Androstane-3 $\alpha$ , 11 $\beta$ -diol-17-one (measures GC metabolites) which has been validated for use in olive baboons using the ACTH challenge test (A. Daspre, M. Heistermann, L. Rosetta and P.C. Lee pers. comm. 2007) and used in other primates' species (Heistermann et al. 2006). The assay was carried out on precoated microtitre plates according to the procedure described by Heistermann et al. (Heistermann et al. 2004). Assay sensitivity of T3 and GC assays at 90% binding was 0.27 ng/well and 3.0 pg/well, respectively. Intra-assay and inter-assay coefficient of variations in both T3 and GC assays were in acceptable range (Table 5.2). Any duplicate above 10% variation, named as a poor duplicate, was re-assessed and any plate contains  $\geq 5$  poor duplicates was repeated. All assay results were then converted to a concentration relative to dry faecal weight, and presented as a nanogram of hormone per gram dry faecal weight. All these laboratory procedures were conducted in Behavioural Ecology and Physiology Laboratory of the Department of Anthropology, Durham University. For detailed description of extraction and hormone assays see Appendix 4-7.

### 5.2.3 Data preparation

In primates, changes in T3 secretion takes 7 to 14 days to respond to environmental factors (van der Lans et al. 2013). T3 excretion in faeces peaks after 21 to 45 hours of secretion, based on dogs (Wasser et al. 2010). Two days excretion lag was accounted in a study of Barbary macaques (Cristóbal-Azkarate et al. 2016). The consideration of time lag is important when

attempting to test the relationship of hormone levels to behavioural events and states. Taking 2 days excretion lag and 7 days response time into account, I averaged ecological, behavioural and climatic data over a 7-day period, from 2 to 8 days before the date of faecal sample collection. There were three behavioural data collection days in this time period in most cases, and two in the remaining cases.

Table 5. 2. Intra-assay variation for high and low concentrations of T3 and GC standards and inter-assay variation of quality controls used in each assay. QCH= Quality Control High, QCL= Quality Control Low

	Intra-assay variation		Inter-assay variation	
	High	Low	QCH	QCL
T3	2.58% (n= 19)	2.84% (n= 18)	9.44% (n= 14)	6.63% (n= 14)
GC	3.7% (n=13)	1.9% (n=14)	10.08% (n= 31)	13.20% (n=31)

*Natural food availability:* Collected monthly, see details in the Chapter 3. In the case of transition periods between months, based on the days falling in the respective months, I weighted and then averaged the food availability data for these two months. For example,  $p$  and  $q$  are the food availability index in December and January, respectively. Then the food availability for the samples collected on 4<sup>th</sup> January (period 27<sup>th</sup> Dec to 2<sup>nd</sup> January) will be-

= (Number of days in December  $\times$  Food availability index in December + Number of days in January  $\times$  Food availability index in January)  $\div$  7

=  $(5 \times p + 2 \times q) \div 7$ .

*Dump food availability:* Based on the number of dumped bags each day, I estimated available dump foods per day (details in the Chapter 3). I averaged available dump foods from 2 to 8 days before the date of faecal sample collection as above.

Similarly, I averaged climatic (temperature) and behavioural (feeding time, daily travel distances) data from 2 to 8 days before the date of faecal sample collection. I also noted the reproductive status of female individuals in the 2 to 8 days before the date of faecal sample collection.

Taking 2 days excretion lag and 14 days response time into account, I also averaged ecological, behavioural and climatic data over a 14-day period, from 2 to 15 days before the date of sample collection, to examine which time period best explains the T3 results, following the procedures outlined above for a 7-day response time.

Unlike T3 hormone, GC hormone levels respond faster, within minutes to a couple of hours in response to environmental factors (Sapolsky et al. 2000). However, there is an excretion lag between hormone in the blood and hormone metabolites subsequently excreted in the faeces. In baboons, peak excretion of steroid hormones in faeces was after 40-50 hours of their secretion in the blood (Wasser et al. 1993). Here, I considered 2 days excretion lag, which is the common practice and also used in other baboon studies (Higham et al. 2009a, MacLarnon et al. 2015). I aligned respective behavioural and ecological data accordingly.

#### **5.2.4 Data analysis**

A Generalized Linear Mixed Model (GLMM) was used to analyse which variables best explain the T3 variations of the baboon group. Natural fruit availability index, daily dump food availability, daily minimum temperature, daily feeding time, daily travel distances and dominance rank were continuous fixed effects and sex was a categorical fixed effect in the model. A second model was run for females only. In this model I fitted females' reproductive status instead of sex as a categorical fixed effect along with the other fixed effects used in the previous model. Individual identity and sample identity were used as random effects in both models. I also performed the same models with behavioural and climatic data averaged for 14 days.

To explore which variables best explain the GC variation of baboons I used two GLMMs. The first included natural fruit availability index, daily dump food availability, daily feeding time, daily travel distances, aggressive interactions and dominance rank as the continuous fixed effects and sex and persecution effects were categorical fixed effects in the model. The second model was for females only and included female reproductive status instead of sex as a categorical fixed effect; other fixed effects were the same as for the first model. Individual identity and sample identity were used as random effects in both models.

Co-linearity between all effects was checked using variance inflation factors, VIF (Field et al. 2012), with a cut-off criterion multicollinearity efficiency value  $>10$  for including variables inside the same model (Myers and Myers 1990). The model fitting was performed using

“lme4” and “lmerTest” packages in R with the “CAR” package used to check the multicollinearity.

All statistical analyses were completed using R (Version 4.0.4, R development core team). All tests were two tailed with a 5% level for significance ( $p < 0.05$ ). For the data visualization I used “ggplot2” with the “cowplot” and “gridExtra” packages in R.

## 5.3 Results

### 5.3.1 Variation in T3 levels

Mean ( $\pm$  SD) T3 level of chacma baboons was  $1613.6 \pm 438.4$  ng/g (range 673.6 to 3436; male= 1604.8, female= 1617.4 ng/g) across the study period. Mean T3 varied seasonally and was higher in summer ( $1806.7 \pm 420.2$  ng/g; male= 1803.7, female= 1834.5 ng/g) than winter ( $1389.3 \pm 342.4$  ng/g; male= 1386.0, female= 1410.6 ng/g; Figure 5.1).

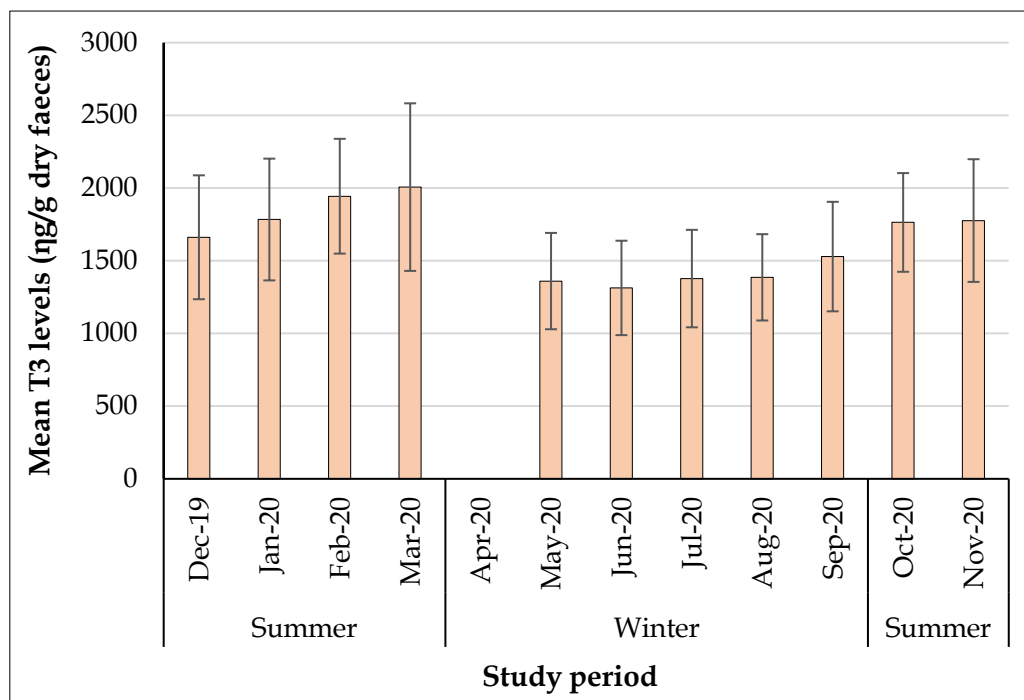


Figure 5. 1. Monthly variations in T3 levels across the study period. Error bars denote standard deviations. Two days excretion and 7 days response lag are considered while labelling X-axis.

### 5.3.2 Factors influencing T3 levels

Using 7-day data for the mixed sex model, T3 levels were significantly predicted by both natural and dump food availability, travel distance and minimum temperature (Table 5.3, Figure 5.2). T3 levels increased when either natural or dump food availability increased, and T3 levels decreased when baboons travelled longer distances. T3 levels also increased with increasing minimum temperature. Feeding time, dominance rank and sex did not impact on T3 levels of the baboon group (Table 5.3).

These results were similar using the 14-day data (Appendix 8).

Table 5. 3. GLMM model for T3 levels (males and females), n= 375. \*reference category was females

Fixed factors/ predictor variables	Estimate	Std Error	t value	p value
Intercept	1441.89	204.62	7.04	<0.001
Natural food availability	0.21	0.06	3.48	<0.001
Dump food availability	2.42	1.05	2.29	0.022
Feeding time	-0.10	0.10	-1.00	0.313
Daily travel distances	-0.07	0.02	-3.18	0.001
Minimum temperature	25.89	8.53	3.04	0.002
Dominance rank	-35.31	19.08	-1.85	0.098
Sex*, male	-199.09	148.46	-1.33	0.218

In the female baboon model, T3 levels for the 7-day data were related to the same four factors as for the mixed sex model, and did not significantly vary between reproductive states (Table 5.4). The results for the 14-day data were similar, except that dump food availability and daily travel distances were not significantly related to T3 levels and did not significantly vary between reproductive states (Appendix 8).

Table 5. 4. GLMM model for T3 levels for females only, n= 263. \*reference category was cycling females

Fixed factors/ predictor variables	Estimate	Std Error	t value	p value
Intercept	1492.78	234.90	6.35	<0.001
Natural food availability	0.23	0.07	3.18	0.001



Dump food availability	3.17	1.27	2.49	<b>0.013</b>
Feeding time	-0.11	0.13	-0.90	0.369
Daily travel distances	-0.07	0.02	-2.68	<b>0.007</b>
Minimum temperature	22.98	10.11	2.27	<b>0.023</b>
Dominance rank	-42.21	19.99	-2.11	0.074
Reproductive status*				
Lactating	-14.32	67.64	-0.21	0.832
Pregnant	-10.81	67.77	-0.16	0.873

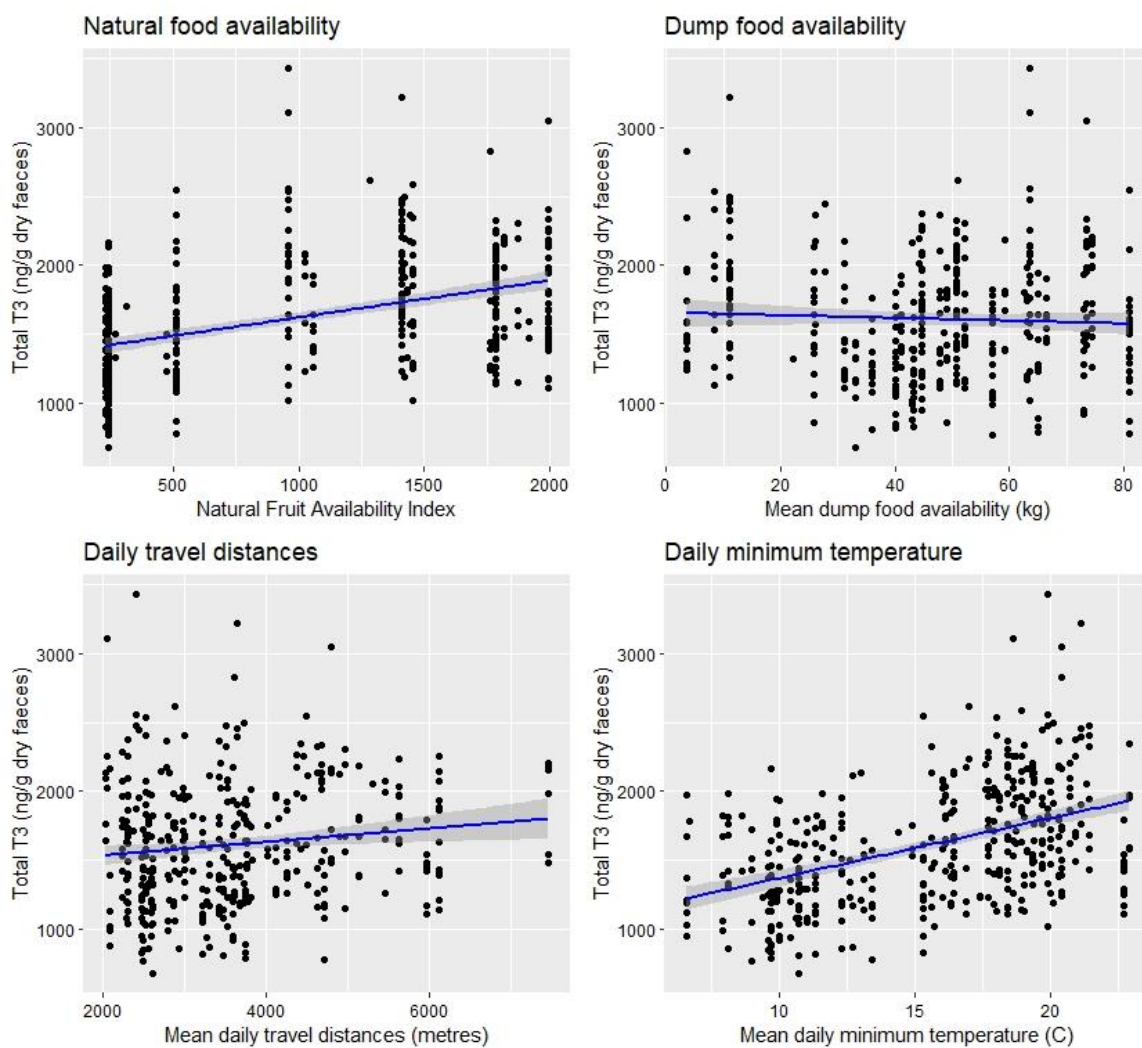


Figure 5. 2. T3 responses as a function of natural food availability, daily dump food availability, daily travel distances and daily minimum temperature. Blue lines indicate the direction of relationships defined by the linear model and the shaded area represents upper and lower limits at 95% confidence interval.

### 5.3.3 Variation in GC levels

Mean ( $\pm$  SD) GC levels of chacma baboons were  $2630.3 \pm 1291.5$  ng/g (range 460.9 to 8894.2; male= 2061.6, female= 2879.8 ng/g) across the study period. Mean GC levels varied seasonally, being higher in summer ( $2819.6 \pm 1371.7$  ng/g; male= 2197.8, female= 3140.0 ng/g) than winter ( $2411.5 \pm 1157.4$  ng/g; male= 1893.8, female= 2602.8 ng/g; Figure 5.3).

### 5.3.4 Factors influencing GC levels

The GLMM for GC hormones for both sexes shows that the GC levels were significantly predicted by natural food availability and sex (Table 5.5, Figure 5.4). GC levels increased when natural foods were available, and females had higher GC levels than males. Dump food availability, feeding time, daily travel distances, aggression, individuals dominance rank and persecution events do not impact on GC levels of the baboon group (Table 5.5).

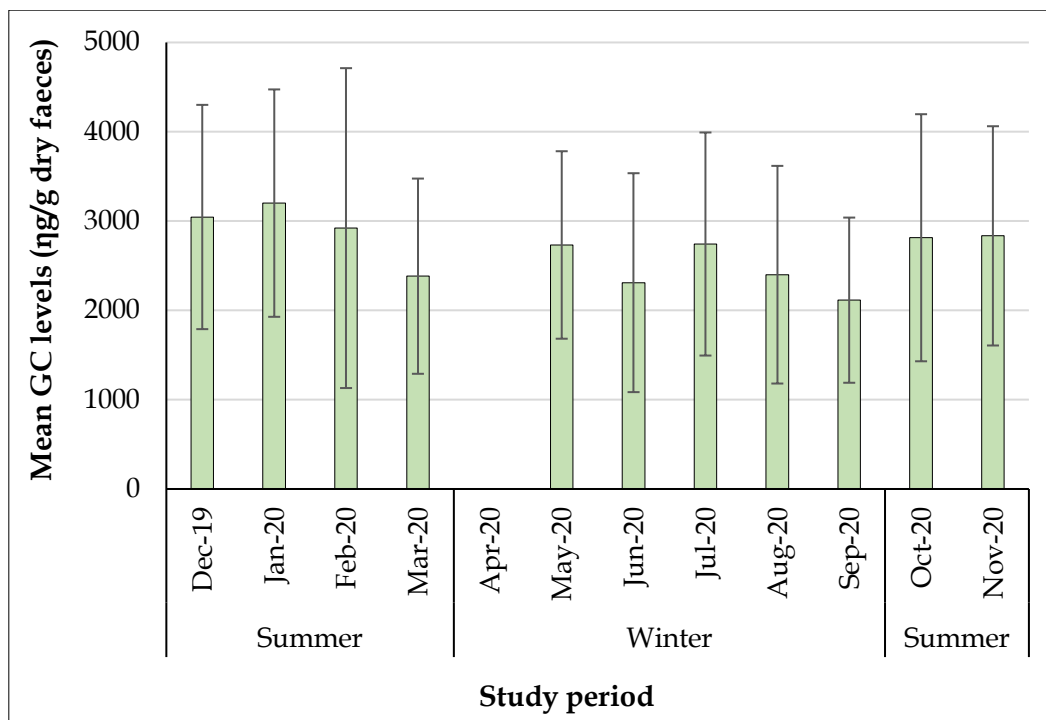


Figure 5. 3. Monthly variation in GC hormone levels across the study period. Error bars denote standard deviations. 2-days excretion lag is considered while labelling X-axis.

Table 5. 5. GLMM model for mixed sexes for GC levels in baboons. \*reference category was no, \*\* reference category was females

Fixed factors/ predictor variables	Estimate	Std Error	t value	P value
Intercept	4028.00	626.80	6.42	<b>&lt;0.001</b>
Natural food availability	0.32	0.12	2.54	<b>0.011</b>
Dump food availability	-0.85	3.74	-0.22	0.819
Feeding time	-0.29	0.22	-1.31	0.192
Daily travel distances	-0.08	0.06	-1.33	0.163
Aggression	9.43	6.24	1.51	0.132
Dominance rank	-125.60	66.27	-1.89	0.093
Persecution effects*, yes	63.08	225.30	0.28	0.779
Sex**, male	-1658.00	523.10	-3.17	<b>0.013</b>

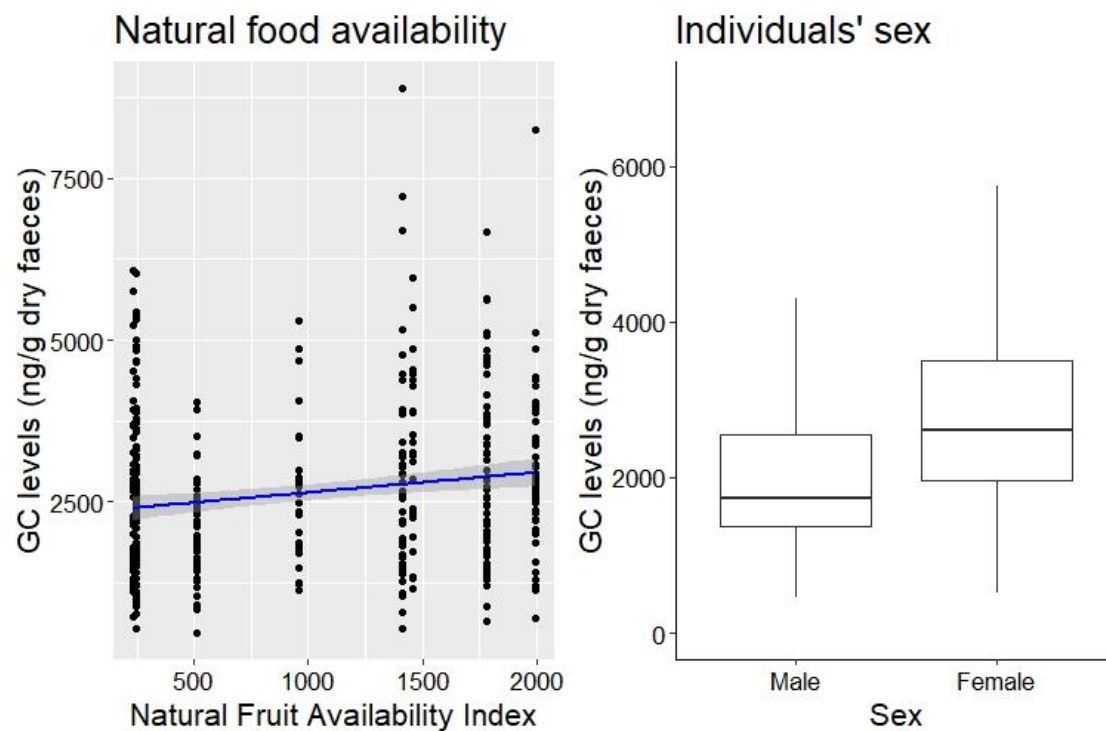


Figure 5. 4. GC responses as a function of natural food availability and sex. Blue line in the scatterplot indicates the direction of relationships defined by the linear model and the shaded area represents upper and lower limits at 95% confidence interval. Boxes in the boxplot represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values; outliers are removed.

The model for only female baboons also showed that GC levels significantly increased when females were involved in more aggressive interactions, while the positive relationship with natural food availability remained (Table 5.6, Figure 5.5). There was no significant difference observed among female reproductive states (Table 5.6).

Table 5. 6. GLMM model for GC levels in adult female baboons. \*reference category was no, \*\* reference category was cycling females

Fixed factors/ predictor variables	Estimate	Std Error	t value	P value
Intercept	3970.14	776.91	5.11	<b>&lt;0.001</b>
Natural food availability	0.37	0.15	2.44	<b>0.015</b>
Dump food availability	-4.11	4.62	-0.89	0.374
Feeding time	-0.35	0.28	-1.22	0.221
Daily travel distances	-0.08	0.07	-1.09	0.275
Aggression	20.75	8.98	2.30	<b>0.021</b>
Dominance rank	-123.60	81.66	-1.51	0.175
Persecution effects*, yes	61.46	276.85	0.22	0.824
Reproductive status**				
Lactating	175.74	243.45	0.72	0.471
Pregnant	180.33	231.09	0.78	0.436

## 5.4 Discussion

The results showed that T3 levels of the Alldays Dump baboons fluctuate with energetic conditions as indicated by both natural and dump food availability; and negatively related to energy expenditure associated with daily travel length. GC levels were positively related with natural but not dump food availability, and they were not related with energy expenditure in daily travel distance. Furthermore, GC levels only relate to levels of agonism in females. These results suggest that the physiology of the baboon group may be impacted by the availability of dump foods, which may provide energetic benefits without enhanced stress levels, at least in males.

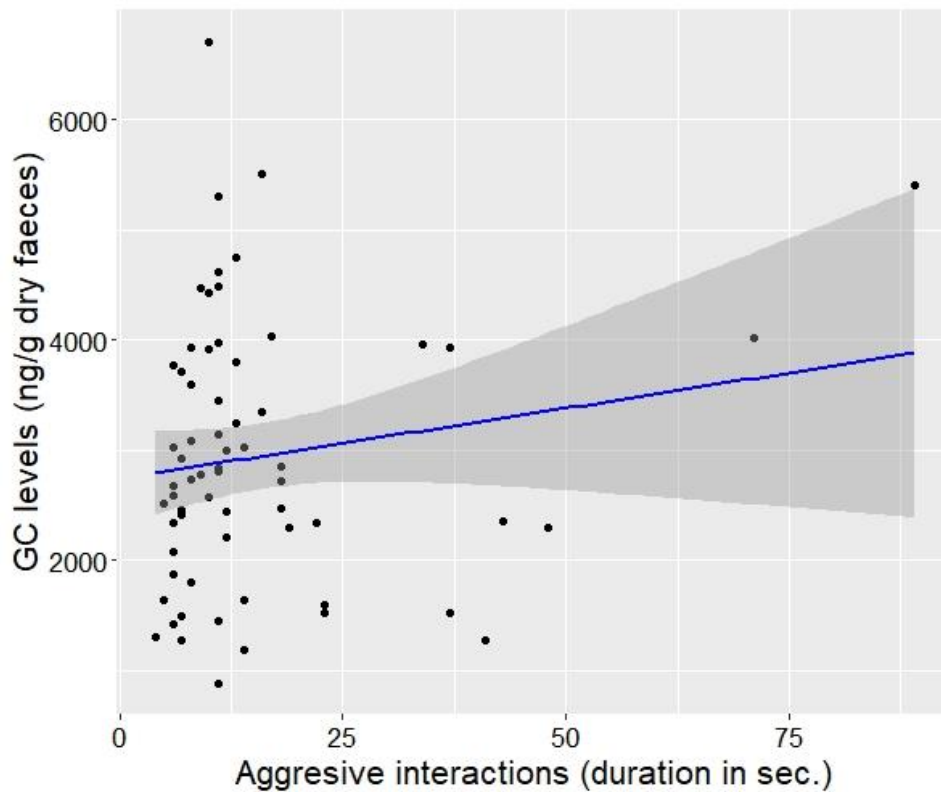


Figure 5. 5. Relationship between aggressive interactions and GC levels in female baboons. Blue line indicates the direction of relationships defined by the linear model and the shaded area represents upper and lower limits at 95% confidence interval.

#### 5.4.1 Hormonal variations in relation to energy acquisition

T3 levels were positively related to both natural and dump food availability, meaning that T3 levels were lower when foods were limited and higher when foods were available. This result is consistent with other studies where the authors showed that T3 levels were related with energy acquisition, increasing and decreasing as food availability varied (Cristóbal-Azkarate et al. 2016, Schaebs et al. 2016, Gesquiere et al. 2018b), presumably reflecting a metabolic strategy of BMR flexibility in response to different conditions.

In wild feeding primates, during limited food availability energy expenditure increased and energy intake decreased that led to negative energy balance, whereas positive energy balance was observed when food was plentiful so that animals maintain their energy balance (Thompson and Knott 2008, Grueter et al. 2014, Gesquiere et al. 2018b). Human foods require less processing time which is energetically less costly in relation to high energetic return, so

their consumption will likely lead to a positive increase in energy balance (Lodge et al. 2013). In addition to natural foods, consumption of dump foods by the study group may provide high energetic advantages, which may help to keep improved energetic conditions.

GC levels were positively related to the natural food availability, which is opposite to my prediction. Various studies in different ecological settings showed that primates' GC levels are negatively related to food availability (Gesquiere et al. 2008, Foerster and Monfort 2010, Carnegie et al. 2011, Gesquiere et al. 2011, Lodge et al. 2013, Gómez-Espinosa et al. 2014, Rangel-Negrín et al. 2014, Charpentier et al. 2018). Although a study on crop-foraging African elephants (*Loxodonta africana*) which showed elevated GC levels, interpreted as being associated with psychosocial stress due to human-elephant conflict (Ahlering et al. 2011). However, the mechanisms or underlying physiological factors mediating this opposite trend of GC response by the studied baboon group remain unclear, which warrants further investigation. Some other factors, however, may have affected the results. First, at the beginning of the study period (Dec- Jan, when natural foods were available), GC levels were higher when there were newly recruited assistants present. The group was habituated to me and already familiar with the variety of people in the dump, but not with these new individuals who spent a lot of time close to the study group. Santiago et al. (2020) reported that faecal GC levels of howler monkeys were positively related to the presence of human disturbance, suggesting that the higher GC levels could result from the physiological stress response associated with fear. Moreover, at the end of the study period (Oct-Nov, when the natural foods were comparatively available), higher GC levels may have coincided with the persecution events occurred at that time (described in the Chapter 6). Second, dump food supply was limited from December to February (Figure 3.2, Chapter 3).

#### **5.4.2 Hormonal variations in relation to energy expenditure**

As predicted, T3 levels were negatively related to the daily travel distance. However, daily travel distances do not have a significant impact on GC levels. This result contrasts with the finding that increases of energetically costly activities such as travel can lead to increase in GC levels in free-ranging howler monkeys (Dunn et al. 2013). The significant negative relation between energy expenditure and T3, and no relation with GC levels suggest that access to energy-rich dump foods may promote baboons to restore their energy reserves and improve energetic conditions for that time when they would have needed it.

In primates, elevated GC levels are highly correlated with intra-species (Dias et al. 2017) and inter-species agonistic interactions (Maréchal et al. 2011), which is also thought to be associated with releasing energy because of metabolic demand of aggression (Beehner et al. 2005). In this study, the combined model (including both male and female data) on GC results showed that GC levels were not affected by aggressive interactions, but the model with only females' baboons showed that GC levels were significantly affected by aggressive interactions. Similar results found in chacma baboons (Crockford et al. 2008), mantled howlers (Gómez-Espinosa et al. 2014) and chimpanzees, *Pan troglodytes* (Thompson et al. 2010) that the females' GC levels increase when they participate in agonistic interactions. This suggests that females are more sensitive to psychosocial stressors than males, which can be supported by several studies that females' GC levels increase when they experience psychosocial stressors such as male immigration (Beehner et al. 2005, Engh et al. 2006b), infanticide (Engh et al. 2006b) and predation (Engh et al. 2006a).

### **5.4.3 Hormonal correlates with thermoregulation**

The T3 levels were positively related to the minimum temperature, which is opposite to the expected relationship for a thermoregulatory function (Cristóbal-Azkarate et al. 2016, Thompson et al. 2017). This difference with other studies could be explained by the nature of temperature variation at the field site. Like a typical tropical environment, the study area does not have large seasonal swings in thermal conditions. However, the area is characterized by wet summers associated with high temperatures and precipitation, and dry winters with lower temperatures and low/no precipitation. Higher precipitation in summer may make baboons' body fur wet, and in conjunction with this, minimum temperature may create a cooler experienced thermal environment for the baboon group (Hill et al. 2004). The positive relationship between minimum temperature and T3 levels may as a response of cold thermal pressures, as experienced by other primates living in tropical climatic conditions (Nowack et al. 2013, Thompson et al. 2014, Thompson et al. 2016).

### **Conclusion**

The increasing T3 levels during energy acquisition and decreasing T3 levels during energy expenditure suggest that baboons carefully allocated energy, as well as coordinated between behavioural and physiological strategies to maintain energy balance. The baboons had energetic advantages due to the abundance of food available through multiple sources. The GC levels may be impacted by the dump resources, which most likely the reason for the lack

of the usual relationships between GC levels and energy acquisition and expenditure. This result suggests that GC levels of the studied baboons were not as simple and straightforward function of food availability and aggression, and instead, other control factors may involve within it that also need to consider explaining the results.



## **Chapter 6. Impact of human persecution events on the behaviour and physiology of baboons in a human-modified habitat**

### **6.1 Introduction**

Due to increasing human populations, land transformation and associated loss of natural habitat, many animals live in close proximity to humans (Stone et al. 2015, Chowdhury et al. 2020). This proximity can provide benefits through providing access to food and building materials for animals such as rodents and small mammals (Hulme-Beaman et al. 2016). But for many animals, anthropogenic environments lead to negative interactions where foods, space and other resources are shared with humans (Kaplan et al. 2011, Hoffman and O'Riain 2012a). Animals can adapt and even thrive in human-modified habitats, although in most cases the interactions with humans have negative impacts (McLennan et al. 2017), often referred to as human-wildlife conflict. It has become increasingly important to understand how animals respond to these 'conflict' situations to survive in anthropogenic landscapes.

Many primates become habituated to living in close contact with humans to access shared resources and in Chapter 3, I showed that baboons living in a human modified habitat occupied a reduced home range that likely reduced their use of natural foods due to the energetic benefits obtained from resources at a garbage dump. Nevertheless, the baboons had higher anxiety levels while using anthropogenic food resources (Chapter 4). In general, competition for shared resources often leads to conflicts between primates and humans (Warren et al. 2011). Direct conflicts and other associated human activities may negatively affect activity, diet, reproduction and the overall health of these primates (Higham et al. 2009b, Maréchal et al. 2016b). In some cases these conflicts lead to permanent injuries, and even death (Beamish 2010).

Human-induced baboon deaths occur through shooting, vehicle collisions and contact with power lines (Beamish 2010) while there is natural predation by leopards, lions, hyaenas and crocodiles (Busse 1980, Cowlshaw 1994, Cheney et al. 2004); both are common in baboon populations throughout Africa. Although animals behave in ways to minimize the risks. Deaths, either through natural predation or through human interference, are unpredictable, uncontrollable, sometimes traumatic and could potentially cause chronic anxiety to individuals who witness such events (Engh et al. 2006a). Furthermore, injury resulting from these events, may adversely affect the locomotory, foraging, and reproductive activities of these injured individuals (Cheney et al. 2006, Beamish and O'Riain 2014). In addition to direct harmful effects to animals, gun shooting might also indirectly affect other animals in the same environment through toxic metal pollution (Arnemo et al. 2016).

In primates, the negative impacts of predation and human interference are manifested through their behaviour and physiology. Behavioural responses include self-directed behaviours (SDBs) and vigilance. SDBs have successfully been used as behavioural measures of anxiety in several primate studies (Maestriperi et al. 1992, Higham et al. 2009a, Maréchal et al. 2011), with higher rates of SDBs associated with predation events in brown lemurs, *Eulemur fulvus* in Berenty forest, Madagascar (Palagi and Norscia 2011). Barbary macaques, *Macaca sylvanus* in the Middle Atlas Mountains, Morocco, showed higher rates of SDBs and aggression when tourist-macaque interactions occurred (Maréchal et al. 2016a). Chacma baboon groups in Namibia increased their vigilance when they were in areas of high risk of predation (Cowlshaw 1997a). Behavioural differences have also been observed in animals that are injured due to natural predation or human persecution. Injured chacma baboons in Cape Peninsula, South Africa, spent less time feeding and more time in resting and moving than non-injured baboons (Beamish 2010). Injured chimpanzees, *Pan troglodytes* in Budongo forest, Uganda, reduced their moving time by half compared to non-injured members, although injury did not affect feeding time (Munn 2006). Similarly, primate habitat use and ranging behaviour is influenced by predation risk (Hill and Weingrill 2007, Willems and Hill 2009, Coleman and Hill 2014). There was evidence that when the group size was small, baboons avoided high-risk habitats and used low-risk habitats (Cowlshaw 1997b) and spent more time close by refuges (Cowlshaw 1997a).

Glucocorticoid (GC) levels represent an important tool to measure physiological responses to stressors. Chacma baboons in Okavango Delta, Botswana, showed higher GCs in months when predation occurred, and for several days when predators separated the group members,

compared to baseline levels (Engh et al. 2006a). Females who lost their close relatives showed the largest increase in GC levels (Engh et al. 2006a). Similarly, females in all reproductive stages had higher GCs during months with infanticide attempts (Engh et al. 2006b). Elevation of GCs has also been found in injured animals; for example, injured African elephants, *Loxodonta africana*, in Kruger National Park, South Africa, had higher GCs levels than normal, with the level of increase varying dependent on the degree of injury (Ganswindt et al. 2010).

Social support through increased grooming and other affiliative interactions appears to be particularly important in mitigating the adverse effects of deaths and injury in primates (Carter 1998, Engh et al. 2006a). Grooming and other positive social interactions appear to increase in stressful conditions; for example, female chacma baboons in Okavango Delta temporarily broadened their grooming network to include more partners after the death of close relatives from predation (Engh et al. 2006a). On the other hand, negative social interactions, such as aggression, decreased amongst female baboons during a stressful situation (Beehner et al. 2005).

The Alldays Dump Group regularly visited a dump site in Alldays, South Africa, and spent on average three hours per day and 45% of their total feeding time on dump foods (Chapter 3). The baboons showed commensal relationships with dump workers (Chapter 4), but local people and sometimes residents dumping their rubbish showed aggressive behaviours towards the baboons through chasing, clapping and throwing of stones. From December 2019 to the end of September 2020, the baboon group was followed regularly for data collection and there were no challenges in alpha male position, no male immigration, no emigration, no infanticide attempts and no predation attempts during this period. One adult female, however, died in June 2020, presumably of natural causes. After this relatively stable period, two shooting events occurred at the baboons' sleeping site causing significant mortality and injury:

**Event 1:** I found two dead juvenile baboons (one male, one female) close to their preferred sleeping site – the water tower – on 28 Sep 2019 at approximately 8 am while conducting plant phenology assessments. After inspecting the dead bodies, I found signs of two bullet holes in the chest of one baboon and one bullet wound in the thigh of the other juvenile. Given the corpse texture and maggot infestation I estimated that the shooting occurred at least one day before (the baboons were not followed on 26 and 27 Sep 2020). I also inspected the water tower area and could not find any fresh faeces, suggesting that the group did not sleep at the water

tower the previous night. Following the event, and on censusing the group, two infants (around ten months old) were also missing, but despite an extensive search of their home range the bodies were not located. I could not find any apparent physical injury to other individuals.

**Event 2:** In the very early morning of 17 October 2020, five minutes after dawn, I was heading to the water tower to conduct a follow day for behavioural observations when I saw the alpha male running from the nearby main road towards an open area, halfway between the dump and the water tower. I followed him and saw other group members arriving at the same location from different directions. I observed physical injuries to some individuals (details in the Results section-Table 6.2) and heard groaning vocalisations (especially from a high-ranking adult female) although the group were then quiet for most of the day. After a census, I found that a high-ranking adult female, her 8-month old baby, and a juvenile were missing and subsequently found the three bodies at the water tower site at the end of the day. On inspection, each body had 2-3 bullet holes, although the size of the wounds was slightly smaller compared to previous shooting event.

Studies on the effects of human persecution on baboons, and primates more generally, are rare. The shooting events thus provide an opportunity to observe the behavioural and physiological responses to human persecution in a commensal baboon group, and to explore whether social interactions play any role in mitigating the persecution effects. The description of the events indicates significant behaviour and ranging changes following the persecution. Moreover, from what I know about the physiological responses to non-human predation and infanticide, I expect similar impacts from human persecution. I test the following hypotheses and predictions (Table 6.1).

Table 6. 1. Hypotheses and predictions for this chapter

Hypothesis	Predictions
<p>1. Activity and ranging behaviours of the baboons will be affected by the persecution events due to the risks and mortality involved.</p>	<p>a) After the persecution events grooming and moving will increase while feeding and resting will decrease compared to pre and post event levels.</p> <p>b) Physically injured animals will rest and groom more, have higher rates of SDBs and spend less time feeding and moving compared to non-injured baboons.</p> <p>c) Daily travel length and distance of sleeping site from the shooting location will be longer, travel speed will be higher and ranging area will be larger after events compared to pre and post event periods.</p>
<p>2. Behavioural anxiety and physiological stress levels will be influenced by the persecution events, because these events are potentially stressful for the baboons.</p>	<p>a) Compared to pre and post events time periods, SDB rates will increase after the persecution events.</p> <p>b) Compared to pre and post events time periods, individuals' GC levels will be higher after persecution events.</p> <p>c) GC levels of injured baboons will be higher compared to non-injured baboons.</p>
<p>3. Baboons will mitigate the negative effects of persecution events by increasing positive social interactions and decreasing negative interactions.</p>	<p>a) Rate of grooming will increase after persecution events, while rate of aggression will decrease.</p>

## 6.2 Methods

For a detailed description of the data collection methods see Chapter 2.

### 6.2.1 Data preparation

*Proportions of activity* (e.g., feeding, grooming, moving, resting and others) for each day were estimated from scan data (section 2.4.2, Chapter 2). I divided the number of records of each category of the behaviour for a follow day (for example, day 1, 2, 3.....,120, 121) by the total number of behavioural records for the respective day (Back et al. 2019). I multiplied the proportion by 100 to get percentage of records.

*Persecution time periods:* I categorized behavioural observations and faecal samples into time periods based on the dates of the shooting events. These categories were 'Pre events', 'After event 1', 'After event 2' and 'Post events' (Figure 1). Since the 2<sup>nd</sup> event happened after 19 days of 1<sup>st</sup> event, I considered these 19 days as 'After event 1'. To make the data even for comparison between events, I considered 19 days after 2<sup>nd</sup> event as the 'After event 2' period. One month before the 1<sup>st</sup> event and one month after the 'After event 2' were considered as 'Pre events' and 'Post events', respectively (Figure 6.1).

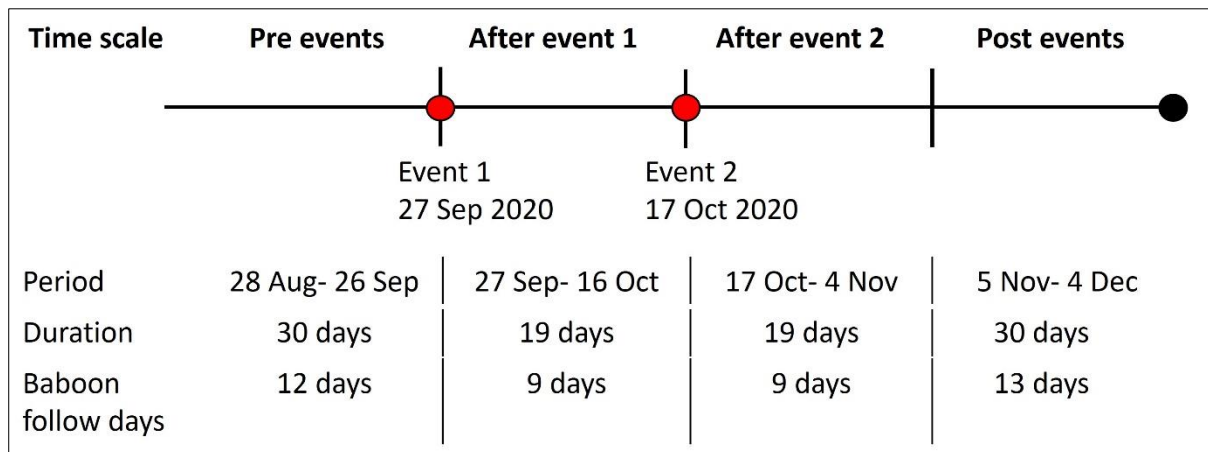


Figure 6. 1. Persecution time periods and components. Red dots indicate date of occurrence and black dot indicates end of study period.

*Injured* baboons were physically injured due to the shootings based on visible signs of injury such as cuts with bleeding or disorderly body hair, eye injuries or limping.

*Daily travel lengths* were determined based on shortest distance between consecutive GPS point locations taken every 30 minutes. Daily travel lengths were calculated using GPS data from successful follow days only. See Chapter 3, data preparation section 3.2.3, for details.

*Travel speed* was the distance the baboon group travelled per hour for the first hour of the day journey. Here, I have considered only the first hour of the day journey as an indication of whether they left sleeping site quickly.

*Distance of the sleeping site from the shooting site* was considered as the shortest distance between the shooting site, and their last location of the study group on each follow day. For this analysis only successful follow days were used. These two GPS points for each day were imported into ArcGIS, then I made a line feature using the data management tool (points to line) and then re-projected to the Universal Transverse Mercator (UTM) map coordinates using zone 36 S (for South Africa) and WGS-84 ellipsoid in the projected coordinate system. Using the calculate geometry function of ArcGIS finally I calculated the distance from the shooting site to the group's daily last location.

*Ranging area* of the baboon group was estimated through Kernel density estimation, using the reproducible home ranges ("rhr") package in R (Chapter 3, section 3.2.3). Here, ranging area for each persecution time period was calculated based on the locations the baboons visited during that time period.

*Rate of behaviours* (SDBs, grooming and aggression) was determined from the focal sampling data. Rate of a behaviour per minute was calculated for each focal sample by dividing time spent in the activity (seconds) by observation time (minutes). Preparation of physiological data was described in the Chapter 5. I considered two days GC excretion lag time when I aligned physiological data across the above-mentioned time periods (Heistermann et al. 1996, Higham et al. 2009a).

## **6.2.2 Data analysis**

I used a one-way ANOVA to compare the percentage of each category of behaviour across the persecution time periods, as the data were normally distributed for all behaviours (Shapiro-Wilk normality test,  $p > 0.05$ ) and had equal variance across categories (Levene Test,  $p > 0.05$ ). Tukey HSD post-hoc tests were used for the pairwise comparisons between categories.

I used the non-parametric Wilcoxon test to test the behavioural differences between injured and non-injured baboons, as the percentages of behaviours were not normally distributed (Shapiro-Wilk normality test,  $p < 0.05$ ).

I used a Kruskal-Wallis non-parametric ANOVA to compare the ranging behaviours across the persecution time periods. Some ranging behaviours were normally distributed, while others were not, so I adopted a uniform approach. Dunn's post-hoc test was used for the pairwise comparisons between two categories. I used the "Bonferroni" method to perform Dunn's test using "FSA" with the "dunnTest" packages in R.

I used Generalized Linear Mixed Models (GLMM) to assess the effects of persecution events on behaviour and physiology. I ran four models for SDBs, GC levels, grooming and aggression. In all models I included persecution time periods and age-sex as categorical fixed effects, and also included daylength in both the grooming and aggression models. In the GC model I included injury status and dominance rank alongside the persecution time periods and age-sex fixed effects. Individual identity was included as a random factor in all models. Co-linearity between all effects was checked using variance inflation factors, VIF (Field et al. 2012), with a cut-off criterion multicollinearity efficiency value  $>10$  for including variables inside the same model (Myers and Myers 1990). The model was performed by using "lme4" and "lmerTest" packages of R-language and the "CAR" package was used to check the multicollinearity.

All statistical analyses were completed using R (Version 4.0.4, R development core team). All tests were two tailed with a 5% level for significance ( $p < 0.05$ ). For the data visualization I used "ggplot2" with the "cowplot" and "gridExtra" packages in R.

## **6.3 Results**

### **6.3.1 Effects on group size**

The group size of the study baboon group was 25, before persecution events. Seven baboons died in the two events, with an additional four individuals having physical injuries (Table 6.2). Juveniles and infants accounted for 6 out of 7, or 85% of the deaths.



Table 6. 2. Apparent individual effects of persecution events on the baboon group. Number in parenthesis indicates group size after that event.

Individual Identity and social status	Age-sex class	Event 1 (21)	Event 2 (18)
Hound, alpha male	Adult male		Right eye severely wounded
Eggo, high-ranking	Adult female	Lost her infant	Buttocks wounded
Leah, high-ranking	Adult female		Dead
Ruby, mid-ranking	Adult female		Scar on the face
Soshi, mid-ranking	Adult female		Red scar on the ribs
Juveniles		One male and one female juvenile dead	One male juvenile dead
Infants		Two male infants missing	One infant dead

### 6.3.2 Comparison of activity budgets across the time periods

All behaviours fluctuated across the persecution time periods. Nevertheless, there were no significant differences found in percentage of feeding, grooming, resting and moving across the persecution time periods (ANOVA; feeding,  $F(3,39) = 1.31$ ,  $p = 0.286$ ; grooming,  $F(3,39) = 1.90$ ,  $p = 0.145$ ; moving,  $F(3,39) = 1.34$ ,  $p = 0.275$ ; resting,  $F(3,39) = 0.95$ ,  $p = 0.428$ ; Figure 6.2).

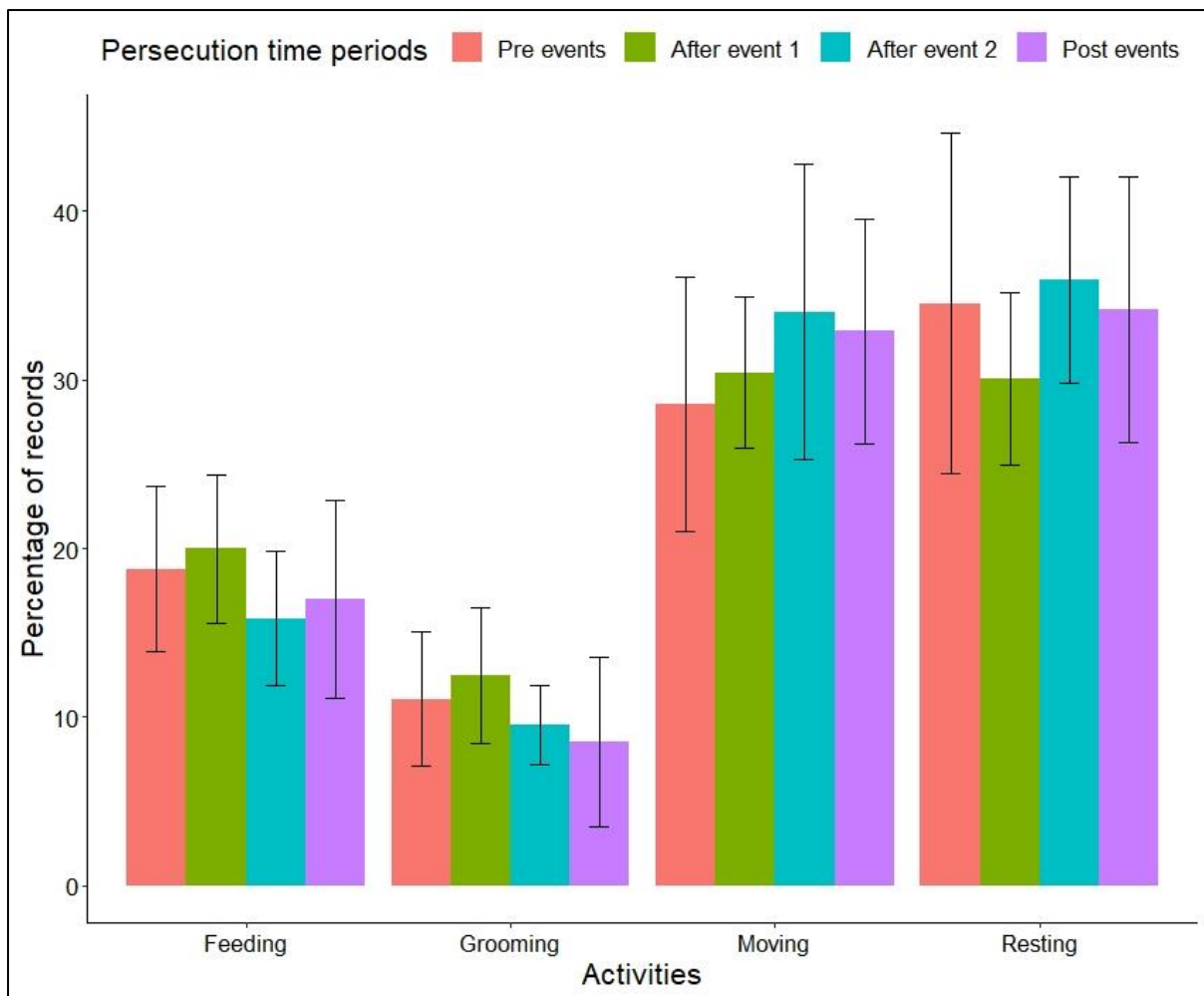


Figure 6. 2. Variation in four major activities across the persecution time periods. Error bars indicate standard deviations.

### 6.3.3 Comparison of activities between injured and non-injured baboons

After the persecution events, changes in feeding, resting and vigilance significantly differed between injured and non-injured baboons; feeding rate decreased while resting and vigilance rates increased in injured baboons (Wilcoxon test; feeding,  $W= 337$ ,  $p < 0.001$ ; grooming,  $W= 578.5$ ,  $p = 0.299$ ; moving,  $W= 1113.5$ ,  $p = 0.833$ ; resting,  $W= 1533.5$ ,  $p < 0.001$ ; vigilance:  $W= 994.5$ ,  $p= 0.033$ ; SDBs,  $W= 126$ ,  $p = 0.248$ ; Figure 6.3).

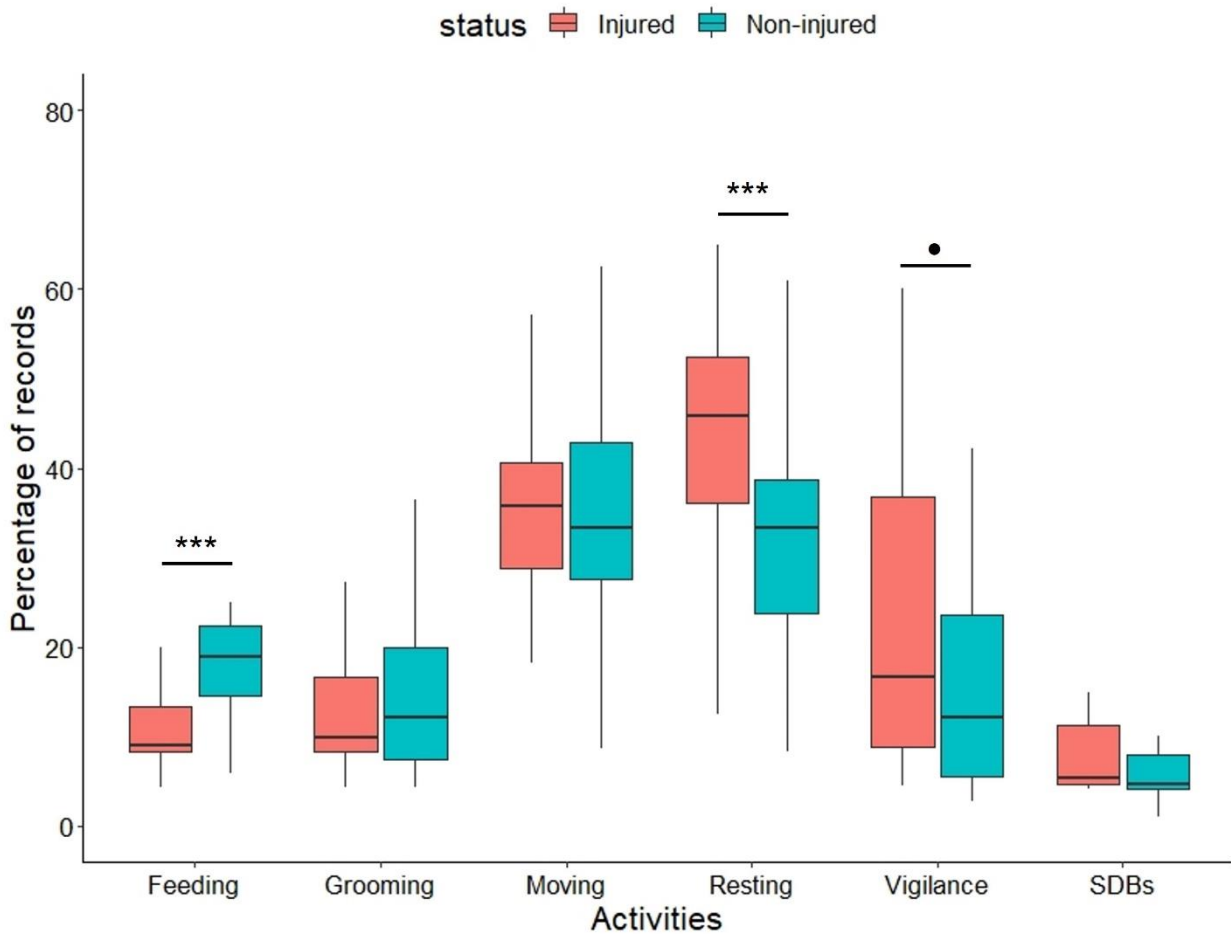


Figure 6. 3. Comparison of behaviour between injured and non-injured baboons during 'After event 2'. Boxes represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values. Horizontal bars above the boxes indicate significant differences. p value, '\*\*\*'  $\leq 0.0001$ , '\*\*'  $\leq 0.001$ , '\*'  $\leq 0.01$ , '•'  $\leq 0.05$ . Physical injury was only observed after the 2<sup>nd</sup> event so the data during 'After event 2' period were used for this analysis.

#### 6.3.4 Effects on ranging behaviours

Travel speed in the first hour of the day differed significantly between the persecution time periods (Kruskal-Wallis test;  $\chi^2 = 7.91$ ,  $df = 3$ ,  $p = 0.047$ ). Post hoc pairwise comparison showed travel speed increased significantly in After event 1 compared to pre events period (Figure 6.4A). Distance of sleeping site from persecution location also differed significantly across the persecution time periods (Kruskal-Wallis test;  $\chi^2 = 23.89$ ,  $df = 3$ ,  $p < 0.001$ ). Post hoc pairwise comparison showed the distances were significantly increased in After event 2 and post events periods compared with pre events and After event 1 periods (Figure 6.4B). Similarly, daily

travel length differed significantly across the persecution time periods and was longer after human persecution events (Kruskal-Wallis test;  $\chi^2 = 8.01$ ,  $df = 3$ ,  $p = 0.045$ ). Post hoc pairwise comparison showed there were significant increases in daily travel length between pre and post events periods (Figure 6.4C). The ranging area was also significantly larger after the persecution events (Kruskal-Wallis test;  $\chi^2 = 38.00$ ,  $df = 3$ ,  $p < 0.001$ ). Post hoc pairwise comparison showed ranging area during After event 2 was significantly bigger than pre and post events periods, and After event 1 was also bigger than pre events time (Figure 6.4D).

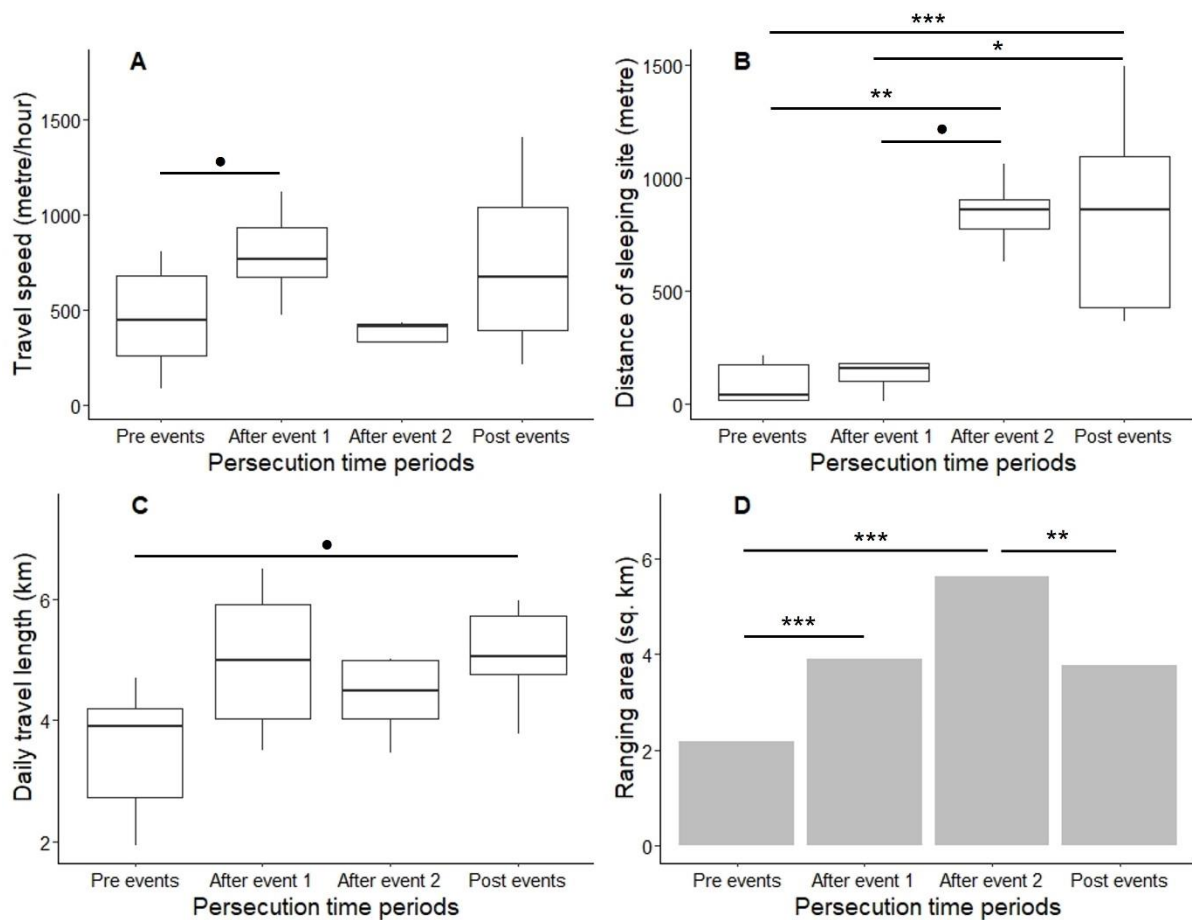


Figure 6. 4. Ranging behaviours of the baboon group across the time periods. Boxes represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values. Horizontal bars indicate significant differences. Kruskal-Wallis followed by Dunn's test; p value, '\*\*\*'  $\leq 0.0001$ , '\*\*'  $\leq 0.001$ , '\*'  $\leq 0.01$ , '•'  $\leq 0.05$ .

### 6.3.5 Effects on behavioural anxiety and physiological stress

Rate of SDBs was significantly increased after both events compared to their respective pre event time periods, with no difference between the pre and post event time periods. SDB rates

returned to the original pre-event levels after the two events (Table 6.3, Figure 6.5). There was no difference observed between age-sex classes (Table 6.3).

Table 6. 3. GLMM analysis for the rate of SDBs, n= 1443. <sup>a</sup>reference category Pre events; <sup>b</sup>reference category adult female.

Predictor variables	Estimate	Std. Error	t value	p value
Intercept	1.57	0.18	8.68	<0.001
Persecution time period <sup>a</sup>				
After event 1	0.89	0.19	4.50	<0.001
After event 2	0.43	0.21	2.09	0.036
Post events	-0.16	0.18	-0.86	0.390
Age-sex <sup>b</sup>				
Adult male	-0.42	0.29	1.45	0.212
Sub-adult male	0.05	0.38	0.130	0.902
Adolescent female	0.19	0.35	0.56	0.585

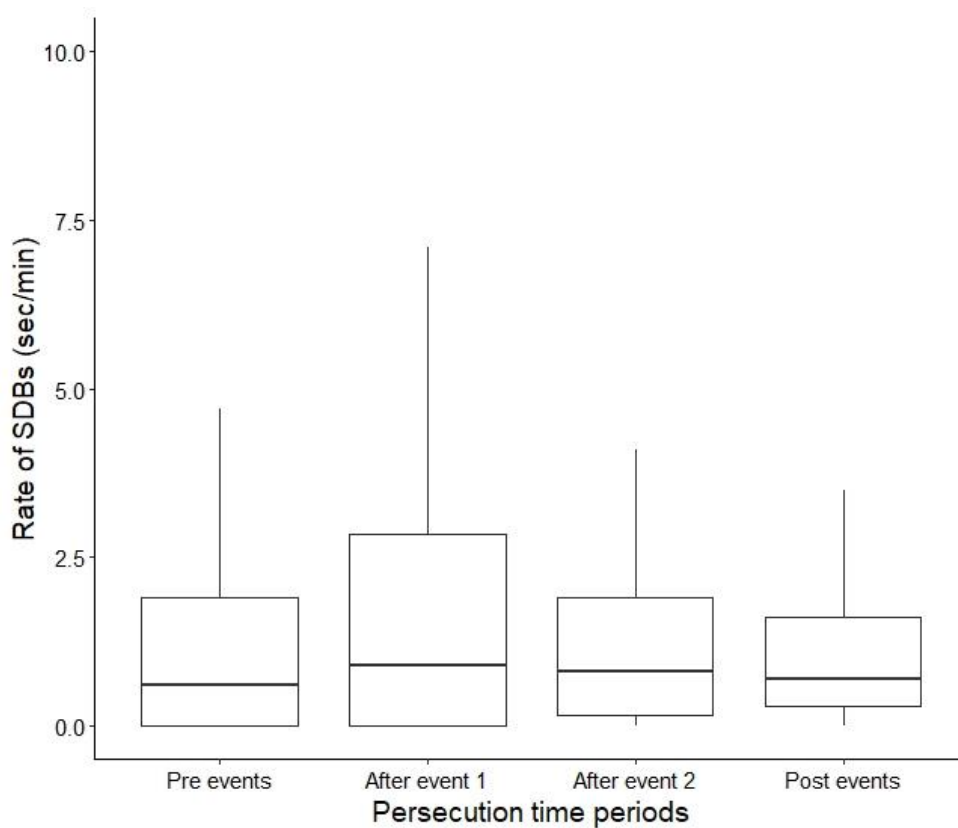


Figure 6. 5. Rates of SDBs across the persecution time periods. Boxes represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values.

GC levels significantly increased after both events and continued into post events time, compared to pre events time period (Table 6.4, Figure 6.6). There was no difference observed in GCs due to dominance rank, injury status or age-sex classes (Table 6.4).

Table 6. 4. GLMM analysis of GC levels across the time periods, n= 160. <sup>a</sup>reference category pre events; <sup>b</sup>reference category injured baboon; <sup>c</sup>reference category adult female.

Predictor variables	Estimate	Std. Error	t value	p value
Intercept	2675.58	819.17	3.26	<b>0.010</b>
Persecution time periods <sup>a</sup>				
After event 1	550.13	216.77	2.54	<b>0.012</b>
After event 2	607.88	283.49	2.14	<b>0.033</b>
Post events	1048.36	245.80	4.27	<b>&lt;0.001</b>
Injury status <sup>b</sup> , non-injured	-144.56	400.36	-0.36	0.718
Dominance rank	-6.51	102.09	-0.06	0.951
Age-sex <sup>c</sup>				
Adult male	-1048.31	772.54	-1.35	0.221
Sub-adult male	-1146.78	816.50	-1.41	0.206
Adolescent female	-559.78	633.54	-0.88	0.410

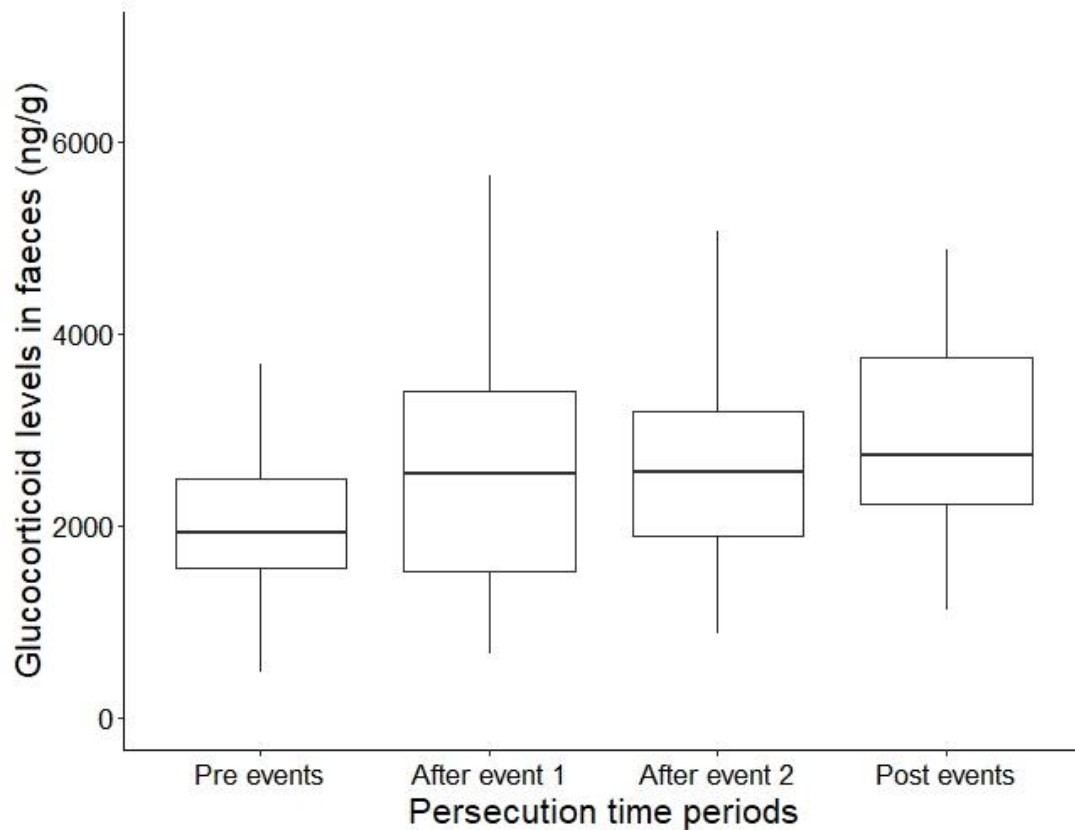


Figure 6. 6. Average GC levels across the persecution time periods. Boxes represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values.

### 6.3.6 Effects on social interactions

The GLMM analysis showed that the persecution effects influenced rate of grooming, grooming was significantly decreased in After event 2 and post events periods compared to pre events time period (Table 6.5, Figure 6.7). Adult males and sub-adult male groomed significantly less than adult females (Table 6.5). Persecution events did not influence the rate of aggression (Table 6.6).

Table 6. 5. GLMM analysis for the rate of grooming, n= 1443. <sup>a</sup>reference category Pre events; <sup>b</sup>reference category adult female.

Predictor variables	Estimate	Std. Error	t value	p value
Intercept	-60.50	36.38	-1.67	0.095
Persecution time periods <sup>a</sup>				
After event 1	-4.11	2.17	-1.89	0.058
After event 2	-6.62	3.19	-2.13	<b>0.033</b>

Post events	-11.98	4.65	-2.58	<b>0.010</b>
Daylength	0.10	0.05	2.02	<b>0.042</b>
Age-sex <sup>b</sup>				
Adult male	-5.89	1.18	-5.00	<b>0.002</b>
Sub-adult male	-6.88	1.53	-4.48	<b>0.005</b>
Adolescent female	-0.29	1.68	-0.18	0.860

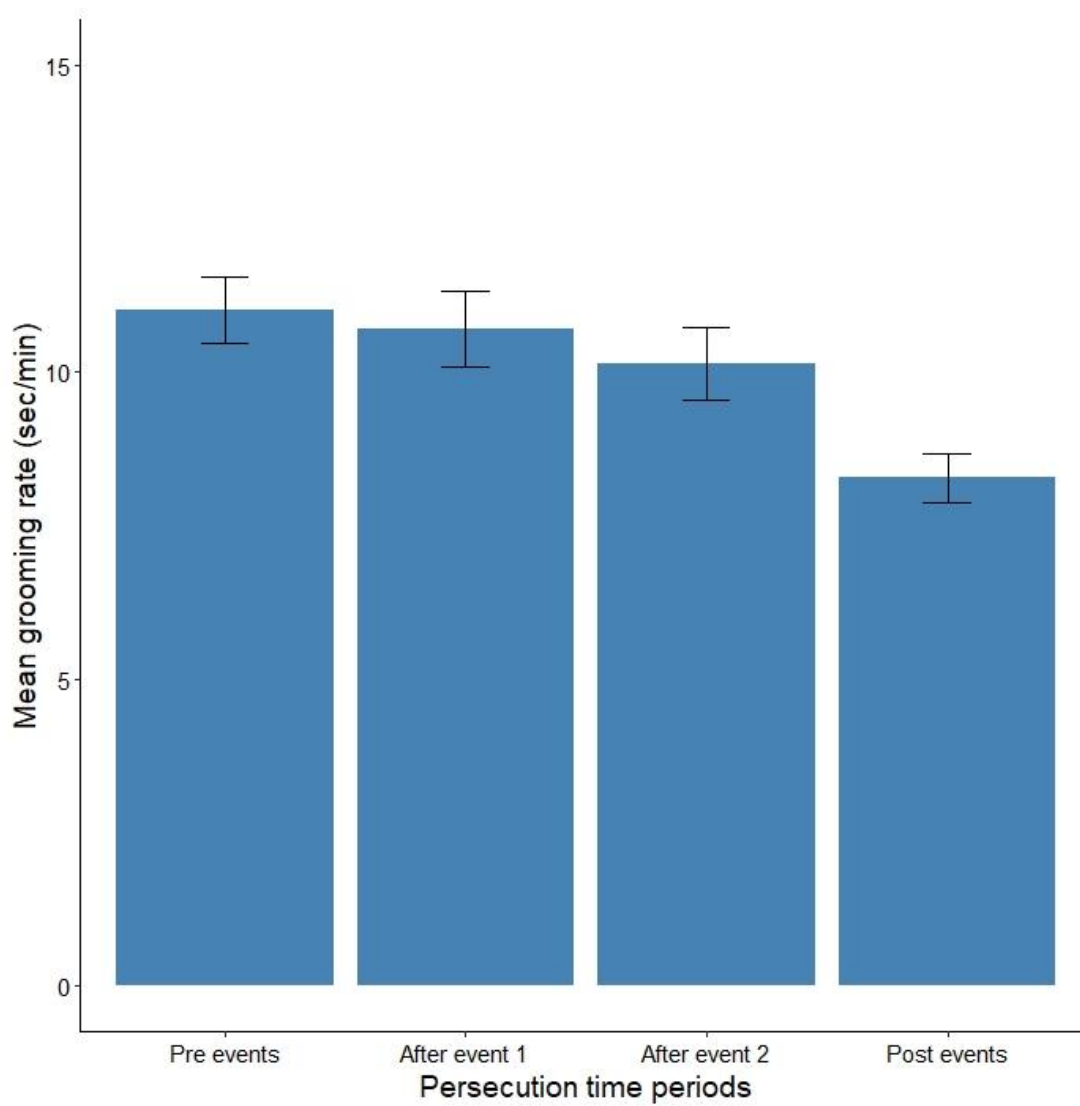


Figure 6. 7. Mean grooming rates across the persecution time periods. Error bars indicate standard errors.



Table 6. 6. GLMM analysis for the rate of aggression, n= 1443. <sup>a</sup>reference category Pre events; <sup>b</sup>reference category adult female.

Predictor variables	Estimate	Std. Error	t value	p value
Intercept	0.63	1.14	0.581	0.561
Persecution time periods <sup>a</sup>				
After event 1	-0.04	0.06	-0.69	0.488
After event 2	-0.11	0.09	-1.13	0.258
Post events	-0.04	0.14	-0.34	0.736
Daylength	-0.0007	0.001	-0.43	0.666
Age-sex <sup>b</sup>				
Adult male	0.05	0.04	1.26	0.252
Sub-adult male	0.02	0.05	0.37	0.727
Adolescent female	0.10	0.05	1.85	0.081

## 6.4 Discussion

Group size of the Alldays Dump Group was greatly reduced after the human persecution events, with juvenile and infant baboons most susceptible to the shootings. While the shooting events did not affect the baboons' overall activity budgets, there were impacts on ranging behaviours. Travel speed increased in the first hour following departure from the sleeping site after the first event; distance of sleeping site from the shooting location increased after the second event. The baboon group travelled longer daily distances after the events, and ranging area increased after both events and remained higher in the period after both events. The baboons who were physically injured fed less, rested more and were more vigilant than non-injured baboons immediately after the injuries. The baboons showed more behavioural anxiety and physiological stress after both events compared to pre events time period; anxiety levels but not GC levels returned to the original levels within the study period after the two events. Shooting events affect grooming interactions; grooming decreased after both events, which continued until the end of this study, although shootings did not affect aggression. The results indicate that the shootings had a very significant impact on the behaviour, and anxiety and stress levels of the baboons.

### **6.4.1 Shootings and their effects on group size**

The baboon group had a commensal relationship with the dump workers (discussed in Chapter 4), but many local people, including children, may possess different attitudes and show aggressive behaviours toward baboons. Many people consider baboons to be the greatest nuisance animal in the region (Findlay 2016). Although shootings occur when animals forage on crops (Kaplan et al. 2011, Mesele et al. 2014), and to obtain bushmeat in other regions (Mwangi 2019), the shootings observed here appear unrelated to these contexts. Over five years of mortality data on chacma baboons in the Cape Peninsula showed that shooting was the second highest human-induced cause of baboon deaths (after vehicle collisions), and it increased over time (Beamish 2010). It seems likely that shootings are a major cause of mortality across the baboons' range.

The group size was greatly reduced after shooting events with over a quarter of the group members killed. Although juveniles and infants were the most vulnerable, one adult female died in the second shooting. She was estimated to be older than other females and was observed remaining at the rear of the group due to slower movement. Physically challenged chacma baboons in the Okavango Delta were more susceptible to predation due to their slower and cumbersome locomotion (Cheney et al. 2006), and this may account for why this adult female was killed in the shooting event.

### **6.4.2 Activity budgets and ranging behaviours**

There were no significant differences in activity budgets at the group level due to the persecution events. At an individual level, however, injured baboons fed less, rested more and spent more time vigilant than their non-injured counterparts. Like other social animals, baboons move as a cohesive group and injured individuals are forced to travel the same distances as the other members. As daily travel length increased after shootings, the injured individuals compensated for their higher moving time by resting more. As resting and vigilance are compatible, injured baboons scanned their surroundings while resting. The increased moving and resting time affect their foraging budgets. Further investigation showed that after shooting events injured baboons' feeding rate on dump foods was higher than non-injured baboons, suggesting that injured baboons probably compensated their reduced feeding time by increasing foraging on dumped foods, which was most likely the easiest way to compensate the feeding deficit. Similar compensation patterns were also

observed in chacma baboons in the Cape Peninsula, where injured baboons foraged more on crops and other anthropogenic food sources than natural vegetation (Beamish 2010).

Persecution events affected the baboons' ranging behaviours. Travel speed increased after the first event, and the distance of the sleeping site from the shooting location increased after the second event. Both shootings occurred at the water tower, sleeping site. After the first event, the baboons retained the sleeping site, but left the site quickly everyday morning, which was probably a strategy to avoid the potential risk of shooting. However, after the second event, they shifted the sleeping site, possibly due to the cumulative effects of the two events. Again, after the second event, they visited new ranging area where I had never been with them before, resulting in longer travel distances and larger overall ranging area. Nevertheless, they continued visiting the dump on a daily basis.

#### **6.4.3 Behavioural anxiety and physiological stress**

As predicted, baboons' anxiety levels, measured by SDBs, increased after both persecution events. Similar responses have been noted in wild brown lemurs in southern Madagascar, where SDBs increased after predatory attacks (Palagi and Norscia 2011). Several primate studies have also shown that SDBs increased under anxiety-inducing conditions, such as interactions with tourists (Maréchal et al. 2011), aggressive interactions (Maestripieri et al. 1992, Troisi 2002), and having dominant individuals nearby (Troisi and Schino 1987, Castles et al. 1999). This suggests that baboons were more anxious after the shootings than before shooting events.

The persecution events were also associated with a significant increase in GC levels in the baboons. This is very similar to responses found in a chacma baboon group in Okavango Delta where female GC levels significantly increased when predation and infanticide occurred (Engh et al. 2006a, b). The GC levels remained elevated during post events period and had not return to the initial pre events levels by the end of the study. This suggests that the physiological effects may be prolonged beyond the 19 days used for analysis. GC levels of female chacma baboons were higher in the four weeks following a predation event (Engh et al. 2006a) and an infanticide attempt (Engh et al. 2006b), which is consistent with this finding. The results also showed that there was no significant difference of GC levels between injured and non-injured baboons. This result suggests that witnessing baboons being killed and losing peers may be more important to a rise GC levels than individual injury.

#### **6.4.4 Social interactions**

The rate of grooming varied in relation to the persecution events, and unexpectedly, the grooming rate decreased following the first persecution event. Several studies have suggested that grooming has a function to decrease stress and anxiety (Boccia et al. 1989, Shutt et al. 2007), and chacma baboons extended their grooming network following predation events (Engh et al. 2006a). The study results do not fit this pattern and the back-to-back shooting and loss of young baboons within a short period may have damaged stable grooming networks. Usually, female baboons restrict most of their grooming to a small number of individuals (Engh et al. 2006a), and the loss of close grooming partners, and particularly the three infants in this study, could have resulted in a decrease in overall grooming time.

The persecution events affecting the Alldays Dump Group did not have significant impact on the rate of agonistic interactions. Similar responses found in a wild feeding chacma baboon group in Okavango Delta where the rate of aggression among female baboons remained unchanged during socially stressful situations such as a male immigration to the group (Wittig et al. 2008).

#### **Conclusion**

In this chapter, I showed the behavioural and physiological effects of one of the major causes of the human-induced death of baboons. Activity budgets of baboons who were physically injured altered after the persecution events, with all baboons showing more behavioural anxiety and physiological stress after the shootings. Ranging behaviour also varied after the persecution, and while the water tower continued to be used as a sleeping site after the first event, the group changed sleeping site after the second shooting event. Nevertheless, dump resources remained important, and while the baboons' relationship with humans remained commensal at that location, the risks and costs associated with living in a human-modified habitat had profound impacts on behaviour and physiology due to the lethal interactions at their sleeping site.

## Chapter 7. Overall discussion

As a result of human encroachment into wildlife habitat, urbanization and increasing human populations, co-occurrences of human and primates are increasing across range countries. Living close to humans, some primates have adapted using their dietary flexibility to include human foods into their diet. The main aim of this study was to investigate what a human rubbish dump contributes to a baboon group as a potential human food source, and what the impacts are of accessing this food source on the baboons' behaviour and physiology.

### 7.1 Impacts of dump foods on baboon behaviours

Feeding time of the Alldays Dump group of baboons was significantly less than both wild foraging chacma baboons and other anthropogenic foraging baboon groups. The difference from naturally foraging baboons is expected, but the difference from other anthropogenic foragers indicates that dump foods were nutritionally richer and/or required less processing than other anthropogenic food sources, satisfying individuals' foraging demands quickly (Fa 1986), and allowing them to increase other activities, such as resting (Saj et al. 1999). Resting time was almost double that of naturally foraging chacma baboons and similar to other anthropogenic foraging baboons, as expected. Decreasing feeding time and increasing resting behaviour was also observed in other primate taxa having access to other human foods (Malik 1986, Altmann and Muruthi 1988, Saj et al. 1999, Unwin and Smith 2010, Jaman and Huffman 2013).

The studied baboon group ranged over a comparatively smaller area and travelled shorter distances compared to naturally foraging chacma baboon populations elsewhere. Unlike natural foods, which are usually distributed heterogeneously, are unpredictably available, and may require longer travel distances to meet nutritional requirements (Ganas and Robbins 2005), dump foods were predictable, and relatively homogeneously distributed. Consequently, the group was able to satisfy their nutritional requirements within a small ranging area. This

pattern of ranging behaviours is commonly observed in the other primates incorporating anthropogenic foods into their diet (Anderson 1981, Altmann and Muruthi 1988, Saj et al. 1999, Warren 2003, Higham 2006, Strum 2010, Van Doorn et al. 2010, Hoffman and O'Riain 2011, Hoffman and O'Riain 2012b).

It was expected that Alldays Dump baboons' dietary diversity and feeding time would vary according to seasonal changes in food availability, and that priority access to the dump foods would depend on the baboons' social status. But the study results showed that baboons of all age-sex classes fed more on dump foods than on natural foods in both seasons. In addition, their natural diet was less diverse compared to that of wild foraging (Norton et al. 1987, Barton 1989, Kunz and Linsenmair 2008, Ellwanger 2020, Pebsworth 2020) and anthropogenic foraging baboon groups elsewhere (Boug et al. 1994, Okecha and Newton-Fisher 2006, Henzi et al. 2011). It is probable that increased availability and easier accessibility of the dump resources throughout the year influenced these results.

Unlike crop foraging and human provisioning, dump foraging is apparently risk free, in terms of people's interests in a dump and baboons accessing food there. The dump was not closely managed, and no deterrent methods were used against baboons. In addition, dump resources contained high energy foods which were replenished frequently. The high degree of behavioural and dietary flexibility by the studied baboons compared to their natural and anthropogenic counterparts strongly suggests that dump foods can be considered as an extreme form of potential anthropogenic food source.

## **7.2 Impacts on behavioural anxiety**

The integrated approach used to measure behavioural anxiety, assessed through self-directed behaviours, aggression and vigilance, revealed that the baboons showed more behavioural anxiety when they were in the dump compared to when they were outside. Dump foods were highly concentrated in a constant location and very predictable, as other human food sources (Saj et al. 1999, Ilham et al. 2018). Several studies report that anxiety-inducing intragroup aggression is related to the concentration of resources (El Alami et al. 2012, José-Domínguez et al. 2015, Ilham et al. 2018). The concentrated dump resources and resulting aggression may influence increased anxiety levels of the studied baboons. However, unexpectedly, known social and anthropogenic stressors, such as the presence of baboons from different groups and humans nearby, which are recognised causes of animal anxiety, did not significantly affect

overall anxiety levels. Instead, the studied baboon group may have benefited from the presence of humans and other baboon groups on the dumps.

### **7.3 Impacts on physiological stress**

The hormonal results showed that the studied baboons did not show variable energetic stress related to dump food availability, and only females showed psychosocial stress related to aggression, suggesting their higher sensitivity to psychosocial stressors (Beehner et al. 2005, Engh et al. 2006a, b). The fact that the baboons were behaviourally anxious in the dump but the variation of dump foods did not affect their energetic stress levels, suggests that the anxiety experienced by the baboon group may be triggered by relatively mild stressors which may not be sufficient to induce adrenal activity to release cortisol hormone (Higham et al. 2009a). In Barbary macaques not all levels of anxiety were associated with glucocorticoid secretions (Maréchal et al. 2011). A study of captive hamadryas baboons suggested that SDBs may reflect acute emotional responses, whereas elevations of glucocorticoids require a potentially severe social threat (Pearson et al. 2015). Together, these suggest that increased anxiety in the dump was associated with competition between conspecifics over the concentrated dump resources, which was not strong enough to elevate glucocorticoid levels in the studied baboons. The availability of dump foods may relieve the baboons from energetic and psychosocial stress, the latter at least in males, but these resources may be the cause of increased short-term anxiety to the baboons.

### **7.4 Impacts on physiological energetics**

As expected, thyroid hormone levels, which are an index of basal metabolic rate, were positively related to both dump and natural food availability and negatively related to daily distance travelled, suggesting similar relationships with energy acquisition and energy expenditure, respectively, presumably reflecting the maintenance of energy balance. Similar energy maintaining strategy has been observed in other wild feeding primates living in seasonally varied habitat (Thompson and Knott 2008, Grueter et al. 2014, Gesquiere et al. 2018b).

The results also showed that thyroid hormone levels did not significantly vary either between sexes or between reproductive stages in female baboons. This result is unexpected in the context of the high energetic demands during pregnancy and lactation periods in females (Dias et al. 2017, Gesquiere et al. 2018b), and mating activities in males (Kaack et al. 1980,

Petter-Rousseaux 1984, Cristóbal-Azkarate et al. 2016). These results suggest that improved energetic conditions, achieved through consuming high-quality dump foods, may help to reduce further energetic demands during the highly energy-demanding reproductive stages.

## **7.5 Threats and challenges living in anthropogenic habitat**

Primates living in human-modified habitat face multifaceted challenges including ecological constraints and human-wildlife conflicts, and in the case of pest species, the challenges are even more intense. Baboons are one of the most nuisance animals, considered as a pest throughout the African continent (Webber and Hill 2014). Since the study area is mostly dominated by game farms, owning firearms was commonplace. It was also observed that people used firearms for unauthorized purposes, such as shooting birds. Baboons' pest status and unregulated use of firearms posed a great threat to the baboon group. The study group experienced two shooting events, which severely affected the baboons through the deaths of several individuals, and those who survived experienced higher anxiety and stress levels.

## **7.6 Weakness and limitations of this study**

In this study I initiated a novel approach of estimating dump food availability, based on the weighing of foods in a bag and counting the number of dumped bags. As observed in other novel initiatives, I also faced some issues that need to be acknowledged, and appropriate cautions need to be placed while interpreting the related results.

First, collecting the number of daily dumped bags was a challenge and estimation of bag numbers was even more challenging. The size of the dumped bags was not always even and in the case of big dumping trucks there was a high chance of being significantly over or under in the estimates of bag number recorded. As the number of dumped bags was the main driver for dump resources, maintaining a regular log with fairly accurate counting is important to get a good picture. To collect this data, I had to depend on the security guards, who were not regular and confident in this regard.

Second, it is important to maintain appropriate caution while interpreting the results of biweekly dump food availability. Most of the dump foods were either processed, cooked, prepared for humans, or vegetables and fruits that usually degrade quickly. Due to their degradable nature, dump foods were completely rotten within a short period of time. So, the estimated quantity of available dump foods in a biweekly food assessment block was not available across those 15 days; rather it represented food availability for shorter period.



Finally, the field data collection was interrupted by Covid restrictions for a period of seven weeks, which was completely unavoidable. By chance, this period was the time of seasonal transition. Data collection during the seasonal transition would help to understand in closer detail how the baboons moved through the transition in relation to their behaviours and physiology.

## **7.7 Potential future studies**

This study opens an avenue for future studies on the impacts of dump feeding. For example, a future study could focus on how intensive utilization of human foods influences disease prevalence and overall health conditions, as well as the impact of diseases and/or health risks on the energetics and stress levels of the baboons. I found plastic pieces, different sizes of worms, most likely helminths (thread worms), and cestodes parasites (ribbon-like worms) in the faeces while collecting samples. However, I did not collect or identify these parasites, which was beyond the scope of this study, but this is very important to consider regarding health issues. This could be achieved through clinical investigation or non-invasive parasitological analysis of faecal and urine samples or a combination of both. Another study could focus on quantifying actual energy intake from the dump foods as well as from the surrounding natural foods, which would help to draw a better picture of energetic importance of dump foods and how baboons' dump energy intake varied with the seasonally fluctuating natural foods.

## **Conclusion**

This study addresses some existing research gaps by investigating a combination of both the behavioural and physiological responses of a chacma baboon group to garbage-feeding. For the first time, behavioural and measures plus faecal measures of glucocorticoid and thyroid hormones to get anthropogenic foraging wild chacma baboons. This study also initiated a novel approach of estimating food availability in the dump, which could be used as a baseline for similar research in future. The results showed that, dump foods contributed foraging and dietary shifts to a greater extent than for baboons feeding on natural foods and even other human foods. The ranging patterns were also modified, home range and daily travel length both decreased compared to wild foragers. Dump foods also provided energetic benefits to the studied baboons. These results emphasizes that dump feeding could be considered as an extreme form of anthropogenic feeding. However, there were some significant costs in terms

of anxiety, physical injury and death associated with living close to the human population surrounding the dump resources.

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# Appendices

## Appendix 1- License issued for transporting faecal samples from South Africa

 <b>Animal &amp; Plant Health Agency</b>	<div style="border: 1px solid black; padding: 2px; display: inline-block;">                 Authorisation No: ITIMP21.1172             </div>
<p><b>EUROPEAN COMMUNITIES ACT 1972</b></p> <p>The Trade in Animals and Related Products Regulations 2011 (as amended)                  Animal By-products (Enforcement) (England) Regulations 2013,                  Animal By-products (Enforcement) (Scotland) Regulations 2013,                  Animal By-products (Enforcement) (Wales) Regulations 2014.</p>	
<p><b><u>AUTHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH AND DIAGNOSTIC SAMPLES</u></b></p> <p>The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of The Trade in Animal and Related Products Regulations 2011 authorises:</p>	
<div style="border: 1px solid black; padding: 5px;">                 Professor Ann MacLarnon                  Hatfield College                  Durham University                  North Bailey                  Durham                  DH1 3RQ             </div>	<p><i>Name and full address of importer responsible for consignment</i></p>
<div style="border: 1px solid black; height: 30px; width: 100%;"></div>	<p><i>Full address of destination premises (if different from importer)</i></p>
<p>to land in England, in accordance with the conditions set out below,</p>	
<div style="border: 1px solid black; padding: 5px;">                 Faeces from wild baboons, intended for particular studies or analyses only. (Not for resale).             </div>	<p><i>Product</i></p>
<p>from</p> <div style="border: 1px solid black; padding: 2px; display: inline-block;">                 South Africa             </div>	<p><i>Countries of origin</i></p>
<p>at</p> <div style="border: 1px solid black; padding: 2px; display: inline-block;">                 All ports and airports in England             </div>	<p><i>Ports of entry</i></p>
<p><b>This licence expires on 2 years less one day from the date of signature.</b></p>	
<p>Signed: </p> <p>Name: Anthony Williams                  Officer of the Animal and Plant Health Agency                  authorised by the Secretary of State.</p>	<p>Dated: 27/08/2021</p> <div style="text-align: center;">  </div>
<p>Page 1 of 4</p>	



## Appendix 2- Ethical approval for this study

**Ethical Approval: ANTH-2019-05-13T13:11:53-xxxv76** 🔍 ✓

Dear Rahman,

The following project has received ethical approval:

Project Title: *Behavioural and hormonal responses to anthropogenic food sources in chacma baboons, Papio ursinus*;  
Start Date: 01 August 2019;  
End Date: 31 December 2020;  
Reference: ANTH-2019-05-13T13:11:53-xxxv76  
Date of ethical approval: 28 August 2019.

This project has been approved by the Animal Welfare Ethical Review Board, subject to approval of health and safety arrangements by your department or other appropriate health and safety committee.

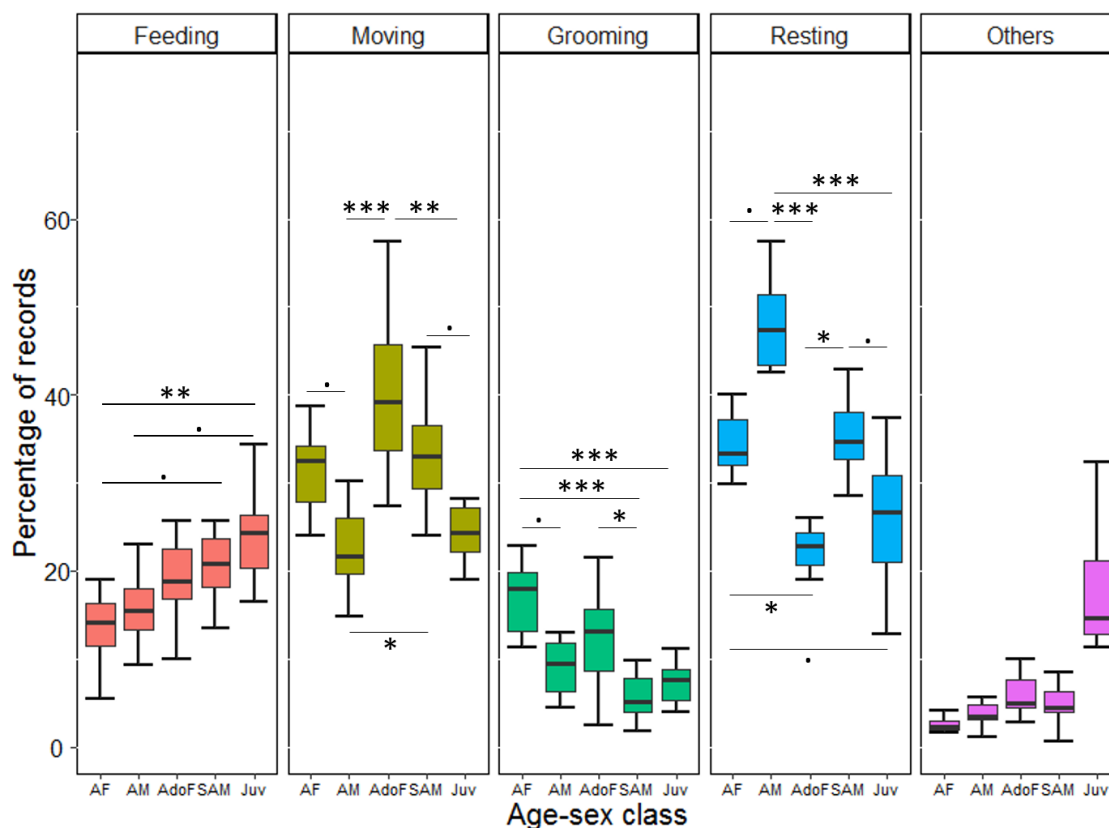
AWERB requests a brief end of project report at the conclusion of all approved projects: see <https://www.dur.ac.uk/research.innovation/governance/ethics/process/awerb/reports/>. Please be aware that if you make any significant changes to the design, duration or delivery of your project, you should contact [research.policy@durham.ac.uk](mailto:research.policy@durham.ac.uk) for advice, as further consideration and approval may then be required.

If you have any queries regarding this approval or need anything further, please contact [research.policy@durham.ac.uk](mailto:research.policy@durham.ac.uk)

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If you have any queries relating to the ethical review process, please contact your supervisor (where applicable) or departmental ethics representative in the first instance. If you have any queries relating to the online system, please contact [research.policy@durham.ac.uk](mailto:research.policy@durham.ac.uk).

### Appendix 3- Age-sex differences in activity budgets of the studied baboons



Supplementary Figure 1. Percentage of time spent in different activities across age-sex classes of the Alldays Dump Group. AF= Adult female, AM= Adult male, AdoF= Adolescent female, SAM= Sub-adult male, Juv= Juveniles. Boxes represent the interquartile ranges and horizontal lines represent the medians; whiskers indicate minimum and maximum values. Symbols indicate significant differences between age-sex classes (Dunn's test: p value, '\*\*\*'  $\leq 0.0001$ , '\*\*'  $\leq 0.001$ , '\*'  $\leq 0.01$ , '•'  $\leq 0.05$ ).

### Appendix 4- Preparation of frozen samples for Enzyme Immunoassay

#### Freeze drying and grinding of samples

The frozen faecal samples were freeze-dried (FreeZone 4.5 Liter Benchtop Freeze Dryers, Labconco) at around  $-50\text{ }^{\circ}\text{C}$  temperature and around  $0.003\text{ pa}$  pressure for approximately 48 hours. Caps of the sample bottles were slightly loosened, so that moisture from the samples could be drawn out. Between freeze-dried batches I cleaned and sanitized the sample reservoir with 1:10 distal solution. After freeze-drying, I transferred the samples to a micro-safety cabinet (model- Bio3/1 +R 1.2M, Envair) for grinding.

Grinding was carried out with the airflow off settings in the micro-safety cabinet, to prevent very light powder flowing around the cabinet. I used a heavy-duty dry and wet grinder (model WEG60K, Waring commercial) for this purpose. A dried sample was placed in the grinder and run for about a minute. A scrap paper was used under a sieve (500  $\mu\text{m}$  diameter) to collect faecal powder. I dumped any remaining in the sieve into an autoclave bag and banged the sieve couple of times in the bin to make sure all unwanted matter fell off the sieve. The faecal powder was then poured back into its bottle. I cleaned the grinder, metal scoop and working surface with 1:10 distal, and wiped them dry with paper towel. I did not clean the sieve with distal because it is difficult to dry and all unwanted matter should come off with a good bang.

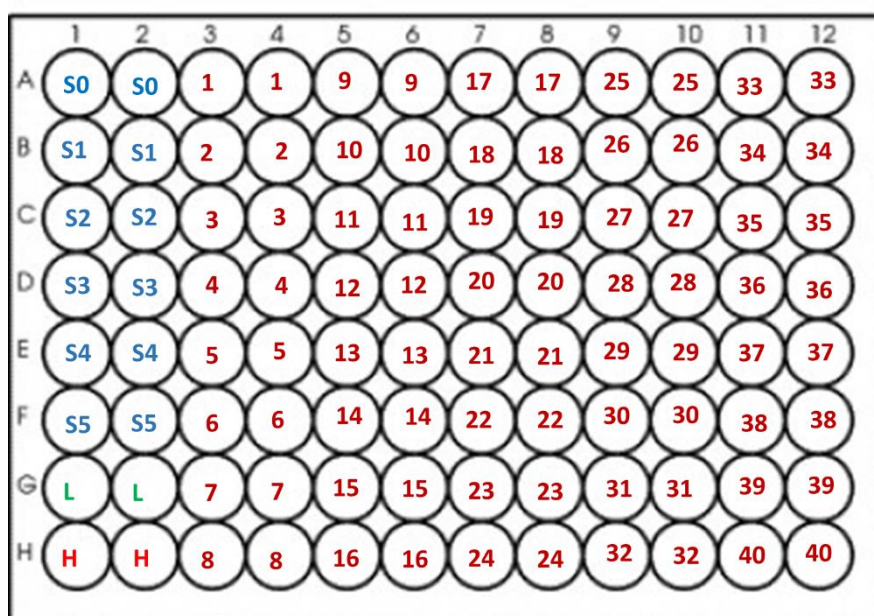
### **Hormone extraction and storage**

I weighed out 0.1 g dry faecal powder into prelabelled 15 ml centrifuge tubes by using a metal spatula. I rinsed this spatula with 70% methanol and dried before using again. Then I added 3 ml 80% methanol to each tube containing dry faecal powder. The tube was capped immediately to prevent evaporation. I repeated this procedure for all samples. The samples were then agitated on a tube shaker (Fisher ANA Multi-tube vortexer, model no- 945092) at speed ~7 for 10 minutes. The tubes were then centrifuged at 4000 rpm for 12 minutes at 4°C. The resulting supernatant was poured off into prelabelled 2  $\times$  1.5 ml microcentrifuge tubes without disturbing the pellet. I then stored the tubes in -20 °C freezer until further analysis started.

### **Drying and resuspension of hormonal extracts, and running T3 assays**

For analysing T3 hormones, the samples needed an extra step whereby the extracted frozen samples were dried and resuspended with de-ionized water. I took sample extracts that were stored in the freezer and vortexed them thoroughly, then centrifuged them for 1-2 minutes to pellet the sediment. I took 180  $\mu\text{l}$  extract and transferred this to a prelabelled glass tube (12 $\times$ 75 mm). The tubes were then placed in a sample concentrator (Techne Dri-Block®, model no DB100/3), whose temperature was pre-fixed at 45 °C. Nitrogen flux was then conducted in the glass tubes. The sample concentrator was placed in the micro safety cabinet, and I kept the airflow on in the cabinet while flowing Nitrogen gas. This combined drying method (heat and gas simultaneously) took around 35-45 minutes to dry all samples. I reconstituted the dried samples with 240  $\mu\text{l}$  of deionized water and vortexed for 10-15 seconds or until they were

dissolved completely. The samples were then analysed with an ELISA kit. If the plate was not made immediately, the tubes were sealed and stored in the fridge at 4 °C.



Supplementary Figure 2. Layout of Total T3 assay plate; S0-5= Standards, 1-40= Samples, H= Quality Control High, L=Quality Control Low.

## Appendix 5- Enzyme Immunoassay principle

The basic principle of the EIA used in this study is a competitive reaction between an unknown concentration hormonal metabolite (the antigen) present in the faecal sample and a known concentration labelled antigen.

Competitive binding process  $[Ab] + [Ag] + [Ag^*] = [AbAg] + [AbAg^*] + [Ag] + [Ag^*]$

Where Ab= antibody (known quantity), Ag = antigen (unknown quantity), Ag\*labelled antigen (known quantity)

The labelled antigen competes with the unknown antigen in the sample solution to bind to an antibody which originally raised against the antigen. The success of this competition is negatively related to the relative concentration of the unknown antigen. After any unbound antigen has been removed by washing, streptavidin peroxidase is added which binds with the bound labelled-antigen, followed by a chromogenic substrate (TMB) which binds to the bound streptavidin peroxidase causing a change colour. The degree of colour change is therefore negatively related to the concentration of the unknown antigen in the sample. The

precise concentration of the hormone in the sample can then be determined by measuring the optical density of the solution.

These reactions took place on a plate consisting of 96 wells. In order to determine the exact relationship between the optical density of the solution in one of the wells and the concentration of the hormone metabolite in that well it is necessary to run a series of the competitive reactions with solutions containing known concentrations of the antigen (standards). A curve can then be created which describes the relationship between the optical density and the known metabolite concentration. The precise concentration of the metabolite in each well can then be determined from its optical density using this curve.

## **Appendix 6- Plate coating and ELISA procedure**

### **Plate coating- takes three days**

#### **Day 1:**

- Prepare a solution of 1mg/ml IgG and add certain amount of coating buffer to it.
- Dispense this mixture 250  $\mu$ l/well.
- Cover plates with cling film and leave overnight at 4 °C.

#### **Day 2:**

- 1) Pour off the IgG and coating buffer solution from plates.
- 2) Bang the plates dry on some paper towel on the bench.
- 3) Dispense 300  $\mu$ l of Assay Buffer / 1% BSA into each well.
- 4) Cover the plates with cling film and keep at 4 °C overnight.

#### **Day 3:**

- 1) Pour off the solution and blot plates dry. Freeze at -20 °C for storage.

### **ELISA procedures- takes two days**

Faecal extracts and standard solutions were diluted in assay buffer. A reference standard curve was created from eight serial dilutions of a known concentration standard (12,500 pg/50  $\mu$ l), generating nine different concentrations in the range of 2.44-625 pg/50  $\mu$ l (Supp. figure 3). The previously coated plate was used to conduct this assay.

	1	2	3	4	5	6	7	8	9	10	11	12
A	BL	BL										
B	Zero	Zero	S 4	78								
C	S 9	2.43	S 3	156			QCH1	QCH1				
D	S 8	4.87	S 2	312			QCL1	QCL1				
E	S 7	9.75	S 1	624								
F	S 6	19.5							QCH2	QCH2		
G	S 5	39							QCL2	QCL2		
H												

Supplementary Figure 3. Layout of GC assay plate; S1-9= Standards and the corresponding values denoting concentration of that standard, QCH= Quality Control High, QCL=Quality Control Low. Rest of the wells get samples.

#### Day 1:

*Step 1: take out the plate and reagents from the freezer and leave until they reach room temperature*

- a coated plate
- aliquoted standards and quality controls (yellow=standard, purple=QCH, blue=QCL)
- aliquoted biotin labelled steroid (antigen)
- aliquoted steroid-specific antibody

*Step 2: preparation of reagents*

- make fresh assay buffer or use previously made that stored in the fridge (can be used up to one month)
- prepare standards by following instructions on the top sheet
- add 5.5 ml (5500  $\mu$ l) assay buffer to biotin labelled steroid (antigen) and mix thoroughly
- add 5.5 ml (5500  $\mu$ l) assay buffer to antibody and mix thoroughly

***Step 3: wash the plate and dispense the prepared reagents (follow the order below)***

- wash the coated plate 3 times with plate washer
- dispense 100 µl assay buffer to blank and 50 µl to zero well
- dispense 50 µl standards to specific wells
- dispense 50 µl quality controls to specific wells (purple tube=QCH, blue tube=QCL)
- dispense 50 µl samples or H & L to respective wells
- dispense 50 µl biotin labelled steroid (antigen) to all wells
- dispense 50 µl antibody to all wells, except blank

***Step 4: seal the plate and incubate in the fridge***

- seal the plate with cover film and place on the plate shaker for 10 minutes
- incubate the plate in the fridge for overnight

**Day 2:*****Step 1: take out the plate from fridge, leave to reach room temperature and then wash 3 times in plate washer******Step 2: prepare and dispense fresh enzyme solution for streptavidin reaction***

- take 30 ml assay buffer (leave to reach room temperature), add 1 µl Streptavidin-POD-conjugate and stir well through clock and anti-clockwise rotating
- dispense 150 µl to each well.
- cover the plate and incubate on the plate shaker for 45 minutes

***Step 3: wash the plate, prepare and dispense substrate solution for colour reaction***

- wash the plate 3 times in plate washer
- take 30 ml substrate buffer from fridge and leave until reaches room temperature. Add 500 µl TMB (20 mg in 5 ml DMSO) and 100 µl of 0.6% H<sub>2</sub>O<sub>2</sub> (30 µl in 1.75 ml water) to this solution and mix thoroughly by clock and anti-clockwise rotating
- dispense 150 µl this TMB mixture to each well
- cover the plate (make sure dark condition) and incubate on the plate shaker for 45 minutes

**Note:** the desired blue colour might reach before 45 minutes, or after 45 minutes, so need to watch it for appropriate colour so that the zero (blank deducted) reading comes with ~1

***Step 4: Stop the reaction and read the plate***

- stop the reaction by dispensing 50  $\mu$ l stop solution (2M H<sub>2</sub>SO<sub>4</sub>)
- read the plate in a plate reader with appropriate template

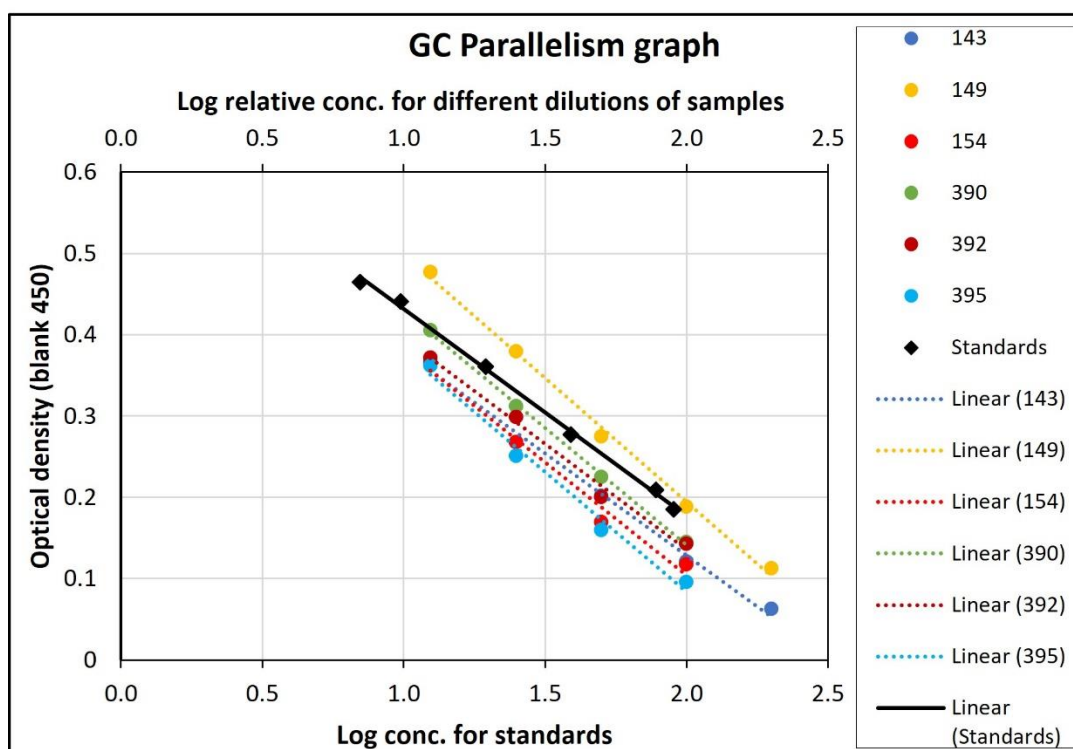
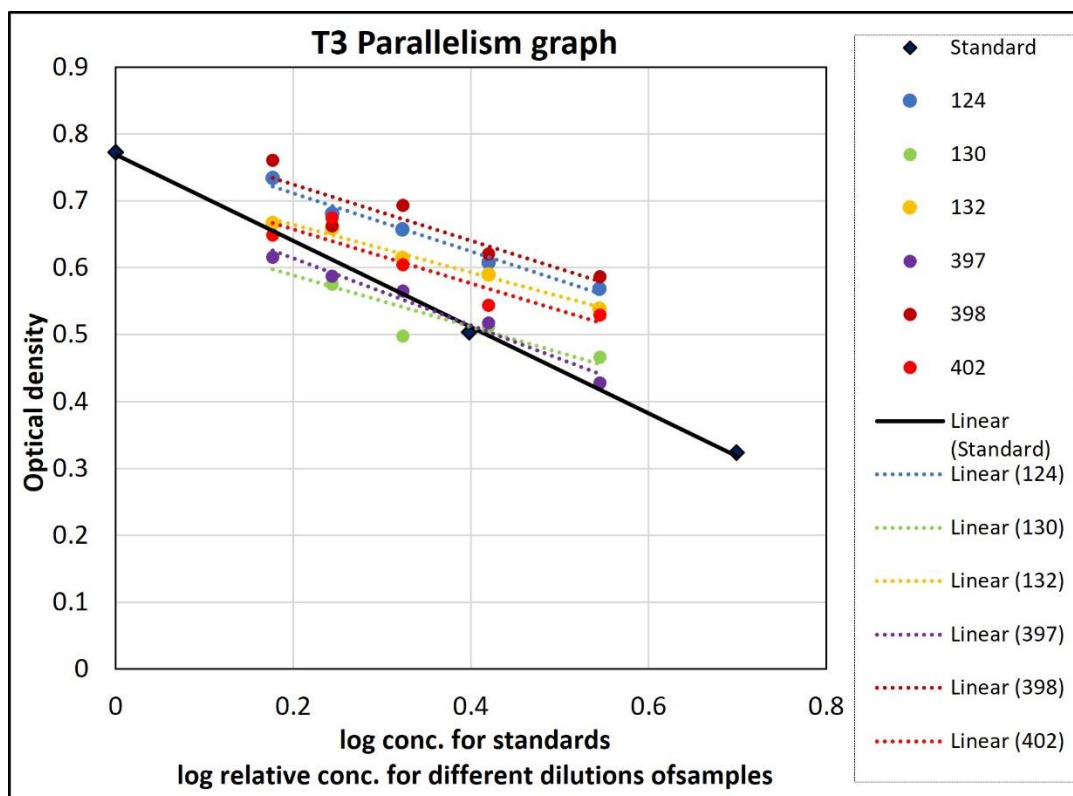
Before running the sample plates, plate tests and dilution and parallelism tests, were conducted. Standards, quality controls and samples were run in duplicates and the samples were repeated in next plate if there was more than 10% variation between the duplicates, called poor duplicate. And the whole plate was repeated if there were more than five poor duplicates occurred in a plate.

## **Appendix 7- Dilution and parallelism tests**

Dilution tests allows to determine which dilution factor gives the most central value of the optical density of the most samples fall within the linear range of the standard curve. Five different dilutions were used in these tests. Dilution tests were carried to see whether sample dilutions diluted in parallel. For example, would a sample diluted by a factor of 3 be measured, using the curve, as 3 times weaker than the original? Ideally, doubling the dilution of the sample may not produce the same change in measurements as doubling the dilution of the standard, because the impurities in the sample extracts. The sample extracts were prepared from faeces which contain all sorts of different compounds can interfere with the reactions. Parallelism tests were carried out in order to determine whether the sample dilutions reacted similarly to the solution used to construct the standard curve. However, my aim was to test all samples at the same dilution, or as close to this as possible.

Six samples, three pair of individuals, were selected for these tests (Supp. table 1 & 2). I choose samples from two extreme food availability conditions i.e. when natural foods were available and limited. I also accounted individuals' sex and reproductive class while selecting samples for these tests. For T3, each extracted raw sample was dried in conjunction with Nitrogen flux and heat, and then reconstituted with 180, 240, 300, 360 and 420  $\mu$ l of deionized water to give a series of dilutions (details in the sub-section drying and resuspension of hormonal extracts in appendix 4), while for GC, the samples were diluted by assay buffer in 1:20, 1:40, 1:80, 1:160, 1:320 dilutions and then run on a plate alongside the respective standards. In both





Supplementary Figure 4. Parallelism graphs for T3 (top) and GC assay (bottom). X axis for standard = log concentration of standards as prepared, within the linear range; X axis for samples = log of relative sample concentration as prepared (i.e. the inverse of the dilution), scaled to fit nicely on the same graph as the standard points. The number in the figure legend denotes the sample number.

### Samples selected for dilution and parallelism test

Supplementary Table 1. Details of faecal samples used in dilution and parallelism tests for total T3. Absorbance readings (optical density) at different dilutions for each sample. Linear range of the standard curve for this dilution plate was 0.773-0.324.

Food availability/ season	Date of collection	Individual ID	Age-sex class	Age-sex & reproductive status	Sample no	Different dilutions				
						180 µl	240 µl	300 µl	360 µl	420 µl
limited foods / winter	26/05/2020	Hound	Adult male	NA	124	0.569	0.608	0.657	0.681	0.734
"	27/05/2020	Eggo	Adult female	Cycling	130	0.467	0.512	0.498	0.576	0.617
"	29/05/2020	Fiona	Adult female	Lactating	132	0.539	0.59	0.615	0.659	0.667
food available/ summer	17/11/2020	Eggo	Adult female	Pregnant	397	0.428	0.518	0.566	0.588	0.616
"	17/11/2020	Hound	Adult male	NA	398	0.587	0.621	0.694	0.663	0.761
"	17/11/2020	Fiona	Adult female	Cycling	402	0.53	0.544	0.605	0.675	0.649

Supplementary Table 2. Details of faecal samples used in dilution and parallelism tests for GC. Absorbance readings (optical density-blank 450) at different dilutions for each sample. Linear range of the standard curve for this dilution plate was ~0.465-0.185. The values fall outside of the linear range are marked as *Italic front*.

Food availability/ season	Date of collection	Individual ID	Age-sex class	Age-sex & reproductive status	Sample no	Dilution factors				
						1:20	1:40	1:80	1:160	1:320
limited foods / winter	08/06/2020	Eggo	Adult female	Cycling	143	<i>0.063</i>	<i>0.121</i>	0.202	0.268	0.368
"	09/06/2020	Hound	Adult male	NA	149	<i>0.113</i>	0.189	0.275	0.38	<i>0.477</i>
"	16/06/2020	Fiona	Adult female	Lactating	154	<i>0.048</i>	<i>0.118</i>	<i>0.17</i>	0.268	0.365
food available/ summer	13/11/2020	Hound	Adult male	NA	390		<i>0.145</i>	0.225	0.312	0.406
"	13/11/2020	Fiona	Adult female	Cycling	392		<i>0.143</i>	0.201	0.299	0.372
"	13/11/2020	Eggo	Adult female	Pregnant	395		<i>0.096</i>	<i>0.16</i>	0.251	0.362

cases the diluted samples were in parallel with each other and roughly parallel with the standards (Supp. figure 4).

The results of the T3 dilution test indicated that the samples were diluted with 240  $\mu$ l deionized water gave the optical density values were comparatively most central of the linear range of the standard curve (Supp. table 1). All samples were successfully run with this single dilution. The GC dilution test showed that the samples diluted with 1:160 dilutions gave the most central values of the linear range of the of the standard curve (Supp. table 2). All samples were initially run with this dilution. Although, a few samples (only eight samples, <2% of total samples) were needed to run with different dilutions.

### **Calculation of intra and inter-assay co-efficient variation**

A plate test was run to ensure the intra-assay variations are in acceptable range. For the T3 plate test, standard 4 (5.0 ng/ml) and standard 1 (0.5 ng/ml) were used as High and Low, respectively, and were run in duplicates in place of the samples. For the GC plate test, standard 5 (39 pg/50  $\mu$ l) and standard 7 (9.75 pg/50  $\mu$ l) were used as High and Low, respectively. The co-efficient of variation (CV) for Highs and Lows were calculated using the formula:  $CV = (\text{standard deviation}/\text{mean}) \times 100$ . CV values  $\leq 10\%$  are considered acceptable for intra-assay.

The high and low-quality controls (QCH and QCL) run on each assay plate provide measures of inter-assay variation. The CV was calculated using those values from each plate. CV values  $\leq 15\%$  are considered acceptable for inter-assay.

### **Expressing hormonal values from the assay results**

The following formula was used to convert the assay values to a concentration relative to dry faecal weight. The values (ng/g) resulting from this formula were used in all further analyses.

Hormonal metabolite per gram dry faeces

$$= \frac{\text{assay value} \times \text{dilution factor} \times \text{original extract volume (3000 } \mu\text{l)}}{\text{sample volume for assay (50 } \mu\text{l)} \times \text{original fecal weight for extraction (0.01 g)}}$$

## Appendix 8- T3 analysis averaging 14 days behavioural and climatic data

Supplementary Table 3. GLMM model for explaining T3 levels (males and females), n= 386. Averaging last 14 days behavioural and climatic data. \*reference category female

Fixed factors/ predictor variables	Estimate	Std Error	t value	P value
Intercept	1258.23	222.60	5.65	<b>&lt;0.001</b>
Natural food availability	0.15	0.07	2.09	<b>0.038</b>
Dump food availability	3.05	1.18	2.59	<b>0.010</b>
Feeding time	-0.03	0.13	-0.29	0.767
Daily travel distances	-0.05	0.02	-2.05	<b>0.041</b>
Minimum temperature	36.26	10.31	3.52	<b>&lt;0.001</b>
Dominance rank	-36.81	19.84	-1.85	0.098
Sex*, male	-206.08	154.70	-1.33	0.219

Supplementary Table 4. GLMM model only females. Averaging last 14 days behavioural and climatic data, n= 268. \*reference category cycling

Fixed factors/ predictor variables	Estimate	Std Error	t value	P value
Intercept	1372.60	253.94	5.40	<b>&lt;0.001</b>
Natural food availability	0.19	0.08	2.23	<b>0.026</b>
Dump food availability	2.46	1.41	1.73	0.083
Feeding time	0.03	0.16	0.17	0.863
Daily travel distances	-0.05	0.03	-1.56	0.121
Minimum temperature	28.27	12.56	2.25	<b>0.025</b>
Dominance rank	-42.59	20.44	-2.08	0.076
Reproductive status*				
Lactating	-23.29	67.61	-0.34	0.730
Pregnant	8.15	65.73	0.12	0.901