ENZOOTIC GEOPHAGY BY ELEPHANTS (*LOXODONTA AFRICANA*) IN RELATION TO GEOCHEMICAL COMPOSITION OF MINERAL LICKS IN ADDO ELEPHANT NATIONAL PARK, SOUTH AFRICA

by

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Declaration

I declare that the thesis submitted by me, K.N. Darker, in fulfilment of the requirements for the degree in Master of Science in Zoology at the University of the Free State, is my own independent work. This thesis has not previously been submitted by me or anyone else at another university or faculty. I furthermore concede the copyright of this thesis in favour of the University of the Free State.

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Abstract

Geophagy, the deliberate ingestion of soil, is a common occurrence amongst various animal species including mammalian herbivores such as elephants. Despite the documented instances of soil-eating, and several nonexclusive hypotheses, the real motivation behind the phenomenon remains controversial. In this study, six camera traps were set up throughout Addo Elephant National Park, South Africa at selected geophagy sites which captured visitation frequency as well as the demographic trend of elephant groups during site visits from April 2019 to May 2020. The geochemical and mineralogical composition of soils at these selected geophagy sites were analysed using X-ray diffractometry (XRD) and X-ray fluorescence spectrometry (XRF). Furthermore, the spatial distribution of five collared elephants (three matriarchs and two males) in relation to the six geophagy sites were investigated using kernel density estimations (KDE). Females had larger home ranges that incorporated more geophagy sites than males. Visitation frequency to geophagy sites were estimated using 500 m buffer zones from the centre of each site. Individuals visited at least three or more geophagy sites throughout the study period. Overall, essential elements Na, Ca and Mn were identified as main drivers for geophagic behaviour in the elephants of AENP. These essential elements (Na, Ca and Mn) are important for certain physiological demands such as bone and tusk growth in elephants and reproductive (pregnancy and lactation) demands in females. Geophagy is considered to be a contributing factor of movement patterns and area utilisation and may have important implications for conservation and management.

Dedication

Dedicated to the parentals. Keith & Linda.

Thank you for always being on your knees and being so supportive and invested in my passion.

Here’s to breaking generational curses. May knowledge and wisdom, qualifications, and success follow for generations to come.

…sodat almal sal sien hoe GROOT is ons GOD.

Acknowledgements

To my supervisor, thank you for the amazing opportunity to work alongside these gentle giants. I have learned a lot during this entire process which has shaped me into who I am today. Thank you for the journey, the experiences, the advice and the long nights. We made it! To everyone who was involved in my study at Addo Elephant National Park, a big big thanks. A special mention to Portia Chake. thank you for your assistance in keeping me safe, the long hours, the patience. Charlene Bissett, Lizette Moolman, and Anban Padayachee thank you for the role you played and for making it possible. It was an honour to work with SANParks and their team.

To my family and friends who braved the elements and tent living with me, I am ever thankful. Keith, Linda, Brandon, Uncle Marius, Joaquín, Chanel, Natashia, Surene and AJ, I appreciate you all so very much. Another special thanks to my mom and dad for every single contribution to my study, whether it was financial, motivational or simply just a listening ear, it meant the world to me and kept me going. I would also like to extend thanks to Prof. Daryl Codron for statistical advice. Dr Adriaan van der Walt from UFS geography department and Henk Butler, for the GIS assistance and Shaquile Barnes for his talented drawing. As well as Dr Johan Joubert at Shamwari Private Game Reserve for his willingness to help.

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List of Abbreviations

AENP	Addo Elephant National Park
AMC	Addo Main Camp
CAM	Crassulacean Acid Metabolism
CEC	Cation Exchange Capacity
CTD	Camera Trap Days
DFA	Discriminant Function Analysis
GI	Gastrointestinal
GPS	Global Positioning Systems
KDE	Kernel Density Estimations
KW	Kruskal-Wallis Test
LOI	Loss on Ignition
OOS	Out of Sight
PCA	Principal Component Analysis
REE	Rare Earth Elements
SANParks	South African National Parks
XRD	X-ray Diffractometry
XRF	X-ray Fluorescence

Ethical Clearance and Permits

The Interfaculty Animal Ethics Committee of the University of the Free State approved the study project along with the procedures, under the reference UFS-AED2019/0118 on the 18th of July, 2019.

Furthermore, research and all data collection in accordance with SANParks regulations were approved under the permit number BUTL-HJB/209-013 issued.

CHAPTER 1

GENERAL INTRODUCTION

1.1 The concept, causes, and consequences of geophagy

The deliberate and frequent consumption of earthy substrates such as clays, soil or sediments, known as geophagy (or geophagia), is a common occurrence among several animal species, including populations of mammalian herbivores and omnivores (Klaus et al. 1998; Chandrajith et al. 2009). Geophagy is hypothesised to be an adaptive, beneficial behaviour in response to a phenomenon known as “pica”, which refers to the craving and intentional consumption of non-food substances (Young et al. 2011; Semel et al. 2019). According to Mahaney and Krishnamani (2003), animals can detect slight variations in the soil composition and would concentrate on a specific area within the same ingested horizon layer. Soil-ingestion among species is encouraged by a physiological need, which may vary in response to seasonal changes, reproductive cycles, and ontogeny, as well as geographical differences, leading to temporal and spatial variation in utilisation (Hui 2004; Blake et al. 2011). Most documented geophagia instances prove that animals are highly selective in the soil substrates they consume (Mahaney and Krishnamani 2003). Geophagy is expected to influence the distribution and densities of wildlife and is crucial for nutritional budgeting (Klaus et al. 1998; Milewski 2000). In the context of animal nutrition and considering the large role minerals and therefore, elements play in geophagy, it is important to clarify the differences in terms used throughout this study. The majority of interdisciplinary literature refers to ‘minerals’ differently and as an all-encompassing term for nutritional elements and/or chemical compounds. However, in this study, I will refer to minerals as naturally occurring chemical compounds, while single chemical elements will be referred to as elements.

The mitigation of mineral and elemental deficiencies is frequently mentioned as the immediate cause of geophagy (Weir 1969; Kreulen and Jager 1984; Krishnamani and Mahaney 2000; Stephenson et al. 2011). This theory has gained such widespread acceptance that most locations where geophagy is seen are referred to as "mineral licks," "soil licks," or "natural licks." Numerous research supports the idea that elemental supplementation is the most plausible cause for soil consumption, especially for inorganic elements like sodium (Na), manganese (Mn), potassium (K), and sulfur (S) (Sienne et al. 2014). Despite numerous documented instances of different animal species consuming soil, it is still unclear what the true motivation behind geophagy is. Natural soil consumption has been linked to several potential advantages, including better adsorption of plant phenols and secondary metabolites (Krishnamani and Mahaney 2000), the prevention of acidosis (Klaus et al. 1998), the prevention of diarrhoea (Krishnamani and Mahaney 2000), and the eradication or elimination of endoparasites in the gastrointestinal (GI) system (Kreulen 1985; Klaus et al. 1998; Krishnamani and Mahaney 2000). Alternatively, geophagy could have no physiological benefits whatsoever and the behavioural phenomenon observed could merely be driven by hedonic sensations (Semel et al. 2019).

Despite all the proposed advantages, opposing views have also suggested several disadvantages associated with soil eating. Animals that practise geophagy often must travel long distances to reach these sites and this could eventually lead to an energetic disadvantage (Stephenson et al. 2011). Other proposed disadvantages derived from soil eating could result in teeth wearing or increasing the risk of intoxication because of persistent utilisation of contaminated soils (Klaus et al. 1998). In addition, sand impaction can be fatal in case of excessive geophagy (Abutarbush and Petrie 2006). The likelihood of sand impaction is influenced by the animal's daily defecation rate and the quantity of soil it consumes. However, despite possible negative effects, geophagy has been reported from regions all over the world, strongly suggesting that the possible rewards of this behaviour must outweigh the costs.

1.2 Elephants as models for geophagy studies

Given that soil eating has a direct effect on the substrate, which can ultimately lead to changes in the terrain of certain areas, geophagy also has important implications for conservation and management (Milewski 2000). This is particularly true for species considered to play an ‘ecosystem engineer’ role in the environment, thus being able to produce significant alterations of their geographical and vegetal characteristics (Valeix et al. 2014). Elephants (Order Proboscidea) are known to practice soil eating as noted in the African savannah (*Loxodonta africana*), forest (*L. cyclotis*) and, Asian (*Elephas maximus*) elephant species across most of their habitats (Spinage 1994). The most striking example of elephants consuming soil is seen in the excavation of ‘caves’ formed by elephants on Mount Elgon's volcanic slopes on the boundary of Kenya and Uganda, as reported by Bowell et al. (1996).

Elephants have a diverse diet as they are mixed feeders; they graze primarily in the wet season and browse primarily in the dry season (Mramba et al. 2018). They can dominate in environments which has a significant amount of low-quality plant biomass. According to the Jarman-Bell principle, large-bodied herbivores, such as elephants, can consume plant material with low digestibility and a high concentration of fibre because of their long intestinal retention times and low metabolic demands (Mramba et al. 2018). Geophagy is therefore motivated by GI diseases in elephants that are remedied by ingesting soil (Ayotte et al. 2006; Sienne et al. 2014), or by detoxifying unpalatable foods (Johns and Duquette 1991; Chandrajith et al. 2009). The latter could be the result of a diet based on more browse than grass as various tree and shrub species contain harmful plant secondary metabolites (Mwangi et al. 2004).

On the other hand, elephant geophagy has also been hypothesised as a mechanism to obtain mineral and elemental supplementation. According to Cherian (2020), mineral and elemental matter accounts for about 4% of an animal's body's weight. For elephants, it is a significant amount as they have an average body weight of 1 800-6 000 kg (Ullrey et al. 1997). A major aspect of fully understanding geophagy is to determine whether animals can discriminate between different elements and minerals in the soil and area. Elephants selectively exploit Na, K, calcium (Ca), and magnesium (Mg)-containing soils as these nutritional elements are typically deficient in their plant diet (Weir 1972). Optimal foraging theories envisage that animals should be able to control diet composition and use foraging tactics that improve energy intake (Ceacero et al. 2010); and due to these necessities of important nutrients, they should seek to ingest additional threshold levels of elements and other essential nutrients.

Furthermore, specific nutrient needs (due to seasonality, changing environmental conditions, sex/age classes, and/or reproductive status) can also play a role in elephant geophagy. Elephants have intricate social systems. They frequently form family groups ranging from two to 30 females with kin of varying ages, or males will form smaller bachelor groups made up of adults and sub-adults (Poole 1994). Elephants may, however, form even smaller groups to limit competition when food is scarce (Wittemyer et al. 2005). Bachelor and family groups forage and utilise the habitat differently. Compared to the smaller females with transiently high reproductive demands, males are more tolerant to low-quality forage. Therefore, compared to males that engage in bulk foraging, females are also more selective about the quality of their forage and generally spend more time feeding (Shannon et al. 2006).

Ultimately, these large-bodied herbivores' activity patterns and behaviour may be impacted by the difference in the seasonal availability of forage.

Holdø et al. (2002) discovered that female elephants in Zimbabwe's Hwange National Park ingested more mouthfuls of soil and expended a larger amount of their daily activity budget ingesting soil than the males. Because Na content in milk and developing foetal tissues is essentially consistent regardless of Na intake, pregnancy and lactation in females impose high demands on Na and other elements (Michell 1995; Blake et al. 2011). Other studies by Kreulen and Jager (1984) and Atwood and Weeks (2003) suggest that Na is the desired element in these soil licks, thus reinforcing the generalised idea about the importance of elephant geophagy on Na intake. However, a preference for salt (NaCl) does not necessarily indicate a deficiency thereof (Phillips 1993). In fact, due to its strong scent, Na might be used by elephants merely as an element-rich site indicator (Sienne et al. 2014). There are numerous other macro- and micronutrients at play in geophagy besides Na. The chemical analysis of geophagy-site soils in the Central African Republic shows significantly higher quantities of K, Ca, Mg, Mn, phosphorous (P) and clay compared to non-geophagic soils (Klaus et al. 1998). In addition, other elements such as chlorine (Cl), and iodine (I) have also been identified as important attractants for geophagy in African forest elephants from Central Africa (Sienne et al. 2014).

Although elephant geophagy undoubtedly has some behavioural adaptations, very few research findings on geophagy include the behavioural aspects of the animals involved. Reports of sex- and age differences are usually represented by nothing more than observational remarks. Elephants perform intentional cyclical migrations to geophagy sites in both arid and forest habitats (Panichev et al. 2013), an observation that suggests that seasonal and periodic movement patterns of elephant populations could be determined by the geographical location of geophagy sites. For instance, elephant population density and movement patterns have been proposed to be dependent on the distribution of clay soils high in Na (Weir 1972). Over the past centuries, elephant populations have become increasingly confined to mere fragments of their original distribution range because of anthropogenic influence, a phenomenon that can severely alter their natural behaviour considering they are naturally nomadic over great distances, moving to and from dispersed lick sites (Mwangi et al. 2004). This means that many conservation areas may not, in the long term, be viable for elephant populations unless appropriate provision is made for nutrient supplementation. A study conducted by Leshchinsky (2015), suggests that the mass extinction of woolly mammoths (*Mammuthus primigenius*), precursors of the modern elephant, was due to geochemical stress caused by mineral and elemental deficiencies. More than 1 500 preserved mammoth bones were analysed, which revealed signs of bone disease such as osteoporosis, osteofibrosis, arthritis and other diseases caused by metabolic disorders due to insufficient essential nutrients. This furthermore emphasises the importance of such resources for elephants. Ultimately ecosystems could collapse without the pivotal role elephants play (Mwangi et al. 2004).

1.3 Aim and objectives of the study

Within this context, this study aims to explore and describe patterns of geophagy displayed by the African savannah elephant, which is the largest and likely most widely distributed of the elephant species. Understanding potential proximate factors may allow researchers to better understand this iconic species' development and reproductive performance, as well as its migratory patterns and forage quality. To achieve that, six geophagy sites were selected throughout AENP which holds one of the highest densities of elephants in the world (Maciejewski and Kerley 2014). The frequency of elephant visits for geophagy was monitored for approximately 13 consecutive months using camera traps, which also allowed the determination of the age class and sex of the individuals evidencing geophagic activity. Additionally, the chemical and mineralogical composition of soil from the different selected sites was analysed. All these data was obtained to address the following key questions and objectives (divided into specific questions):

Key question: What is the geophagy site utilisation pattern and frequency among the elephant population of AENP concerning the geochemical and mineralogical soil properties of selected geophagy sites?

Objective 1: To describe the physiography and geology of the study area.

Objective 2: To determine the geochemical and mineralogical compositions of soils from each selected geophagy site.

> 2a. Which major and trace elements and minerals are found in higher concentrations per geophagy site?

2b. Do geophagy sites differ in elemental and/or mineral composition from each other?

Objective 3: To determine the social structure of the elephants actively utilising the selected geophagy sites.

3a. Is there a difference in the age structure of the elephants using these sites?

3b. Do females utilise these sites more frequently than males?

Objective 4: To determine the visitation frequency to geophagy sites among the elephant population.

4a. Is there an increase in geophagy site visits during specific seasons?

Objective 5: To determine the spatial distribution of the elephant population in the study area in relation to the selected geophagy sites.

5a. Do their movements patterns include visits to geophagy sites?

1.4 Thesis outline

This dissertation is composed of six chapters. In this Chapter 1, I have provided a general introduction and background on geophagy, motivation and the significance as well as objectives of this study. The next chapter describes the study area of AENP, its topography and geology, climate and vegetation as well as the history of the Park and its elephant population. Chapter 2 also provides information on each geophagy site utilised and how these sites were identified.

Chapters 3, 4 and 5 have been compiled as stand-alone manuscripts to some extent, with each its own introduction, methodology, results and discussion. Due to this, there is some repetition between chapters. Chapter 3 addresses the geochemical and mineralogical aspects of the geophagic study. This includes the methods used in order to obtain geochemical and mineralogical data and presents the results and discussion thereof. Furthermore, Chapter 4 presents the behavioural results obtained from camera traps and discusses the relation to geophagic activity. Chapter 5 reports on the results of Global Positioning System (GPS) collar data provided by South African National Parks (SANParks) to assess the spatial distribution of elephants in relation to geophagy sites in AENP. Finally, Chapter 6 summarises the main findings of this study and discusses the importance thereof for future studies and management efforts.

CHAPTER 2

STUDY AREA AND GEOPHAGY SITES

2.1 Location and topography

The AENP, one of the official 19 national parks (SANParks) of the country, is located east of the Sundays River and approximately 70 km north-east of Gqeberha (formerly Port Elizabeth) in the Eastern Cape Province of South Africa (Fig. 1). The Park also forms the eastern extension of the world-renowned Garden Route. More specifically, this study was conducted in the Addo Main Camp (AMC) and Colchester (excluding the Marine Protected Area) sections of the AENP (Fig. 1).

Although the AMC and Colchester sections are separated by the Addo Heights gravel road, together they form one ecological functional unit after the dividing fence was removed in 2006 (Anonymous 2017). Both these sections cover approximately 26 000 ha. The AMC section has the R342 road as its northernmost boundary, while the Colchester section has the N2 highway as its southernmost limit.

Topographically, the landscape is characterised by lowland plains and rolling hills (Fig. 2), varying in height between 71 and 354 m above sea level (Paley and Kerley 1998). Numerous natural water pans or small seasonally flooded depressions are distributed across both sections (Toerien 1972; Paley and Kerley 1998). However, permanent water is only available to animals in the AMC via three artificial dams (Hapoor Dam, Rooidam and Domkrag Dam), as well as three water holes (Marion Baree waterhole, Carols’ Rest, and Gwarrie Pan) fed by pumped groundwater (Landman et al. 2012).

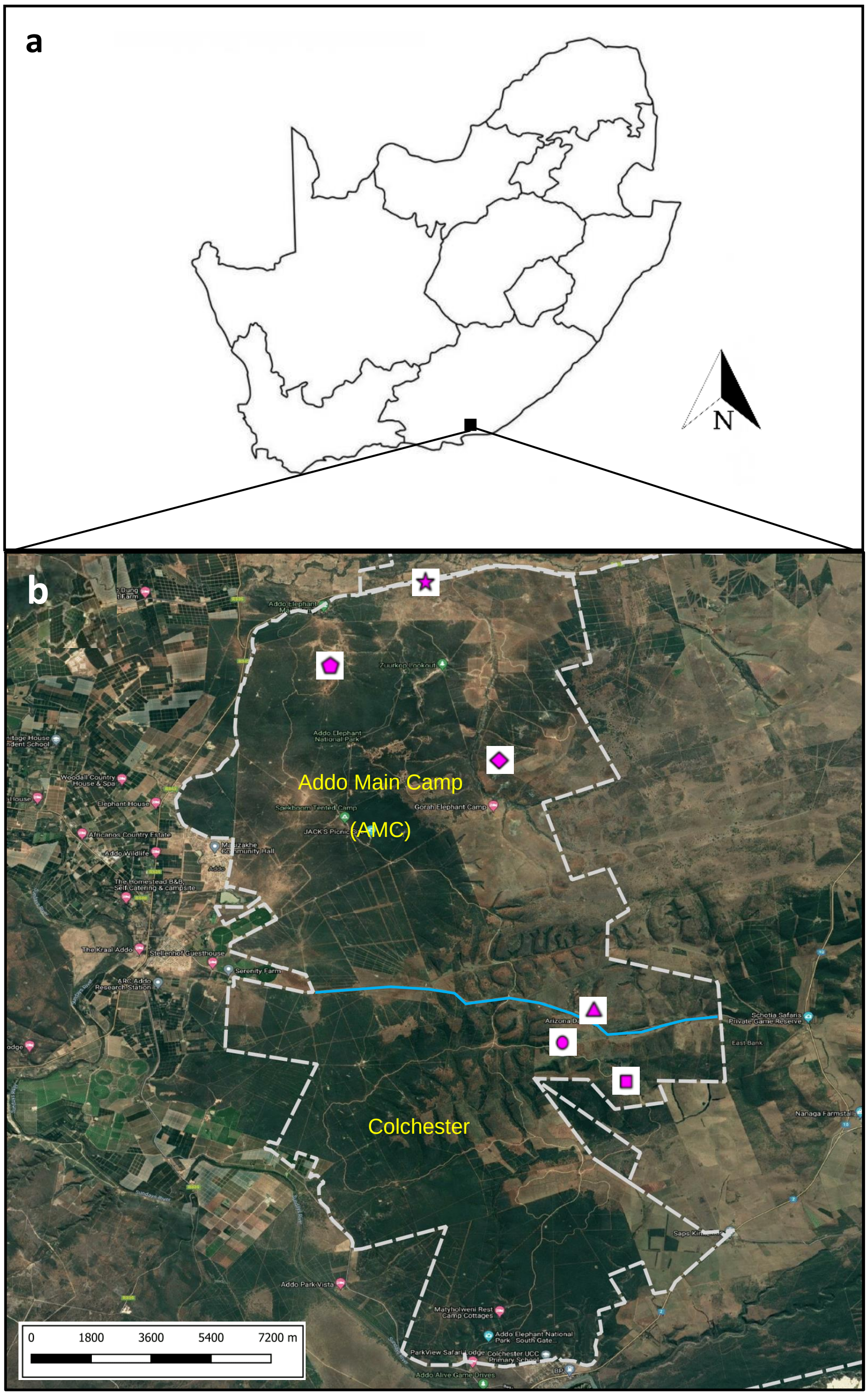

Figure 1. *Geographical location of the study area within South Africa (a) and an aerial view of the two sections within Addo Elephant National Park used for this study (b). The blue line indicates a public road that separates the two sections. Pink markers indicate the geophagy site locations. Aerial view modified from Google Earth ©2021 in QGIS (Pty) Ltd.*

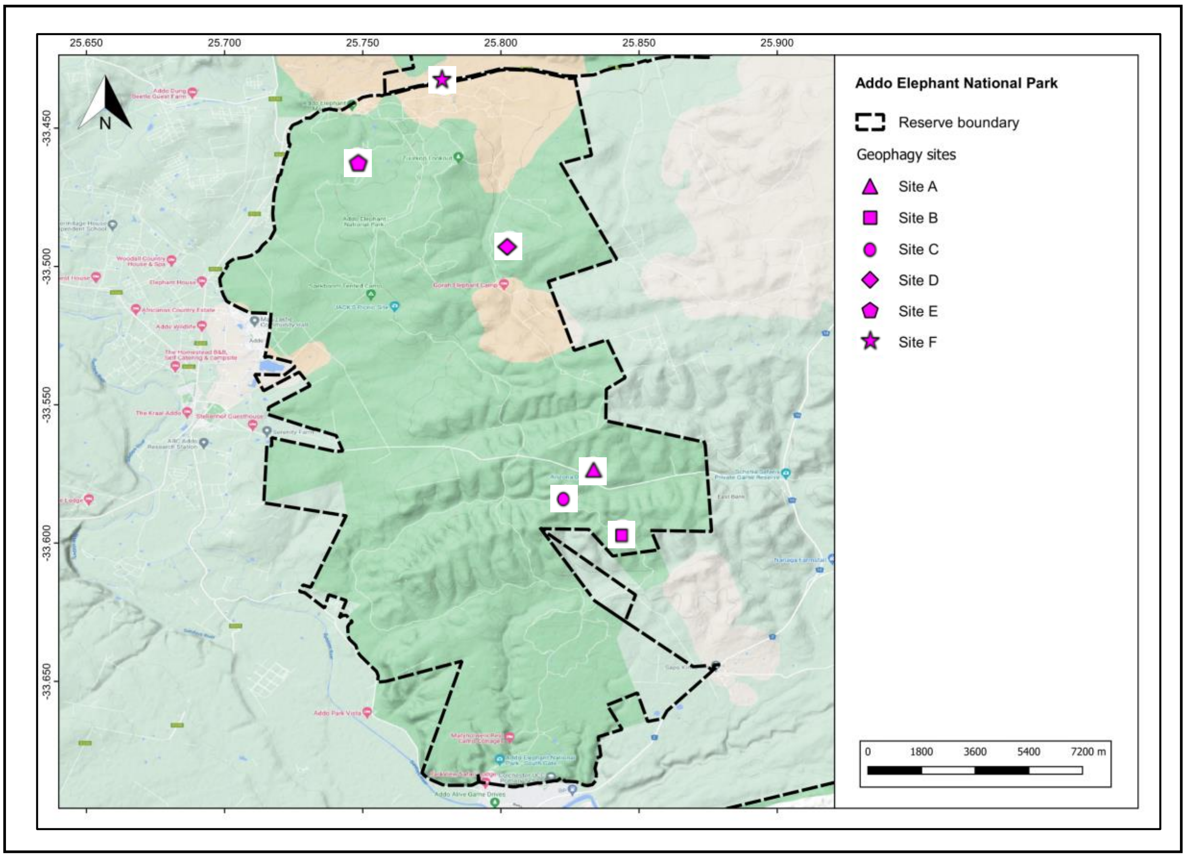

Figure 2. *Landform features of the study area in Addo Elephant National Park, South Africa. Green areas indicate high natural vegetation coverage and light brown areas indicate low vegetation coverage. Pink markers indicate the geophagy site locations across the terrain. Modified from Google Earth ©2021 in QGIS (Pty) Ltd.*

2.2 Physiography and geological background of AENP

The Greater AENP is situated within the largest onshore basin, an undulating south-dipping fault depression, known as the Algoa Basin (Lombard et al. 2001; Muir et al. 2015). Torrential streams eroded the quartzitic sandstone highlands during the Early Jurassic period and continually deposited extensive granitic boulder beds and gravels (Muir et al. 2017). Along the southern foothills of the Zuurberg Mountain range, a notable horizon is the resulting red-brown coarse conglomeratic Enon Formation (McLachlan and McMillan 1976).

Sedimentation of the Kirkwood Formation started towards the end of the Jurassic Period (ca. 140-150 Mya) and reflects the deposition under prevailing fluvial conditions of fine-grained sediments (Muir et al. 2017). Foliage, petrified wood fossils, and calcrete-rich palaeosols (fossil soils) are present in the resulting multi-hued siltstone, red and green mudstone, and subordinate green-grey sandstone (McLachlan and McMillan 1976; Almond 2014; Muir et al. 2017). The Kirkwood Formation yields the most abundant and diverse animal and plant fossils of all the mid-Mesozoic basin deposits in South Africa (Muir et al. 2015). The Kirkwoord Formation underlies the low-lying plains and the Zuurberg Mountains, which are situated in the south and north, respectively (Kakembo et al. 2015). The Algoa Basin was first filled by fluvial deposition, which was followed by an estuary and shallow marine ingression to create the Sundays River Formation, which is a deposit of mudstone and sandstone that ranges in colour from blue-green to grey (Le Roux 2000). The interlayered, subordinate sandstone bands are often iron (Fe)-rich, thus showing dark brown colour (Toerien 1972). Numerous estuarine to marine megafossils, including ammonites, belemnites, bivalves, gastropods, polychaetes, and echinoids, could be observed in the Sundays River Formation (McLachlan and McMillan 1976; Almond 2014). Molluscs of the Bivalvia (previously known as Lamellibranchiata) class, *Trigonia* and *Exogyra*, are extensively spread throughout the Formation (Toerien 1972). The Enon, Kirkwood, and Sundays River Formations make up the Uitenhage Group, which is organised from oldest to youngest (McLachlan and McMillan 1976).

The Sundays River Formation sediments underlie the Park's northern portion (which includes the majority of the camp), while the Kirkwood Formation sediments underlie the Park's southern portion (Anonymous 2017). These formations, which are believed to be cyclic transgressive sequences of shallow marine and estuarine origin, have a striking similarity to surface outcrops and often consist of reddish and greenish-grey mudstones, siltstone, and sandstone (Hattingh and Goedhart 1997). Clays with scattered sandstone fragments are prevalent on bare weathered patches and near dams throughout the park. Rocks appear greenish-grey and may contain secondary limestone and gypsum (Hattingh and Goedhart 1997).

The current configuration of South Africa's south and east coastlines was formed during the Cretaceous Period (ca. 90 Mya). Following this, subsequent fluctuating sea levels had an impact on the development of the landscape to some extent, exposing the sediments to weathering at times (Toerien 1972).

The Coega Platform forms part of the Alexandria Formation near Colchester, as well as the older Grassridge Platform within the AENP near Addo Heights. This formation, which was formed during the Tertiary Period, overlies the Mesozoic Uitenhage Group and is made up of alternating layers of calcareous and quartzitic sandstone, coquinite (cemented shell-rock), and conglomerate with an average thickness of about 9 m (Le Roux 2000). The Alexandria Formation is clearly visible throughout the Park and stands out as a white strip close to the peaks of the hills, especially at the Zuurkop Lookout (Toerien 1972; Anonymous 2006). This white cover layer is also known as the Nanaga Formation, which consists of a dense layer of fine-grained yellowish sandy soils that form the Park's high-lying topography (Almond 2014). The sand and dune rock that make up this layer is also calcareous due to the presence of numerous shell fragments. The Alexandria and Nanaga Formations are two of the five geological groups that make up the Cenozoic Algoa Group.

2.3 Climate

The AENP is situated within the hot semi-arid region of South Africa (Landman et al. 2008; Kakembo et al. 2015) with a mean annual rainfall of 416 mm and an average temperature recorded of 17.8°C between 2005 and 2020 (Fig. 3). Rainfall is non-seasonal, occurring throughout the year, and it is mostly associated with post-cold frontal events (Hoffman 1989) and usually peaks in austral autumn and spring (Landman et al. 2008). Fogs may provide moisture during extended dry times, as indicated by the prevalence of bark and ground lichens (Barratt and Hall-Martin 1991; Paley and Kerley 1998; Vlok et al. 2003). The maritime and continental climates and the altitudinal variation result in a variable type of climate (Aucamp and Tainton 1984). However, according to Irwin et al. (2008), the Park’s climate is best characterised as warm temperate.

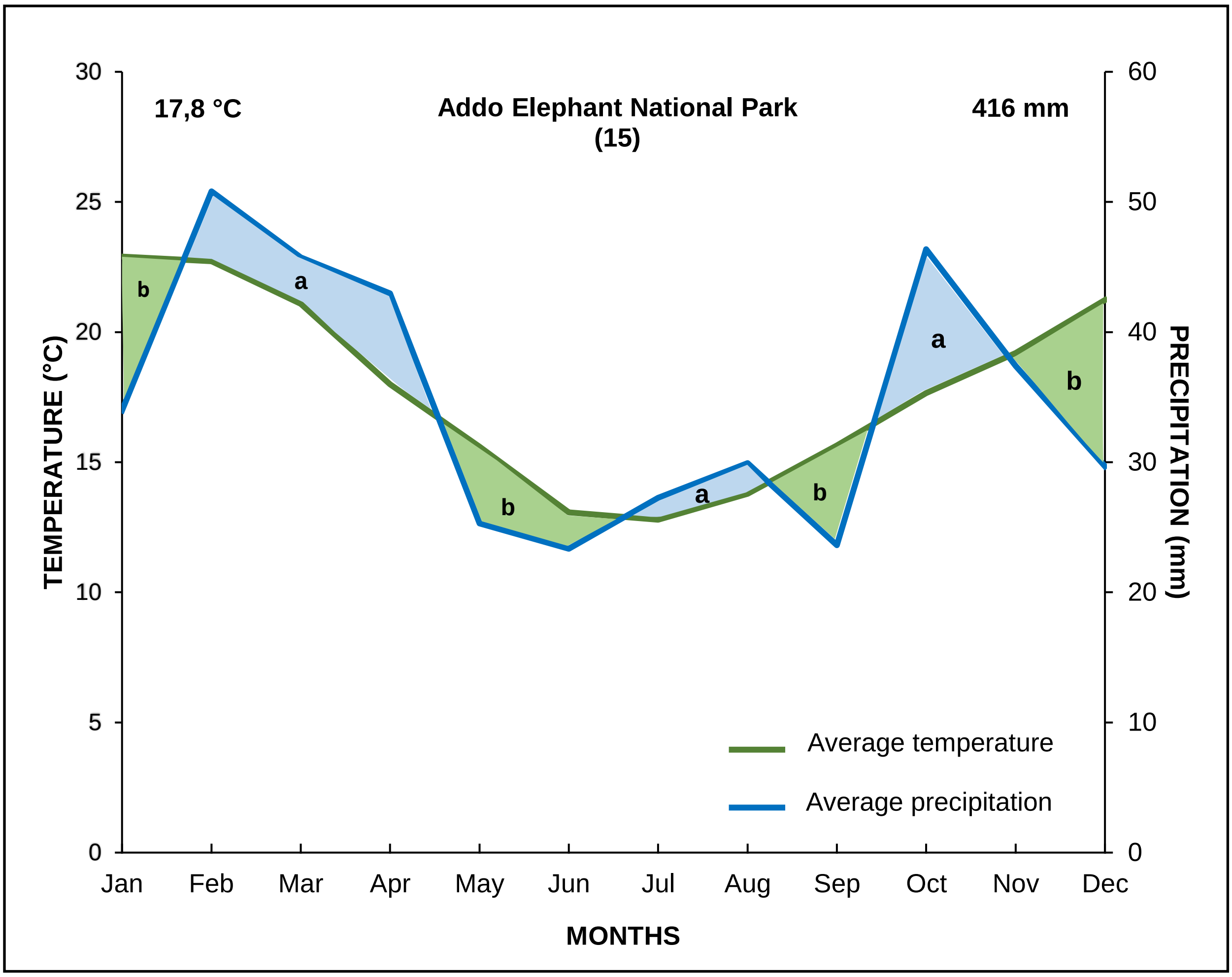

Figure 3. *Climate diagram of Addo Elephant National Park, South Africa, from the period 2005-2020 according to the method of Walter and Lieth (1964). Mean annual temperature and rainfall are indicated in the top left and right corners respectively. Number between brackets indicates years of observation. (a) wet season; (b) dry season. (Data obtained from South African Weather Service).*

2.4 Vegetation

Five of the seven biomes found in South Africa are present throughout all the sections of Greater AENP, these being the Nama-Karoo, Fynbos, Albany Thicket, Grassland, and Wetland (Anonymous 2006), making it the most diverse park on the continent concerning vegetation. This wide variety of terrestrial biomes and correspondent vegetation types found throughout AENP is only possible because of the complex diversity of soils found throughout the Park (Anonymous 2017). More specifically, the AMC and Colchester sections, that form part of the study area, are situated within the endemic-rich subtropical thicket (sub-order xeric succulent thicket) with high vegetation coverage (*vide* Fig. 2). It is also the only national park that contains succulent thickets (Landman et al. 2007; Kakembo et al. 2015). The xeric succulent thicket vegetation group is characterised by a dense growth of succulents, evergreen, and spinescent shrubs, lianas reaching between 2-4 m, as well as herbs, geophytes, and grasses (Henley 2001; Vlok et al. 2003; Landman et al. 2007). As a result, the visibility within the thicket is poor (< 5 m) throughout most of the Park (Whitehouse and Schoeman 2003).

Dominant shrub and tree species found in the area include spekboom (*Portulacaria afra*) covering more than 66% of the AMC, needle-bush (*Azima tetracantha*), wild caper (*Capparis sepiaria*), white milkwood (*Sideroxylon inerme*), and plumbago (*Plumbago auriculata*) (Landman et al. 2007). The grassridge bontveld, which makes up roughly 13% of the region and is found close to the AMC in an area known as Zuurkop, is a combination of woody thickets and small patches of grass veld that are restricted to this highest plateau (Anonymous 2006; Landman et al. 2007; Kakembo et al. 2015). Dominant grass species found include common finger grass (*Digitaria eriantha*), couch grass (*Cynodon dactylon*), broad-leaved panicum (*Panicum deustum*), and red grass (*Themeda triandra*) (Anonymous 2017; Landman et al. 2007).

2.5 Fauna and elephant population history

Initially extending over 2 230 ha, the Park was proclaimed in 1931 to preserve the remaining African savannah elephant population which at the time consisted of only 11 individuals due to extensive ivory hunting locally (Whitehouse and Hall-Martin 2000;

Whitehouse 2002; Anonymous 2006). From the 11 survivors, a single male sired about 28% of offspring born over 15 years (Whitehouse and Harley 2002). The population increased exponentially since the mid-1950s after adequate fencing was deployed and is now home to the second-largest elephant population in South Africa, with more than 480 individuals by the year 2008 (Anonymous 2006; Kakembo et al. 2015). By 2020, the elephant population consisted of 492 individuals for the AMC and Colchester sections alone, (Bissett 2021, pers comm*). Elephants constitute about 85% in biomass of the vertebrate herbivores in the Park (Kakembo et al. 2015). Their population has grown beyond the recommended density limit of a carrying capacity of two elephants per km^2 (Kerley and Boshoff 1997; Boshoff et al. 2002; Owen-Smith et al. 2006).

As the Parks' boundaries expanded over the years, more species have been gradually introduced into the AENP, including some large browsing and intermediate feeder mammalian herbivores, such as black rhinoceros (*Diceros bicornis*), greater kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*), common eland (*Tragelaphus oryx*) and red hartebeest (*Alcelaphus buselaphus*). The bulk of grazing species is comprised of African buffalo *(Syncerus caffer*) and Burchell's zebra (*Equus quagga burchelli*) (Kakembo et al. 2015). In addition, both lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) were introduced by the end of 2003 into the AMC as part of re-establishing the carnivore process in the Park (Anonymous 2006). The AENP is also home to a wide range of terrestrial birds, herpetofauna, and invertebrates with some species listed as Threatened in the Red Data Book (Anonymous 2006).

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2.6 Geophagy sites

2.6.1 Identifying geophagy sites in AENP

The geophagy sites for this study were initially identified using Google Earth™, where vegetation clearings could be seen from above, as well as natural animal pathways that lead to the clearing. During the first visit to the Park, each preliminarily identified location was inspected for signs of geophagic activity that indicated active utilisation. Possible geophagy sites reported by the Parks' officials were also considered and visited to confirm recent utilisation by elephants. Due to the natural dense vegetation found throughout the Park, certain sites could only be reached by foot. Consequently, soil eating could not be directly observed at most of the selected sites, but evidence such as tusk marks, smoothed areas from rubbing, and fresh faecal matter was used.

From the initial ten geophagy sites that were considered, six were finally selected for this study, the remaining four being excluded due to several reasons such as inactivity, flooding, erosion, and exposure to park visitors and tourists. Each of the six selected geophagy sites, posed unique landscapes, textures, and soil colours.

2.6.2 Description of geophagy sites

The major soil type for the AMC and Colchester sections are luvisols. The dominant soils found throughout the study area are mainly calcic and ferric luvisols (Fig. 4). Luvisols form part of the group of soils that are conditioned by the climate in sub-humid forest and grassland areas and have a well-developed soil structure (Spaargaren 2001; Jones et al. 2013).

More specifically, all the geophagy sites, including the areas from where the elephants feed directly, were on vertical and elevated landscapes. They varied from shallow excavations to high exposed soil walls. Soil colours varied from whitish-grey to yellow-brown to reddish or different combinations of these. Due to the physical differences across sites on a smaller scale, it is expected that each site would differ in composition. Alternatively, the sites that are located in the same soil type will be similar in composition.

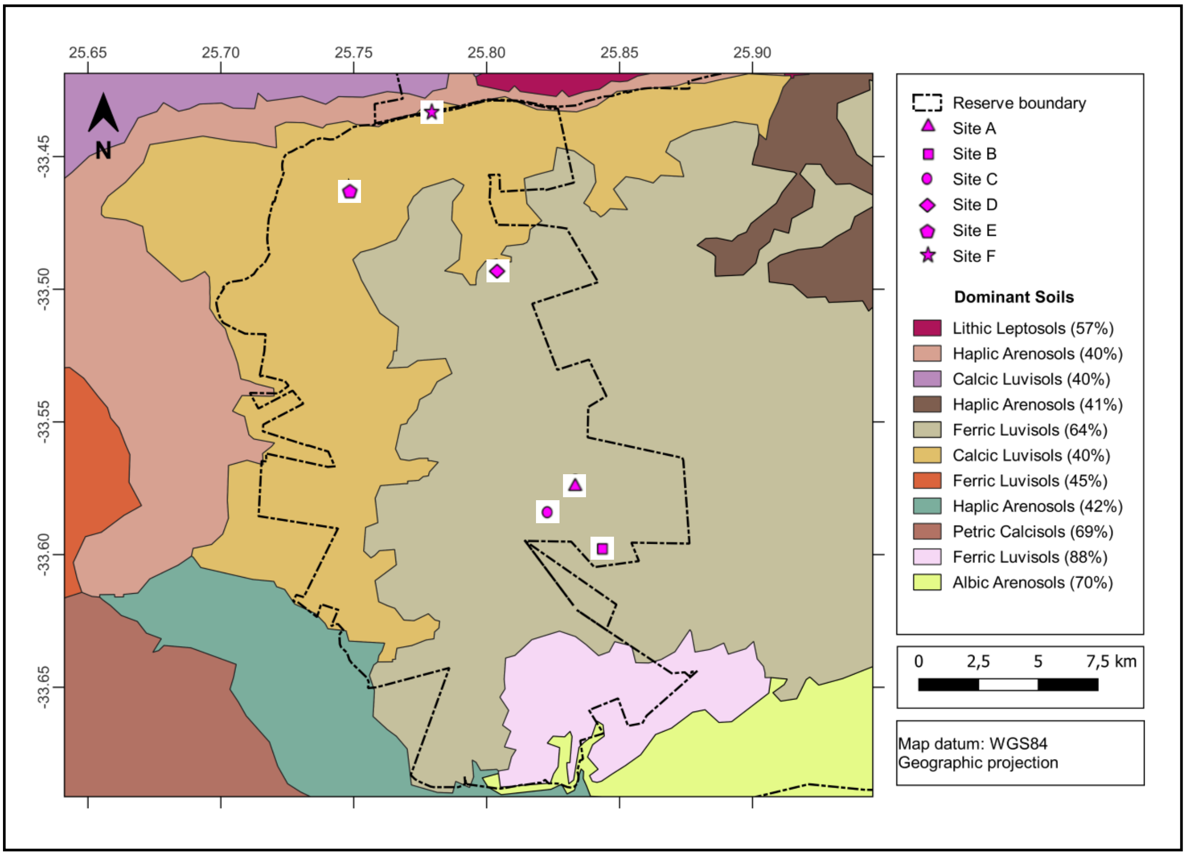

Figure 4. *Classification of dominant soil types according to the method of Batjes (2002) at Addo Elephant National Park, South Africa. Derived from the soil database SORTERSAF, ver. 2.1 for southern Africa. Map generated in QGIS (Pty) Ltd.*

Site A is distinguished by a large east-facing excavation (about 15 m wide) carved into a low-lying hill. This is the only site where the excavation is partly man-made. Excavators are used by park staff to collect soil from this area for use in construction projects throughout the Park, ultimately exposing deeper soil layers. The site is located close to a waterhole and staff housing (Fig. 5). The vegetation in the surrounding area is bare and shows signs of overgrazing. Site B is in a clearing at the top of a slope, roughly 30 m from a tourist road (Fig. 5). The horizontal axis along which soil is actively consumed is approximately 13 m wide. Site C (about 12 m wide) is found along the high walls of a natural deep exposed gulley that forms a natural walkway for animals (Fig. 6). Although the site is very close to a tourist road, it cannot be seen due to the high vertical transects and is accessed by foot. Different soil horizons can be seen along the walls (thick silty to sandy alluvium weathered soils), but geophagy was observed with the focus on the whiter/lighter exposed soils (more calcretised horizon. Site D is located on a hill (Fig. 6). The area where geophagy is observed (about 6 m wide) is on the southern bank of a large depression. The site can only be reached on foot as private roads leading toward the site are overgrown, which also means the site is for the most part undisturbed by human movement. Site E is situated in what appears to be a small dried-up waterhole on a fairly flat landscape and is about 8 m in length (Fig. 7). A few large shrubs are seen near the site; however, most of the surrounding area is rather bare and dry with signs of overgrazing in the area. Lastly, Site F is found on the perimeter of a dried-up dam’s banks. The feeding area about 7 m in length along the edge. It is close to the northern boundary fence of the AMC, as well as train tracks, which are still actively used along the same boundary (Fig. 7). Only on occasion with heavy rainfall, a pool of water will form a few metres from the feeding site. More than one elephant can utilise any of the 6 sites at once.

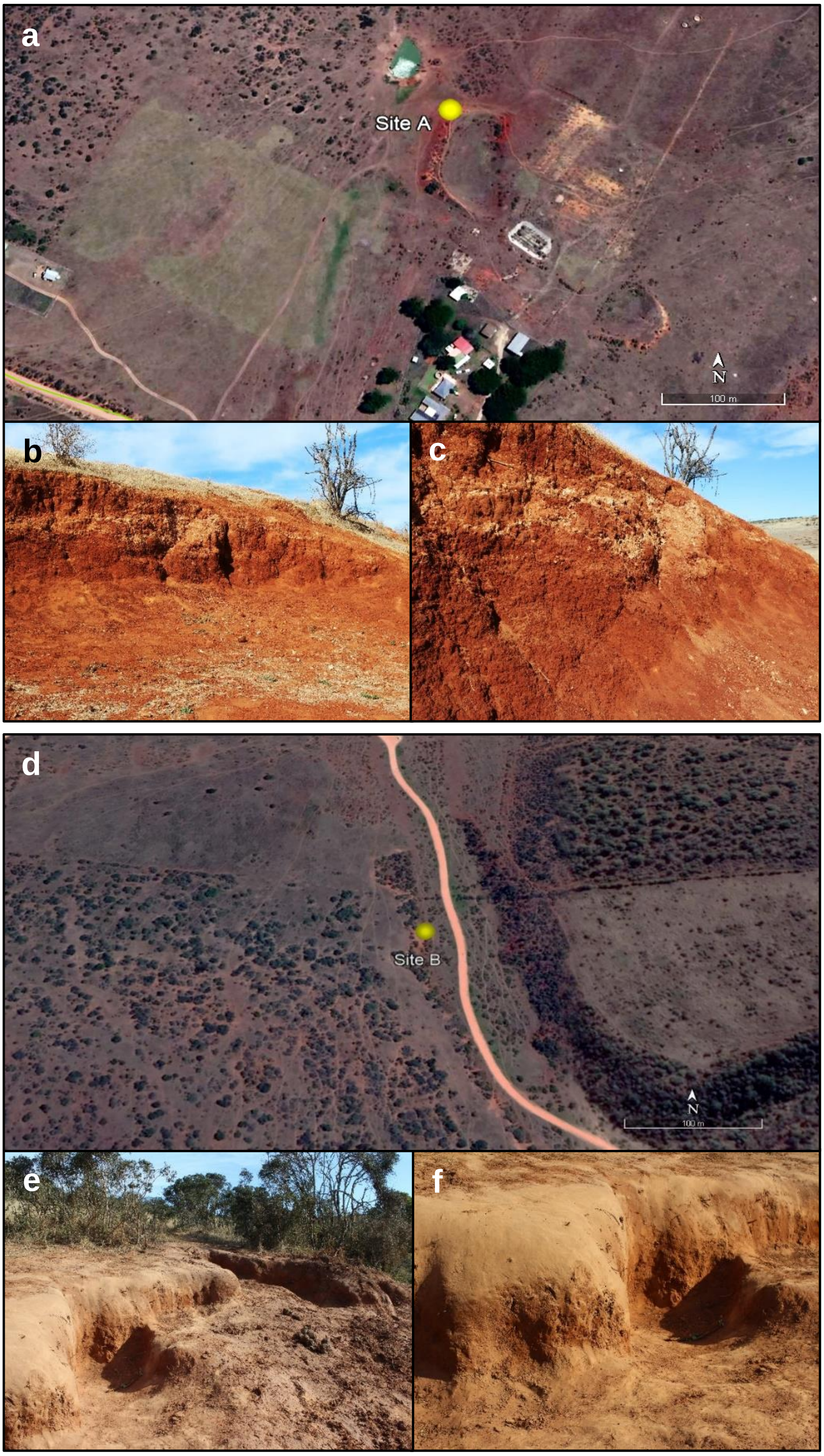

Figure 5. *Aerial view of the location of each geophagy site (yellow marker) illustrating the surrounding landscape for sites A (a) and B (d). Close-up photographs of geophagy sites A (b-c) and B (e-f) utilised by elephants. Aerial views were modified from Google Earth ©2021.*

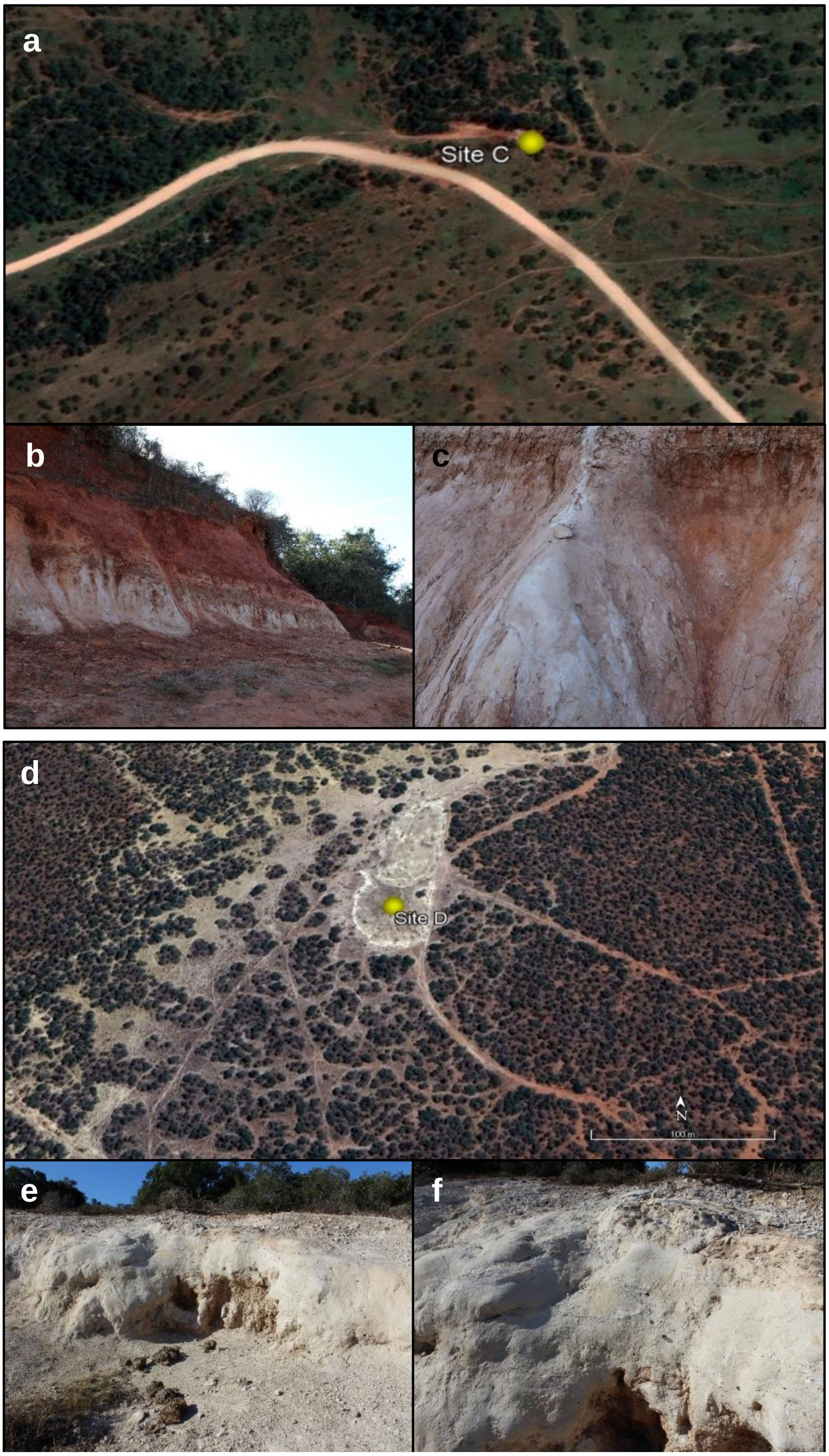

Figure 6. *Aerial view of the location of each geophagy site (yellow marker) illustrating the surrounding landscape for sites C (a) and D (d). Close-up photographs of geophagy sites C (b-c) and D (e-f) utilised by elephants. Aerial views were modified from Google Earth ©2021.*

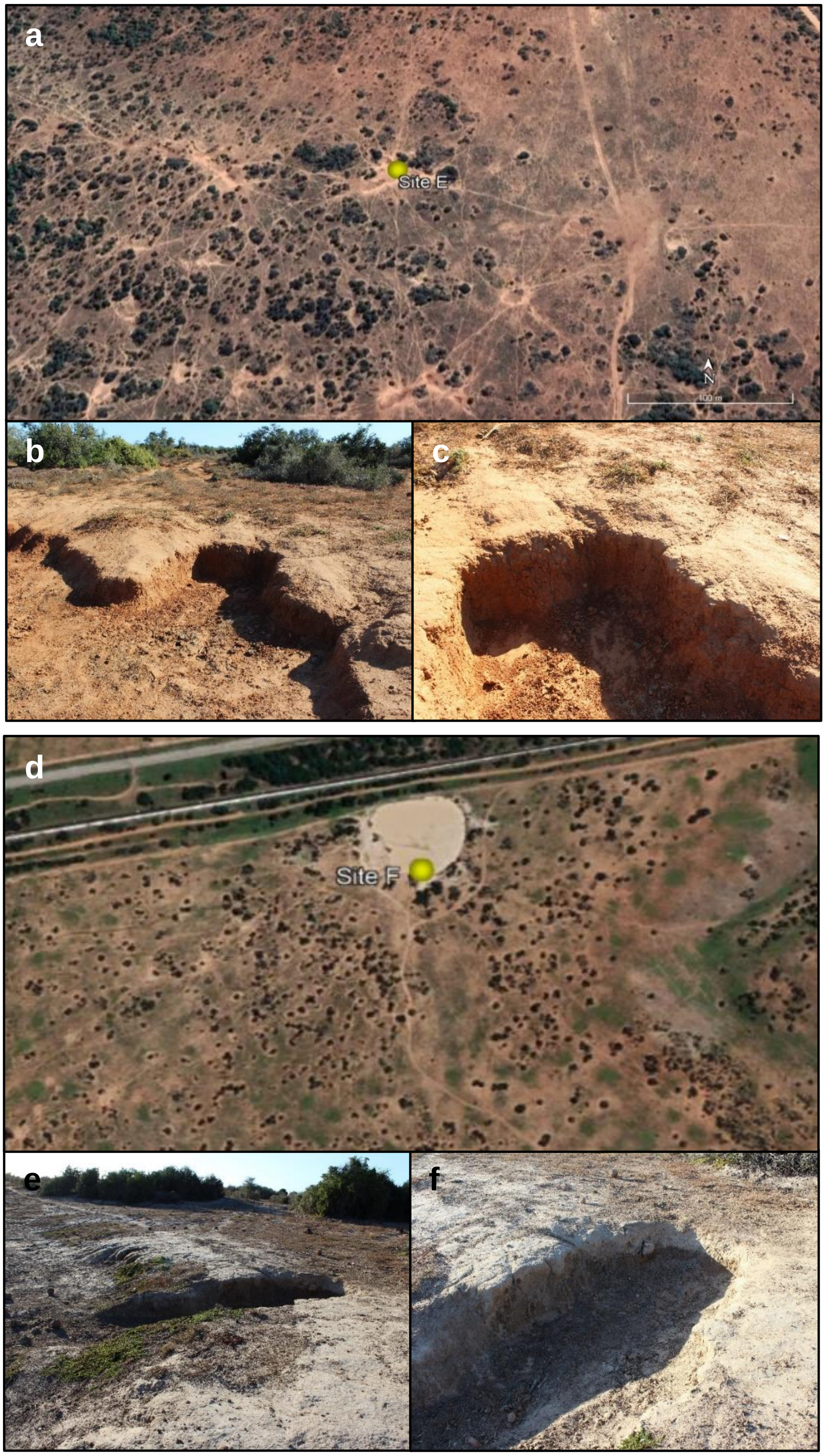

Figure 7. *Aerial view of the location of each geophagy site (yellow marker) illustrating the surrounding landscape for site E (a) and F (d). Close-up photographs of geophagy sites E (b-c) and F (e-f) utilised by elephants. Aerial views were modified from Google Earth ©2021.*

CHAPTER 3

GEOCHEMISTRY AND MINERALOGY

3.1 Introduction

Geophagy sites or soils (also known as mineral licks or kudurs) are natural landscape complexes that feature mineral/elemental soil outcrops that are deliberately ingested by animals (Young et al. 2011). The majority of geophagy sites fall under the lithomorphic or hydromorphic soil types. While lithomorphic geophagy sites are simply exposed rocks that animals actively search for and ingest, hydromorphic geophagy sites are created by mineral water springs where clay particles become saturated with chemical components in a water discharge region (Panichev et al. 2017). These rich natural soils are typically found in older, more stable landscapes, where they have had adequate time to mature, going through several phases of weathering whereby primary minerals have been converted into secondary (clay) minerals (Mahaney and Krishnamani 2003). Primary minerals are found in sand and coarse silt fractions, whereas secondary minerals can be found in clay and finer silt fractions (Karathanasis 2006). Minerals, and therefore certain elements, are required for a variety of physiological and metabolic processes in animals, including structural growth and support, cellular detoxification, osmotic balance, and immunity (Cherian 2020). Essentially all elements considered in animal nutrition can be divided into two groups: major- and trace elements, depending on the amounts required in the diet rather than their physiological value (Cherian 2020).

Geophagia has both beneficial and harmful consequences on animals, depending on the geochemical and mineralogical qualities of the soil consumed (Wilson 2003). Clay deposits, for example, are suggested to aid in the detoxification of the body from anti-nutritional substances by binding noxious compounds or for the relief of GI diseases (Williams et al. 2004; Xu et al. 2004). On the other hand, geophagy could lead to the ingestion of harmful parasites and/or microorganisms or even certain toxic compounds and hazardous metals (Voros et al. 2001).

Elephants, among many other species, have reportedly been observed ingesting different soil types that contain a variety of crystal or mineral compositions (Williams and Haydel 2010). Due to limited research on nutritional mineral and elemental requirements in elephants, domestic equids are often used as a reference model considering that both species have a single stomach and a short, but large hindgut fermentation chamber inhabited by bacteria (Clauss et al. 2003). The mineral status of an animal, according to Jansman and te Pas (2015), is the balance between the dietary intake of an element or nutrient and its biological demand. Evidence for mineral and elemental requirements for elephants is very limited. Nutrient requirements could vary due to the age and condition of elephants (Olson 2004). There are several essential elements known to have important metabolic roles in the mammalian system, where dietary deficiency may result in a clinical deficiency. Elements that are considered crucial for biological functionality include Ca, P, Mg, Fe, K, Mn, Na, selenium (Se) and zinc (Zn) as well as trace elements like copper (Cu), cadmium (Cd), arsenic (As), lead (Pb), uranium (U), and vanadium (V) (Sach et al. 2020).

Given the complex and diverse scenario that represents the geological base of the AENP, this chapter aims to compare geochemical and mineralogical concentrations across the six different geophagy sites selected for this study. This will be achieved by identifying which of these elements and minerals are more abundant in the XRF and XRD analyses. Determining the mineral and elemental availability in AENP at these selected sites is important as it is thought to shape animals, including elephant distributions, and densities (Milewski 2000). It is predicted the geophagy sites that are located in the same soil type will be similar in composition. The geophagy sites situated in the northern section of the Park will therefore be more similar in composition to each other compared to the sites in the south situated in a different dominant soil type. Alternatively, each site would differ in geochemical and mineralogical composition irrespective of underlain dominant soil types. Furthermore, it is expected that quartz (crystalline silica mineral) will be the found across all sampled sites as it ubiquitous in soils (Jones et al. 2013; Panichev et al. 2013). It is therefore predicted that quartz will not be the mineral sought after instead other minerals/elements present in elevated concentrations. Similarly for trace elements, zirconium (Zr) is also considered ubiquitous in nature (Ghosh et al. 1992) and high concentrations thereof is expected across all sites. Lastly, it is predicted that geophagy would be driven by mineral/elemental supplementation and/or deficiencies due to their physiological nutritional demands. However, geophagy could alternatively or non-exclusively be driven by several GI disorders (*vide* Chapter 1).

3.2 Methodology

3.2.1 Soil collection and geochemical analyses

Soil samples were collected from these six established sites at the end of the study period (August 2020), which allowed sufficient time to confirm geophagic activity. The direct feeding area was established after studying numerous camera trap photographs and confirmed in-field with evidence of active utilisation. Three samples (ca. 150 g each) were collected per site (n = 18), each from the following zones; 1) one sample directly from the feeding or licking area; 2) another sample about 1 m away, along the consumed horizontal axis where possible; 3) one control sample, according to the method described by Mahaney and Krishnamani (2003) and Ayotte et al. (2006). The control sites were randomly selected exposed soil between 8-15 m away from the lick site with no sign of utilisation. Each soil sample collected was stored in a labelled paper bag and left to air dry for several days.

All dried samples were subsampled (to approximately 50 g) and ground lightly with a mortar and pestle before being passed through a 2 mm sieve to homogenise the sample for analysis. All subsamples (n = 18) were then stored in plastic containers (Fig. 8) and submitted for semi-quantitative, XRD (X-ray Diffractometry) and quantitative XRF (X-ray Fluorescence), at the Department of Geology of the University of the Free State, Bloemfontein Campus.

Figure 8. *Six of the 18 prepared samples from each of the six geophagy sites showing distinctive colour and hue differences.*

The XRD technique is commonly used to determine the mineral/crystalline compounds in soil sampled by using the diffraction patterns generated by each unique crystalline phase (Loubser and Verryn 2008). The XRD analysis for this study was performed using a PANalytical empyrical diffractometer with a Cu-anode ray tube. The software package Highscore/Sleve was used for phase identification and interpretation. Conversely, the XRF technique is used to determine the chemical composition of soil samples. The loss on ignition (LOI) was calculated for major element analysis by heating the samples to 1050 °C and allowing volatile chemicals to escape until their mass ceased changing. The percentage of weight lost on ignition provides an approximate estimation of the soil's organic composition. Each sample was fused to create beads. For the minor/trace element analysis, all samples were milled using an iron mill before turning the samples into a pressed pellet using Hoechst wax. The Wavelength Dispersive X-ray Fluorescence Spectroscopy (WD-XRF) used for this study was a Rigaku-Primus IV, with a rhodium (Rh) -anode tube, using ZXS software to produce quantitative results.

3.2.2 Soil classification

The Munsell colour chart (1994) was used to categorise the colours of the soils, furthermore hue, value, and chroma were used to depict the colours. On the electromagnetic spectrum, the hue notation relates to the colour shade of the soil (R: red, Y: yellow and YR: yellow-red). The purer the colour of the soil, the higher the hue. The value of a soil colour represents how much light is reflected, or how light it is. The concentration of colour is referred to as the soil's chroma. Low-chroma colours are referred to as weak, but high-chroma colours are described as being highly saturated, intense, or vivid. The mean pH (H_2O) for three subsampled soils as well as the mean cation exchange capacity (CEC) for three subsampled soil was obtained from soil grids through ISRIC - WDC Soils.

3.2.3 Data and statistical analyses

Parametric requirements of the (continuous) geochemical variables were first inspected using the Kolmogorov-Smirnov test. LOI was excluded from subsequent analyses. Several approaches were used in the Repeated Measurement Analyses (RMA) using subsamples (feeding sites, 1 m away and control sites) as within site variation. For each mineral/element as cases, only four of 35 differed significantly. Analyses were performed for each combination of geophagy sites and geochemical condition (mineral/crystalline compounds, major- and trace elements) using all the minerals and elements as cases, only two of 18 were significantly different. Using Sites and Type (individually and combined) as categorical predictors showed a non-significant effect of the within-site source of variation. Data from the subsamples were therefor combined in order to get an average value. Consequently, differences in the mean geochemical values among different sites were analysed using one-way ANOVAs (for normally distributed variables) or Kruskal-Wallis ANOVA (for non-normally distributed ones).

Two multivariate approaches were used to determine if the geophagy site could be separated according to their geochemical composition. First, a Principal Component Analysis (PCA) was performed for the XRF of major and trace elements of the soil (Treguier et al. 2006), independently. Biplots were used to facilitate the recognition of subgroups to determine the basis of site separation. Additionally, a Discriminant Function Analysis (DFA) was performed (again, independently for the major and trace elements) to investigate how the data were distributed in the morphometric space as done by Hasan et al. 2020, according to their geographic origin (using the site as grouping factor). The standard method was used, as well as the substitution model to include all samples in the analysis. Statistical analyses were performed using STATISTICA 7.0 (Statsoft) with a statistical significance set at $p < 0.05$.

3.3 Results

3.3.1 Soil characteristics and colour classification

The descriptive results of the Munsell soil classification are listed in Table 1 for all sites. The mean soil pH values across all sites varied marginally from 6.1 (slightly acidic) to 6.7 (almost neutral), with sites B, C and D showing the lowest pH values. The CEC ranged between 21-25 cmol (+)/kg. Munsell values differed across all sites but could be grouped according to their hues. Sites A, B and E were redder in colour than sites C, D and F which had a yellow to whitish appearance.

Table 1. *Descriptive soil classification of soil per site using colour, mean pH and cation exchange capacity (CEC) values. Soil colour was determined according to the Munsell colour chart and values.*

	SITE A	**SITE B**	**SITE C**	**SITE D**	**SITE E**	**SITE F**
Soil colour	2.5 YR 5/6	7.5YR 6/6	2.5Y 8/3	5Y 8/2	7.5YR 5/6	2.5Y 7/4
pH (H_2O)	6.2	6.1	6.1	6.1	6.7	6.7
CEC (cmol (+)/kg)	23	21	22	22	21	25

3.3.2 Soil mineralogical and geochemical composition

The XRD analysis results identified nine different minerals in total: quartz, calcite, plagioclase, muscovite, gypsum, dolomite, ilmenite, K-feldspar/rutile and clinopyroxene (Table 2). In addition, the quantitative XRF analysis yielded the following ten major oxide elements: silicon dioxide (SiO_2), titanium dioxide (TiO_2), aluminium dioxide (Al_2O_3), ferric oxide (Fe_2O_3), magnesium oxide (MgO), manganese monoxide (MnO), calcium oxide (CaO), sodium oxide (Na_2O), potassium oxide (K_2O) and phosphorus pentoxide (P_2O_5). The XRF analysis also yielded the following 16 trace elements: chromium (Cr), cobalt (Co), nickel (Ni), scandium (Sc), rubidium (Rb), strontium (Sr), yttrium (Y), Zr, niobium (Nb), barium (Ba), thorium (Th), V, Cu, Zn, As and Pb.

The complete XRD analysis results of mineralogical composition found in geophagic soils at sites A-F are presented in Appendix A, Table A1. As predicted, quartz was the most abundant mineral found across all sites except at site D (Appendix A, Table A1), where calcite represented the highest percentage. Quartz concentrations differed significantly among geophagy sites (ANOVA: $F_{5,12} = 18.15$, $p < 0.001$) given the lower concentration of quartz at site D, (mean 32%) compared to the other sites (ranging from 50-73%). The high calcite content (considered abundant, Appendix A, Table A1) of site D (mean 37%) also created significant differences among the sites (K-W ANOVA: H (5) = 13.52, p = 0.019), given the smaller calcite content of sites A, C and E, and its total absence in sites B and F. Overall, plagioclase was the second most abundant mineral found in the soil samples, averaging more than 15% of the total weight, but its abundance did not significantly differ among sites. Muscovite was also common (ca. 10%), but its concentration did show geographical differences (ANOVA: $F_{5,12} = 10.37$, $p < 0.001$), with sites A and E showing slightly higher concentrations than the other sites (Tukey's HSD, all $p < 0.05$). The remaining minerals showed residual concentrations (Appendix A, Table A1) in general and were less commonly found among the sites for example, gypsum only being found at sites A and E, dolomite only at sites A and B and clinopyroxene exclusive to site F (5 wt.%).

None of the minerals show significant differences among the sampling sites. Table 2 provides a data summary of Appendix A, Table A1 where mineral concentrations detected at the feeding site and the control site were compared to determine which non-essential (quartz) and essential minerals were more abundant. Across all sites, with sites A and B as the exception, quartz concentrations were lower at the direct feeding site. Site C had the most different types of minerals (clinopyroxene, K-feldspar and plagioclase) present at elevated levels in the consumed soil sites as opposed to the control. Dolomite and gypsum were the only two minerals not detected at elevated concentrations across all sites.

***Table 2**. Identification of essential and non-essential mineral concentrations (weight %) present at feeding depth soils compared to control soils across all sites A-F in Addo Elephant National Park, South Africa.*

MINERALS	SITE A	SITE B	SITE C	SITE D	SITE E	SITE F
Calcite	X		X	X		
Clinopyroxene						
Dolomite						
Gypsum						
Ilmenite		X				
K-feldspar		X	X		X	
Muscovite						
Plagioclase		X	X			
Quartz			O	O	O	O

X Essential mineral concentration **higher** at feeding area than at control

O Non-essential (quartz) concentration **lower** at feeding area than at control

Calcite $CaCO_3$
Clinopyroxene $(Ca,Na,Mg,Fe,Al,Ti)_2Si_2O_6$
Dolomite $CaMg(CO_3)_2$
Gypsum $CaSO_4 \cdot 2H_2O$
Ilmenite $Fe^{2+}TiO_3$
K-feldspar $KAlSi_3O_8$
Muscovite $KAl_2(AlSi_3O_{10})(OH)_2$
Plagioclase $NaAlSi_3O_8$/ $CaAl_2Si_2O_8$
Quartz SiO_2

The complete geochemical XRF analysis results are presented in Appendix A, Table A2-A7. The most dominant major element was SiO_2 across all sites. However, SiO_2 concentration differed among them (ANOVA: $F_{5,12} = 29.57$, $p < 0.001$), with sites B, C and F showing higher SiO_2 values than sites A and E, and all of them being higher than site D (Tukey's HSD, all $p < 0.05$). Site D also differed from the remaining locations (Appendix A, Table A5) because of its higher CaO concentration (K-W ANOVA: H (5) = 15.37, p = 0.009). RMA showed that Al_2O_3 was the only major element to differ significantly among the geophagy sites ($F_{2,10} = 10.92$, $p = 0.003$), with sites A and E showing significantly higher Al_2O_3 concentrations than the remaining four sites (Tukey's HSD, all $p < 0.05$). The rest of the major elements showed residual concentrations among the sites.

A simplified data summary and of Appendix A, Tables A2 – A7 is provided in Table 3 which highlights the differences of essential major and trace element concentrations detected by the XRF analyses. According to these values, Ca and Na in particular were present at higher or equal levels for most of the sites. Site F on the other hand was the only area containing a higher level of Fe, Mg and As was the most abundant trace elements at higher or equal levels compared to the control, found across four sites.

Table 3*. Identification of essential major and trace element concentrations present at feeding depth soils compared to control soils across all sites A-F in Addo Elephant National Park, South Africa.*

		SITE A	**SITE B**	**SITE C**	**SITE D**	**SITE E**	**SITE F**
Major elements	**Fe**						X
	Mg						X
	Mn	X	X			X	
	Ca	X	O	X	X	X	
	Na	X	X	X		X	X
	K						
	P	X	O		X	O	X
Trace elements	**V**						
	Cu		X		O	X	
	Zn	O					
	As	X	O		X		X
	Pb				O	X	

X Essential element concentration **higher** at feeding depth than at control

O Essential element concentration remained the **same** at feeding depth than at control

The only significant differences of trace elements across the sites were Ba ($F_{2,10}$ = 5.6, p 0.023), Rb ($F_{2,10}$ = 4.79, p = 0.035) and V ($F_{2,10}$ = 6, p = 0.02). The only exceptions were the level of trace elements at site D, (Appendix A, Table A5) ($F_{2,30}$ = 5.92, p = 0.007) and C, Appendix A, Table A4, ($F_{2,30}$ = 4.58, p = 0.018), which were higher for control than for feeding site samples (Tukey's HSD. Site D: p = 0.005; Site C: p = 0.024). Results from univariate analyses (parametric ANOVA and Kruskal-Wallis ANOVA) are given in Appendix A, Table A8. Overall, these tests evidenced that most of the chemical components analysed (minerals, major and trace elements) showed significant differences in their concentrations among the sites (all $p < 0.05$), with the only exceptions of plagioclase (ANOVA: $F_{5,12} = 1.73$, $p = 0.202$), ilmenite (K-W ANOVA: H (5) = 9.51, p = 0.091) and dolomite (K- W ANOVA: H (5) = 7.41, p = 0.191).

Lastly, as predicted the highest concentration for the trace elements was that of Zr (overall mean 746.6 mg/kg), being the most dominant element across all sites, except for site D (Appendix A, Table A5), where Sr and Ba reached higher levels. Therefore, the Zr concentration was significantly different among sites (K-W ANOVA: H (5) = 14.78, p = 0.01). The second most abundant element was Ba (261 mg/kg), which also showed differences among sites (ANOVA: $F_{5,12} = 41.14$, $p < 0.001$). Tukey's HSD pairwise comparisons (all $p <0.05$) showed that sites A (Appendix A, Table A2), E (Appendix A, Table A6) and F (Appendix A, Table A7) (range: 308-367 mg/kg) had significantly higher Ba concentrations than sites D (Appendix A, Table A5), B (Appendix A, Table A3) and C (Appendix A, Table A4) (range: 164-215 mg/kg).

The PCA (results of major elements, Fig. 9) determined that about 72% of the total variance was explained by the first two components. The first one accounted for 39% of the variation, with Al_2O_3, MgO and K_2O as the strongest loading factors, all being negatively correlated with the component (Fig. 9a). For the second component (33% of the variance) the strongest loading factors involved SiO_2 and CaO, each of them respectively showing negative and positive correlations with the component (Fig. 9a). The first axis differentiated three groups (A+E, C+D and B+F) whereas the second one separated site D from the remaining ones, thus creating a combined effect of four groups in total: A+E, C, D and B+F (Fig. 9b).

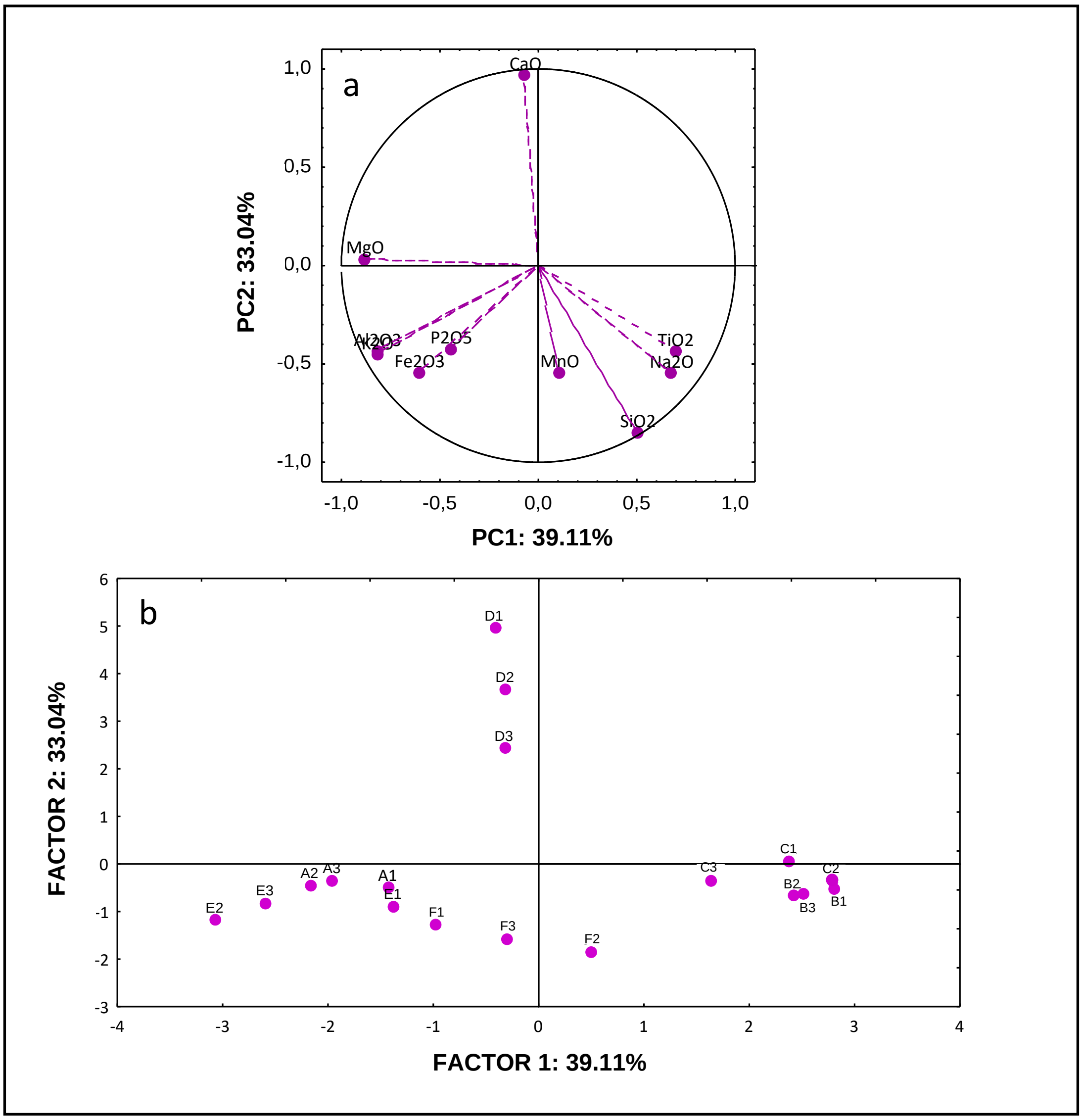

Figure 9. *Principal component analysis (PCA) of major elements (oxides) for all soils sampled at sites A-F. a) loading factors of the first two principal components; b) sites distributed across the first two principal components.*

The DFA analysis of the major elements yielded a significant model of discrimination (Wilks' Lambda: 0.000 approx., $F_{50,17} = 24.703$, $p < 0.000$) with two significant discriminant functions representing 88% of the total variance. The oxides with the largest standardised coefficients for the first function were SiO_2 (5.84), Fe_2O_3 (3.92), CaO (5.33) and K_2O (3.49), whereas SiO_2 (3.10), Al_2O_3 (3.85) and K_2O (4.99) had the largest standardised coefficient for the second function. Squared Mahalanobis distances among the sites were significant except that between sites B and C, which were the closest in morphometric space (distance = 187.57, p = 0.143, Fig. 10). On the other hand, the highest distance was found between sites B and E (distance = 2162.46, p = 0.002, Fig. 10). The classification matrix generated by the model correctly classified all sites with a 100% correct classification for all soil samples.

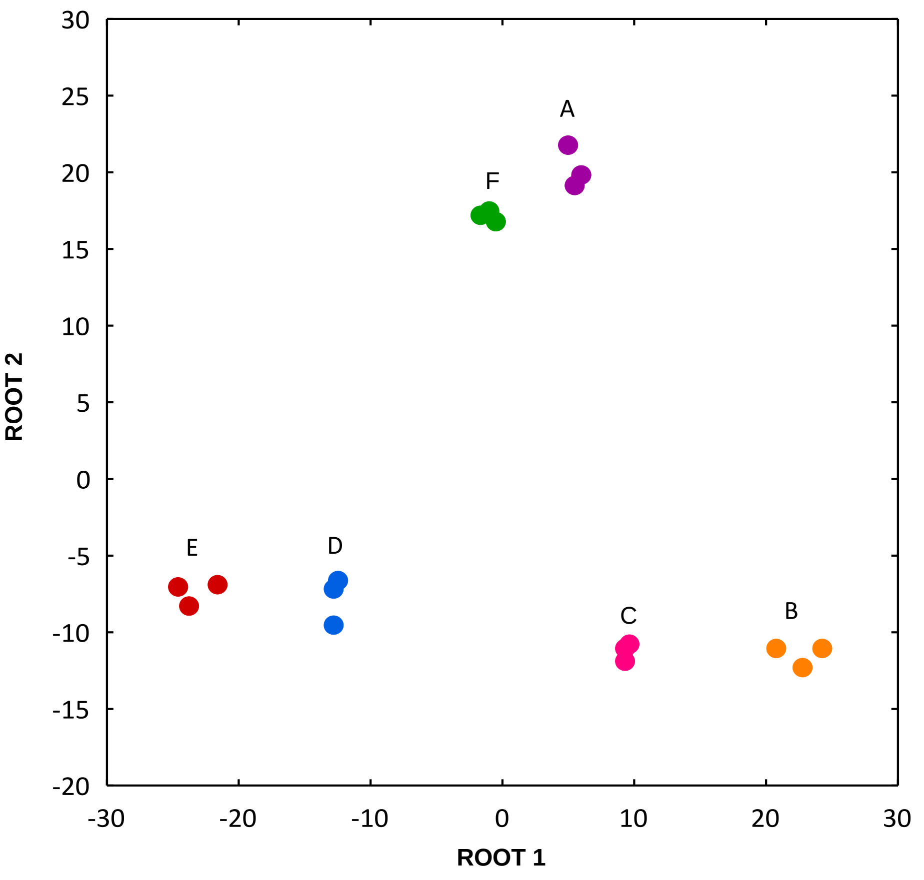

Figure 10. *Discriminant function analysis (DFA) for major (oxide) elements present at sites A- F, where A-F represent each site respective to corresponding plots (88% of total variance accounted for).*

Considering the trace elements, the PCA analysis results indicate that almost 83% of the total variance was determined by the first two components. The first one (56.7% of the variance) includes Sc, Co, Ni, Zn, Rb, Y and Pb as the strongest loading factors. The second component (26.2% of the variance) included Zr and Nb as the most important loading factors (Fig. 11a). The first function differentiated three groups (A + E, B + C + F and D) whereas the second factor separated sites B and site F from the remaining ones, thus creating a combined effect of five groups in total: sites A + E; B, C, D and F (Fig. 11b).

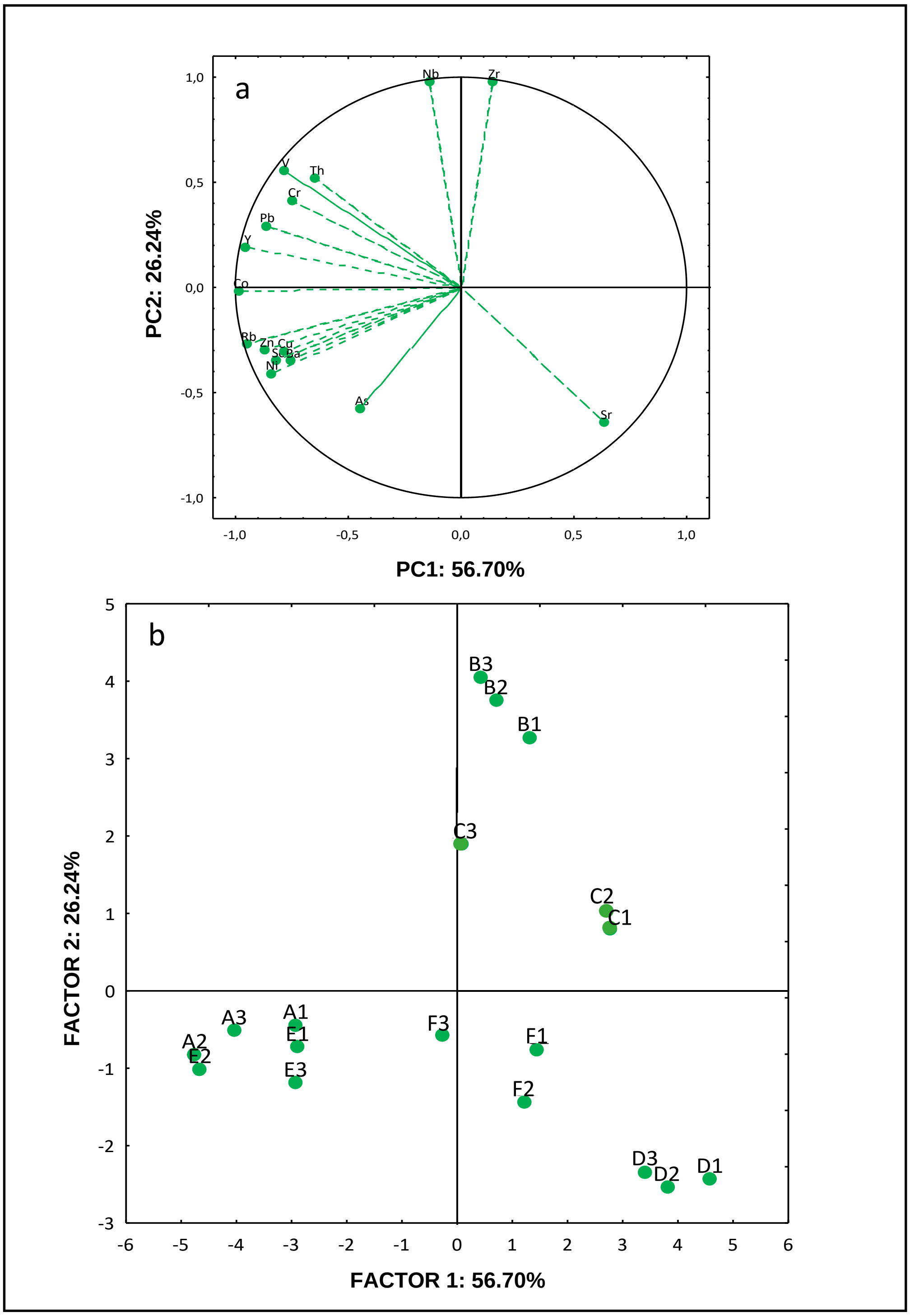

***Figure 11**. Principal component analysis (PCA) of trace elements for all soils sampled at sites A-F. a) loading factors of the first two principal components; b) sites distributed across the first two principal components.*

The DFA analysis of the trace elements (Fig. 12) yielded a significant model of discrimination (Wilks' Lambda: 0.000 approx., $F_{60,8} = 35.803$, $p < 0.000$) with two significant discriminant functions representing 99% of the total variance. The trace elements with the largest standardised coefficients for the first function were Ba (42.25), Y (38.79), Sr (31.04) and V (33.76), whereas Cr (6.24), Co (5.78) and Pb (5.40) had the largest standardised coefficient for the second function. The longest squared Mahalanobis distance was found between sites D and F (distance = 354957.1, $p = 0.013$, Fig. 12). The classification matrix generated by the model correctly classified all sites with a 100% correct classification for all soil samples.

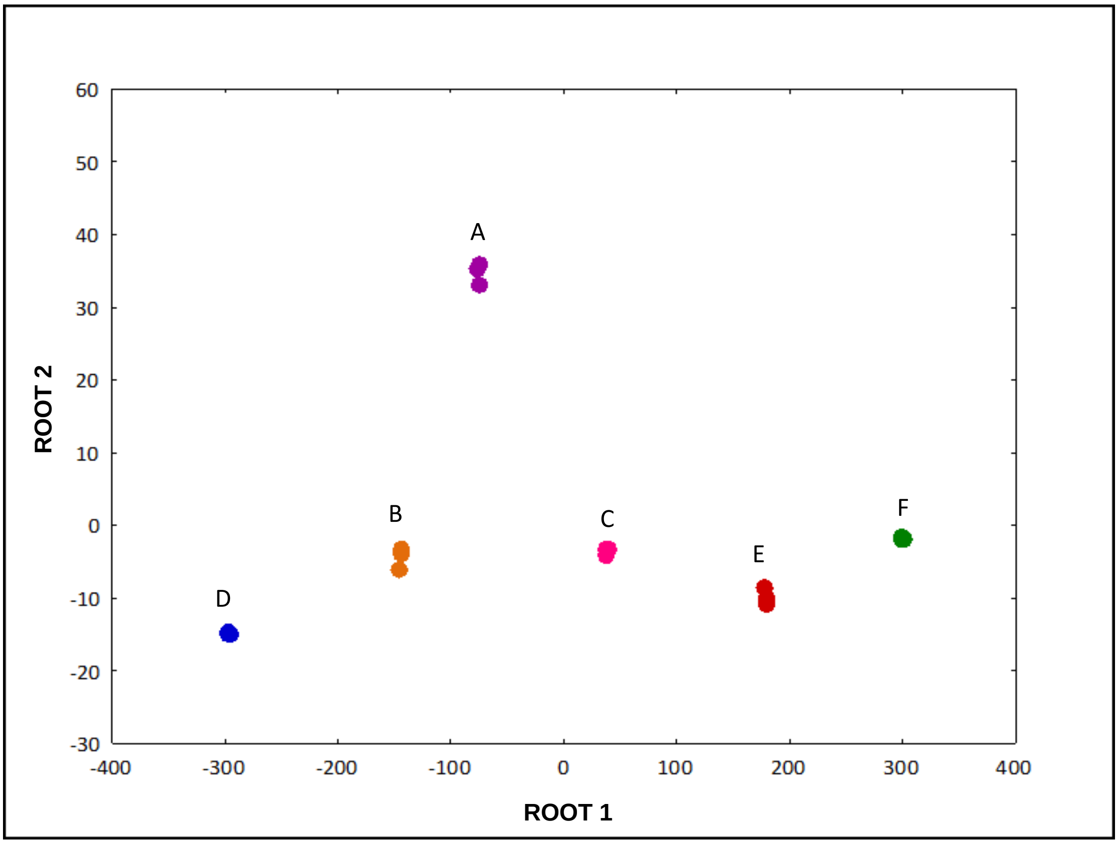

***Figure 12**. Discriminant function analysis (DFA) for major trace elements present at sites A-F, where A-F represent each site respective to corresponding plots (99% of total variance accounted for).*

3.4 Discussion

The study area in AENP is rich in mudstone topsoil, with underlying layers of clay that are exposed due to weathering of the mudstone. Clay soils can generally be seen over sandstone layers except in heavily weathered areas and open parts of the Park such as the dams where sandstone becomes more visible. All geophagy sites were situated in open vegetation clearings in some instances within close proximity to a water source (e.g., site A). More specifically, the dominant soil type for two geophagy sites in the northern part of the study area (sites F and E) is calcic luvisols. Site D lies on the borderline of two dominant soil types, however, considering the high concentrations of Ca found, it can be deduced that site D also has a more dominant calcic luvisol soil type. The other three sites (A, B, and C) situated in the southern section of the study area, are more dominantly covered with ferric luvisols, therefore, splitting the geophagy sites into two distinct groups based on soil types alone. Luvisols at lower elevations typically have a high percentage of clay, a high capacity to hold nutrients, and a good ability to retain water (Archibald et al. 1996; Jones et al. 2013). It was predicted that the geochemical and mineralogical analyses would support similarities across sites underlain by the same dominant soil types, but the PCA results do not support this prediction. Sites A and E are more similar in composition which is striking as these sites are on opposite sides of the study area and each underlain with different dominant soil types.

Soil CEC (mean values) for all sites ranged between 21 and 25 cmol (+)/kg, which has a moderate rating according to Hazelton and Murphy (2007) in terms of the capacity of the soil to hold and exchange cations. Soil pH (mean values) for all sites ranged between 6.1 and 6.7, considered slightly acidic to almost neutral. Site E and F had more neutral mean pH values (both 6.7), and were both located in the north of the

Park. Generally, the pH as well as its buffering capacity in relation to CEC affects the availability of nutrients, minerals, and toxic elements in the soil (Hazelton and Murphy 2007). According to Ngole-Jeme and Ekosse (2015), primary minerals that have a lower CEC ultimately influence the sorption capacity of the soils.

The high concentrations of the primary non-clay mineral quartz (or forms of silicon oxide) found in this study were expected, as it is abundant in soil environments (Panichev et al. 2013). It is the most common product of natural intermediate weathering of various rocks and due to particles deposited by winds (Jones et al. 2013; Panichev et al. 2013). The high abundance of calcite ($CaCO_3$), which is a secondary (clay) mineral (Ngole-Jeme and Ekosse 2015), found in outlier site D could be accounted for by the presence of numerous calcareous shell-rock fragments (Le Roux 2000; Limpitlaw 2010), that are exposed, as seen in Appendix A, Fig. A1. Half (50%) of the mineral composition at the feeding site at site D consisted of calcite, whereas calcite only made up 37% of the composition for the control sample. This is a notable difference, not only compared to the control sample of site D but also the contrasting low concentration found in sites A, C and E (means ranging between 0.7% and 2,3%).

Quartz and plagioclase were the only minerals detected in all samples across all sites. Plagioclase, which was the second most abundant, is a mineral group that consists of a ratio containing Na and Ca and is considered a primary mineral alongside K-feldspar (Hazelton and Murphy 2007), which is found in four (sites B, C, E and F) of the six geophagic soils. According to Taylor and McLennan (1985) and Nesbitt and Markovics (1997), plagioclase is not expected to be present in soils due to its nature to chemically weather and alter rapidly to secondary clay minerals. However, plagioclase feldspars, with respect to europium anomalies (Eu^{2+}), are susceptible to replacing Ca^{2+} in such plagioclase feldspar matrices (Aubert et al. 2001). For all sites, except site D, plagioclase is found in higher concentrations than calcite while certain sites had no record of calcite at all. As the prediction suggests, concentration ratios of Na and Ca could therefore be elements sought after by elephants across the Park. Other studies conducted claim that Na is an attracting mineral for soil eating (Weir 1972; Holdø et al. 2002; Mwangi et al. 2004). In a study conducted in Aberdares National Park, Kenya, licks that were actively utilised by elephants contained high concentrations of Na and I as they are linked in the geochemical cycle (Mwangi et al. 2004). However, in our study, even though low Na concentrations were present, I was not detected in the soil at all. This is somewhat surprising because according to Johnson (2003), I concentrations in the soil are supposed to be high in coastal zones (0-50 km from the sea) and the furthest site for this study is approximately 33 km from the coastline. Soil's ability to retain I is depended on soil properties such as soil texture, temperature and pH (Shetaya et al. 2012). Rainfall is considered the main source for I and factors such as duration and intensity effects to what extent I can infiltrate or drain soils (Shetaya et al. 2012). All the above-mentioned factors might have played a role in the draining of I concentrations by the time soil sampling was done and could explain the low levels. This could potentially be alarming, as I is considered an essential element and deficiency thereof could lead to health problems such as thyroid disease (Lu et al. 2005; Shetaya et al. 2012) Furthermore, compared to previous studies on elephant geophagy, such as Houston et al. (2001), no kaolin was detected in the geophagy soils sampled in AENP. According to Chandrajith et al. (2009), an increase in kaolinite (as well as illite) indicates that soils are extremely weathered.

Additionally, oxides such as Al_2O_3 (8.51% mean), CaO (4.41% mean), Fe_2O_3 (3.36% mean), and K_2O (1.24% mean) were found in moderate to low concentrations across all samples compared to the expected high SiO_2 (73.21% mean). Al_2O_3 was the only element with concentrations significantly higher ($F_{2,10} = 10.92$, $p = 0.003$) at the control and 1 m sites than at the feeding site. Ions such as Ca^{2+}, Al^{3+}, K^+ and Fe^{2+} are all exchangeable cations found in the soils. Similarly, it was found that for the surface soils in south-eastern Australia, Fe_2O_3 and Al_2O_3, as well as the presence of $CaCO_3$, are dependent factors in the dispersion and flocculation states of soils (Hazelton and Murphy 2007). Obasi and Madukwe (2016) also suggest that silica-alumina (SiO_2/Al_2O_3) ratios serve as an indicator of progressive maturity in sandstone. The presence of Fe_2O_3 could be explained by the presence of Fe-containing muscovite and ilmenite. Elements such as Fe and Ca, although present in varying quantities, can act as antacids to help relieve excess acidity in the digestive tract (Wilson 2003; Limpitlaw 2010). The values observed for K_2O are attributable to the K-feldspar detected in the soil. The higher levels of K could be associated with the natural weathering processes of basement rocks and atmospheric deposition (Nderi et al. 2015).

Considering trace elements for the geophagic feeding sites only, the highest concentrations observed were Zr (749.83 mg/kg mean) as predicted, followed by Ba (214.17 mg/kg mean), Sr (101.5 mg/kg mean) and V (78 mg/kg mean). For site B in particular, Zr concentrations were much higher than the rest of the lick sites. Zr, considered one of the ubiquitous rare earth elements (REE), has low solubility and can therefore be used to determine the nature of parent rock and provenance characterisation (Ghosh et al. 1992; Mongelli et al. 2006; Paikaray et al. 2008). However as predicted, by excluding Zr, Ba should be another possible sought after elements across sites. According to Krishnamani et al. (2000), Ba (and Sr) are not of importance for geophagy behaviour. Interestingly, Ba and Sr are found in the calcium-normalized breastmilk of mammals, like walruses, and the concentration found in calves is directly proportional to the bioavailability thereof found in the mothers’ body (Clark et al. 2020). How exactly these elements play a role as possible nutrient drivers for elephants is unknown.

Geophagy is hypothesised to be driven by various and complex functional, physiological and morphological changes and/or deficiencies and/or stress. The mineral/elemental concentrations (and combinations thereof) between and within sites might differ on a finer scale, however results suggest the Na and Ca might be the drivers of geophagy behaviour in the AENP elephant population. Elephants require a high Ca and Na intake, especially for tusk growth and when females lactate (Dierenfeld 2008). Ca deficiency and imbalances could lead to metabolic bone disease (Ensley et al. 1994; Leshchinsky 2015). On the other hand, it is worth mentioning that the excessive amounts of quartz and toxic metals such as Cr and Ni in the soils represent possible health threats for geophagic species (Nderi et al. 2015; Ekosse et al. 2017).

CHAPTER 4

VISITATION FREQUENCY AND BEHAVIOURAL ASPECTS OF GEOPHAGY

4.1 Introduction

Elephants have been documented practising geophagy in several previous studies conducted in different parts of the world: Central African Republic (Ruggiero and Fay 1994), Tanzania (Houston et al. 2001; Kalumanga et al. 2016), Zimbabwe (Weir 1972; Holdø et al. 2002), Kenya (Bowell et al. 1996; Mwangi et al. 2004), and Sri Lanka (Chandrajith et al. 2009). For different reasons, elephant species in different habitats will seek out natural soil licks, which are located where nutrients are concentrated (Klaus and Schmid 1998; Mwangi et al. 2004). These mineral and elemental hotspots are important habitat features that play a large role in determining the behaviour within an individual's home range as well as how the landscape is utilised (Hunter 2017). Geophagy sites may be fixed in space but could only be required at certain periods and therefore may temporally influence their behaviour (Davies et al. 2016).

A study conducted in the Aberdares National Park in Kenya by Mwangi et al. (2004), found that elephants ingested soils with higher concentrations of Na and I. Given the limited availability of grasses in Aberdares National Park, the elephants' diet consists of mainly browse and certain seasonal fruits which generally contain more harmful secondary substances like tannins and alkaloids (Mwangi et al. 2004). On the other hand, in Zimbabwe's Hwange National Park, a study conducted by Holdø et al. (2002) also found that the consumed soil was Na-rich. However, more female elephants were observed ingesting these soils, and it was concluded that geophagy might be driven by the high physiological demands in elephants during pregnancy and lactation. Another geophagy study found that Asian elephants in Udawalawe National Park, Sri Lanka, consumed kaolinite and illite-rich soils (Chandrajith et al. 2009). It is suggested that these soils aided in the detoxification of unpalatable compounds found in their diet instead of nutrient supplementation (Chandrajith et al. 2009).

Several non-exclusive hypotheses exist to explain the role and prevalence of geophagic behaviour and can be divided into two broad categories: protection against gastrointestinal (GI) disorders and nutrient supplementation. Under the protection hypothesis, alleviation of GI disorders can be subdivided into four non-exclusive hypotheses: 1) relief from endoparasites and pathogens in the gut by ingesting adsorptive clays (Krishnamani and Mahaney 2000). 2) Adsorption of plant secondary metabolites and toxins (Pebsworth et al. 2011). Studies by Mwangi et al. (2004) and Chandrajith et al. (2009) have proposed that elephants practice geophagy, particularly for the detoxification of secondary plant metabolites in their vegetation diet. Toxins encountered through their diet include tannins, terpene, alkaloids, and phenols. 3) Ingesting substances like kaolin clays for their adsorptive ability could act as an antidiarrheal agent (Dominy et al. 2004). 4) Antacid effect, as ingestion of clay can assist in the adsorption of organic molecules acting as a buffer in the stomach and gut lining by producing extra mucous secretion (Leonard et al. 1994).

However, the more universally accepted hypothesis explaining this habitual and intentional behaviour is that geophagy supplements dietary mineral and elemental deficiencies (e.g., Klaus et al. 1998; Young et al. 2011; Kalumanga et al. 2016; Pebsworth et al. 2019). Dietary changes may modify the demand for geophagy, resulting in seasonal fluctuations in soil lick utilisation (Blake et al. 2011). Elephants are generalist/mixed feeders with a typical diet of grasses and browse, which could generally lack the adequate nutritional element concentrations to meet their dietary demand (Kalumanga et al. 2016). Deficits in micronutrients can have a negative impact on health status and raise the risk of disease (Rode et al. 2003). Animals also need different nutritional elements during different life stages such as reproductivity and lactation (Tracy and McNaughton 1995; Atwood and Weeks 2003) and for bone (Henshaw and Ayeni 1971) and tusk growth (Whitehouse 2002).

Elephant visitation or group dynamics, as well as the frequency of visits to these sites, can vary from one lick to the next (Tobler et al. 2009). Such variance could be due to differences in soil composition, distances individuals need to travel, topographical accessibility or perhaps be linked to the presence or absence of predators (Izawa 1993; Tobler et al. 2009). The spatial and temporal heterogeneity of resources across the habitat greatly influences the way elephants utilise the landscape (Weir 1972; Ferreira et al. 2017) as well as the dynamics of social structures and group sizes formed (Poole and Moss 1989). Generally, three types of groups are formed in elephants: 1) All-male/bulls' group; 2) cows and calves' groups and 3) mixed groups which consist of bulls, cows, and calves (Moss 1996). A population's age and sex distribution can be affected by factors including calf survival, birth and death rates, conception rates, and other behavioural traits (Dublin and Taylor 1996). Numerous factors influence variation and shifts in group sizes, whether seasonal or long-term, which may have significant implications on the ecology of any ecosystem (Western and Lindsay 1984).

Understanding elephant behaviour and population dynamics may therefore have significant effects on management strategies for elephants. It had already been noted by Kerley and Landman (2006) that the African savannah elephants have been observed to consequently alter the landscape in AENP by excavating soil for consumption, yet it had not been investigated. Therefore, this chapter aims to address the patterns of visitation by elephants to selected geophagy licks located in AENP. It is predicted that elephants, being diurnal animals, will utilise geophagy sites more frequently during the day when they are actively foraging. Alternatively, it could be predicted that visitation frequencies would peak during the night, as this is when most predators are least active, the atmospheric temperatures are lower (lower energetic cost for elephants), human interactions are minimal and/or elephants would possibly engage in geophagy after foraging to mitigate possible GI disorders. Another prediction is that seasonal utilisation would yield an increased and consistent pattern during the colder seasons i.e., winter and autumn. This is usually when vegetation and therefor nutrient availability is lower across the landscape. Alternatively, more frequent utilisation during the spring and summer months could support the hypothesis that more nutrients are required for breeding and reproduction. Due to the high nutritional requirements of reproductively mature females (especially Na and Ca) during pregnancy and lactation, it is predicted that adult females will utilise the mineral rich geophagy sites more often. Alternatively, taking into consideration their sexual dimorphism, males need a higher Ca and P intake than females for bone growth. Similarly, it is also expected that more individuals with tusk than without with exhibited geophagy behaviour due to the higher nutritional demand thereof.

4.2 Methodology

4.2.1 Camera trapping

The use of camera traps is a popular non-invasive technique for examining species composition, structure and abundance, habitation, density, and activity patterns (Swann et al. 2004; Pimm et al. 2015). The AENP has dense vegetation and most of the identified geophagy sites can only be reached by foot, making direct observations dangerous and difficult for a long period of time. Camera traps were therefore considered the appropriate method to continuously capture geophagic events and visits by the animals of the Park without human interaction and influence.

During the first visit to AENP in April 2019, ten initial sites were selected, and a camera trap was deployed at each site at strategic locations depending on the terrain. Considering that geophagy sites were situated within vegetation clearings, camera traps could not be mounted to trees, so modified stands were used instead. Given the limited number of suitable camera traps available, only one camera trap was placed at each geophagy site which adequately covered the geophagy area similar to methods of Pebsworth et al. (2011). More than one elephant could be photographed at once utilising the site at the same time (Fig. 13).

Two different types of cameras were used, Bushnell HD Trophy Cameras and Browning Spec Ops Advantage Trail Cameras, both triggered by an infrared motion-and-heat detector. Similar, to the methods of Blake et al. (2011), all cameras were set to take three consecutive photographs once triggered with a minimum of the 5-min time interval between instances. For the whole study period (April 2019-May 2020) the cameras remained continuously active unless technical errors occurred. Most of the interruptions, however, were caused by the elephants displacing the cameras or damaging them, thus greatly affecting the number of successful camera trapping days at certain sites. The nation-wide lockdown during the Covid-pandemic also contributed to missing data. During this period, travel restrictions and strict SANParks regulations prohibited visits in order to replace batteries, empty SD-cards and restore knocked over cameras. Cameras were serviced approximately every 5 weeks (when possible) to exchange batteries and memory cards, as a preliminary test proved that the batteries would last up to 7 weeks with our set up of choice.

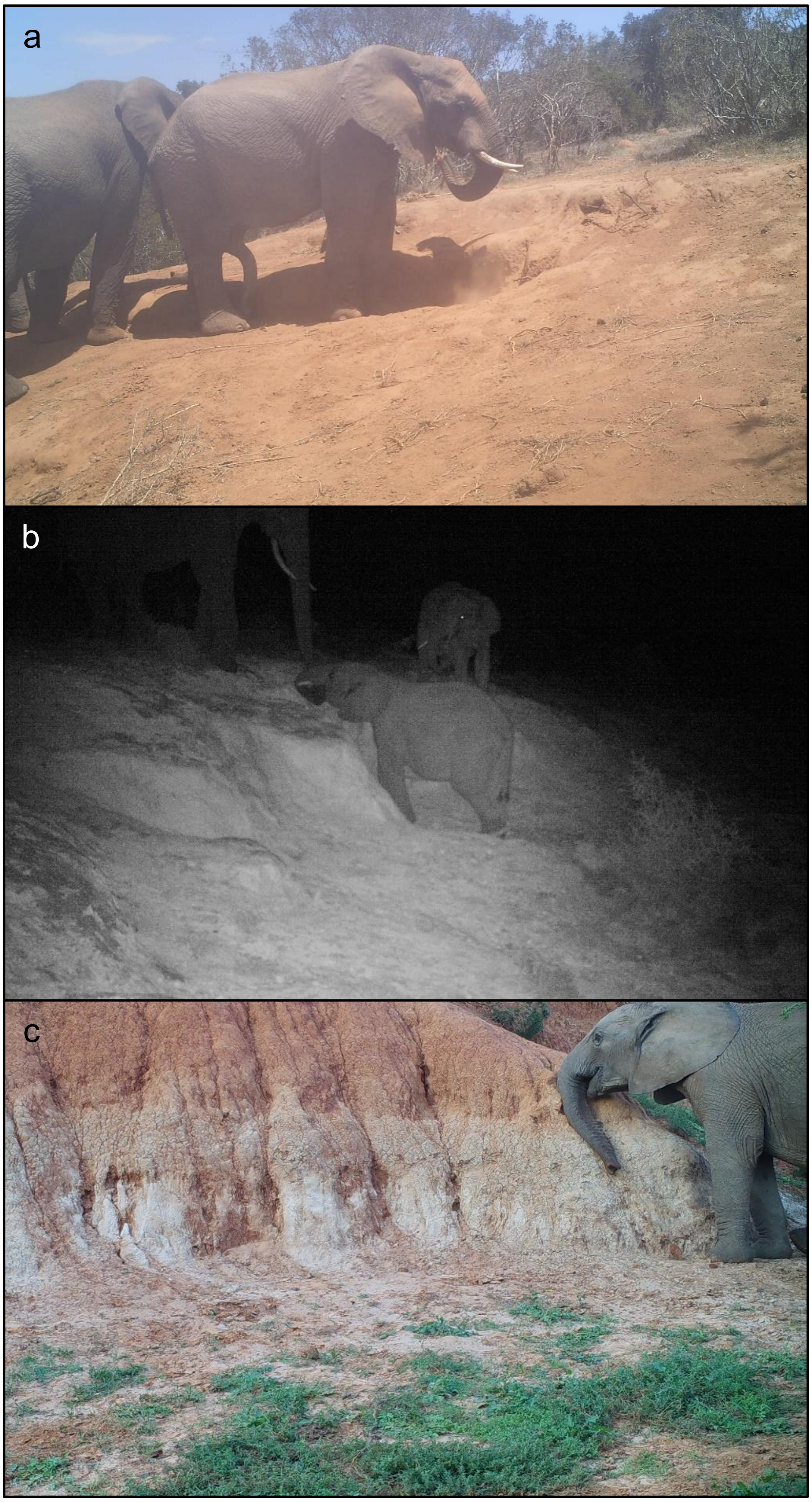

***Figure 13**. Camera trap photographs taken of different individuals utilising geophagy site B (a), site D (b) and site C (c), respectively.*

All photographs were automatically stamped with the date and time once triggered. Based on the 5-min interval setting of the camera, any photograph triggered after that period was considered an independent record, similar to the methods of Srbek-Araujo and Chiarello (2005) and Hamel et al. (2013). Records that included individuals passing by the area, not in close proximity to and/or not interacting with the geophagy site were excluded from all analyses. Whenever photographs contained two or more animals simultaneously utilising a geophagy site, each animal was considered an independent record. All medium and large-sized mammals photographed at geophagy sites were documented. Birds were not included as the camera traps are not always triggered by smaller animals and did also not have a sufficiently rapid response time for fast movements.

Successful camera trap days were calculated from the date each camera was placed in operation to the day the batteries and SD-cards were replaced (i.e., starting a new sequence) or the last photograph taken (based on the date and time stamp on the images). For each geophagic event recorded, the date, time, species, and sex were documented. Furthermore, for all elephant records, additional data such as age class and presence/absence of tusks were also obtained when possible, depending on the conditions of the photos. For instance, if the presence or absence of tusks could not be determined from the photographs, the entries were referred to as “out of sight”.

4.2.2 Sex classification of elephants

Adult elephants are sexually dimorphic in body size and have a few distinguishable external characteristics and shapes. When possible, the sex of the elephants was determined from the photographs deemed suitable. Body size, height, and shape, as well as head shape, the thickness of tusks and genitalia, were considered while sexing the elephants as suggested by Moss (1996).

Full-grown males are generally larger and stand taller than cows of the same age. From a lateral view, the underside of a female's body tends to be parallel to the ground whereas the underside of males slightly slopes upward to their chest (Fig. 14). Bulls have a much broader, bulkier, and rounded head with a sloping forehead, whereas the head shape of females is narrower and longer with a squared forehead. These characteristics are similarly distinguishable in calves as well. Tusk thickness and size also differ among the two sexes, with male elephants having thicker and more tapering tusks compared to the long, slender and more uniform tusks of cows.

From both the lateral and posterior view, the external reproductive organs can be seen. The penis is enclosed in a large forward-facing sheath and from behind the male has a clear ridge that runs down from the anus up to the sheath between the hind legs (Fig. 15). The vulva of the cows usually hangs low between the legs with the opening facing downward (Fig. 15). From behind skin folds are visible which end off squared to the vulva opening.

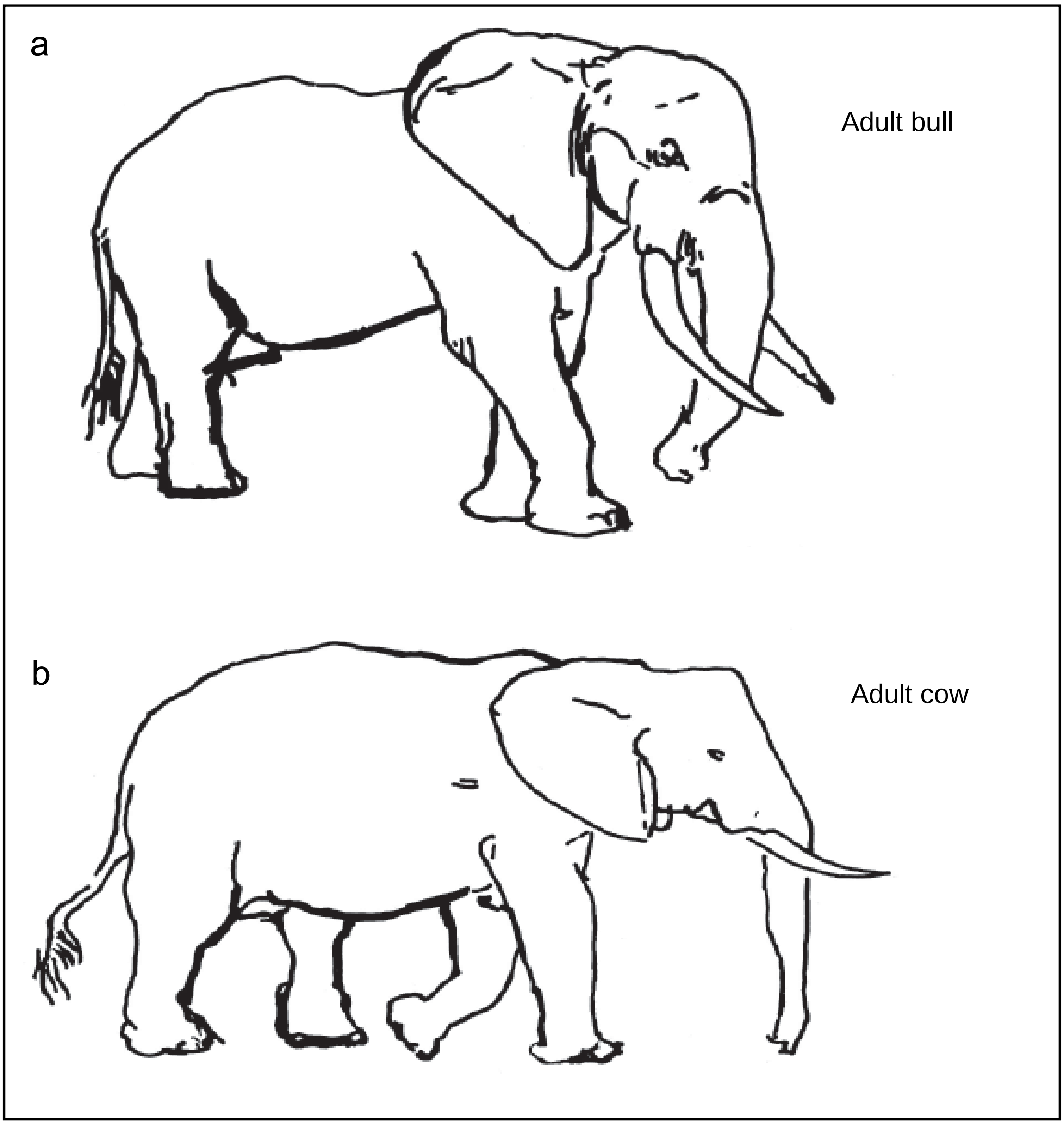

Figure 14. *Visual body shape differences between adult bulls (a) and cows (b) as seen from the lateral view (Modified from Moss 1996).*

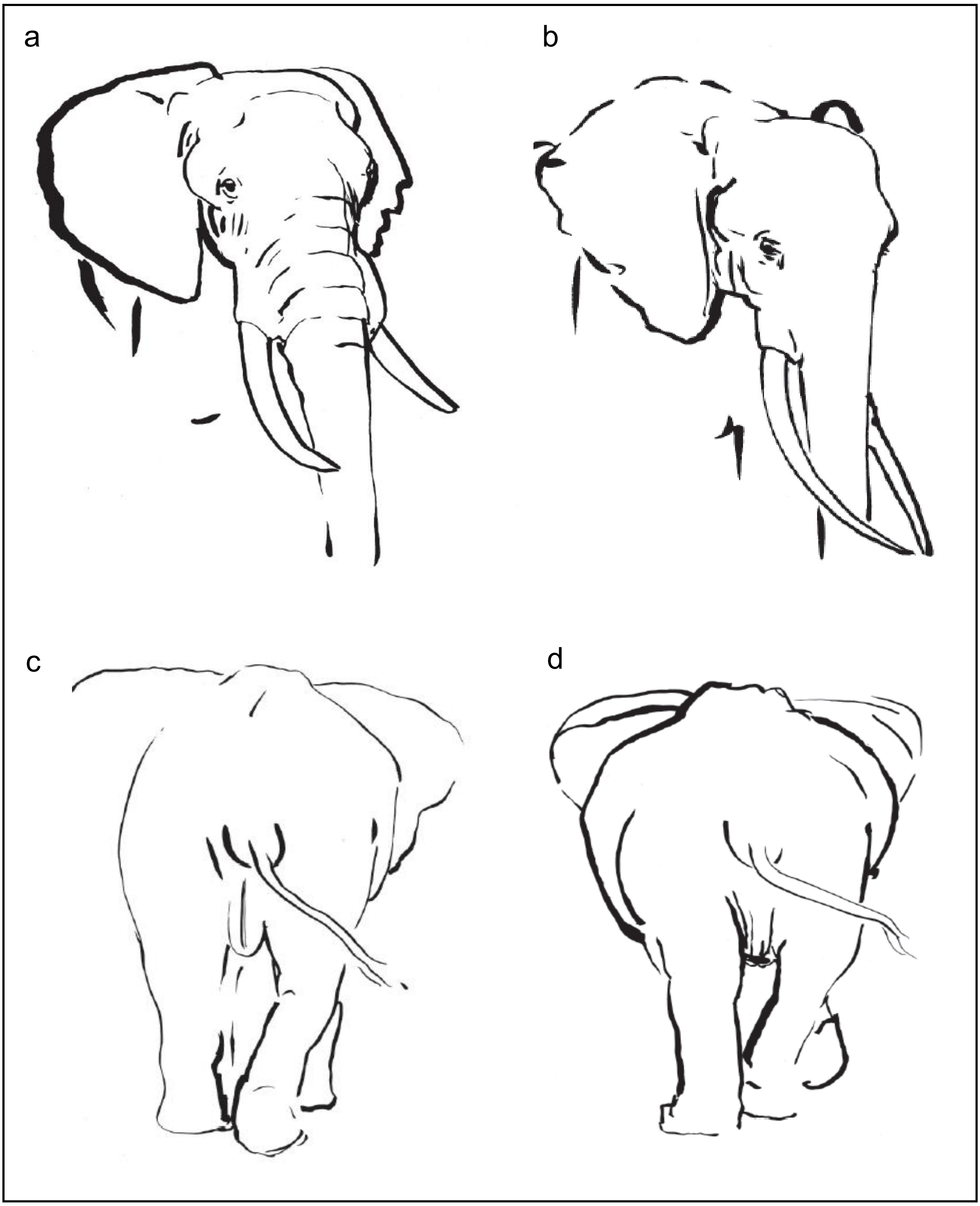

Figure 15. *Head shape difference between an adult bull (a) and an adult cow (b), as well as the posterior view of an adult bull (c) and an adult cow (d) illustrating body shape and genital differences. (Modified from Moss 1996).*

4.2.3 Age classification of elephants

The age of elephants from suitable camera trap images was determined by visual assessment using a combination of characteristics such as physical development, tusk size and shape (when present), back length and size (Fig. 16), and other bodily proportions as suggested by Laws (1966) and Moss (1996). Elephants were aged and divided into one of seven different age classes or categories identified. A modified ageing guide (Table 4) compiled by several authors (Moss 1996; Stokke and du Toit 2000; Whitehouse 2001; Henley 2008) was used throughout the study.

Table 4. *Criteria used for age classification and categorising African elephants based on physical characteristics. All calf proportions mentioned are relative to the size and height of an average adult female. (Adapted from Moss 1996, Stokke and du Toit 2000, Whitehouse 2001, Henley 2008).*

AGE CLASS	AGE (YEARS)	BODY SIZE AND SHOULDER HEIGHT	PHYSICAL DEVELOPMENT AND ATTRIBUTES
0A	0 – 4.9	New-borns can generally fit underneath their mother. The height of calves under five years reaches the anal flap height of the mother.	Yearlings still have a rather short and slender trunk. In some tusk might be absent or stubby (up to about 15 cm in length) become visible.
0B	5 – 9.9	Overall size in height and back length appears to be half or just more than half the mother's size	Young males and females exhibit similar rates of growth and developmental patterns for the first ten years. Tusks, if present, will be about 30cm long. They will appear splayed rather than convergent.
1A	10 – 14.9	Shoulder and back height reach the forehead of the mother. Generally, about three-quarters the size of the adult female.	Tusks of the females are thinner than males and still rather splayed. Young females appear more square than rectangular like older females. The head shape of males starts to slope more noticeably.
1B	15 – 19.9	Females will almost be the same height as the adult mother, whereas males would either slightly exceed the mother's shoulder height or be about the same size as the largest cow in the group.	In young adults, their tusks will start to take on their adult configuration, convergent, straight, or asymmetrical. Breasts may start developing with the pregnancy of their first calf.
2	20 – 34.9	All bulls are larger than the mature females within the breeding herd.	Males are seen in musth from about 25 years old, and their heads are still somewhat narrower than that of a senior bull. Tusk bases are thicker than those of young adults
3	35 – 49.9	Prime bulls become increasingly larger.	Backs are lengthened. Adult bulls have a distinct wide hourglass head shape.
4	50+	Senior bulls have an overall large and heavy body size which can almost double that of females.	Senior bulls and cows have much deeper temporal depressions and appear almost hollow above the eyes. Their ears are generally held lower. Tusk sockets appear more elongated.

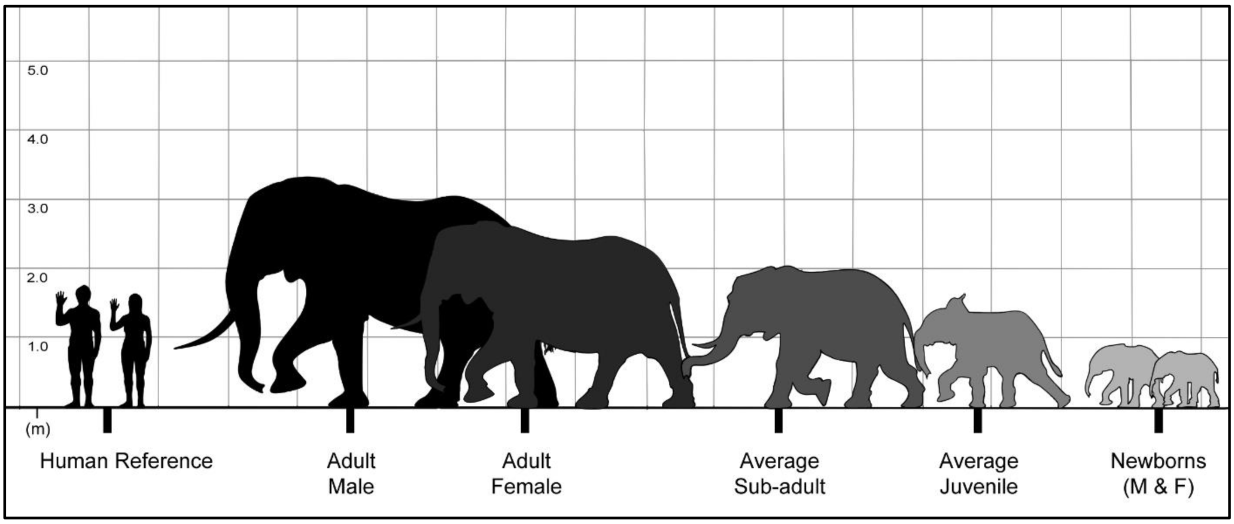

***Figure 16**. Elephant size scaling chart based on average shoulder height and bodily proportions of African elephants. (Modified and redrawn from data published by Henley 2008 and Larramendi 2016).*

4.2.4 Data and statistical analyses

To determine any seasonal variation in geophagy, seasons were classified as spring (September, October and November), summer (December, January and February), autumn (March, April and May) and winter (June, July and August) as suggested by the South African Weather Service. Three time periods were identified within a 24-hour period: morning, afternoon and night, similar to the methods of Evans (2006). The time duration for each period was categorised in accordance with the monthly sunrise and sunset times for the Addo region (Table 5, data obtained from www.timeanddate.org). 'Morning' periods started with the dawn, 'afternoons' ended after dusk followed by 'nights' that ended with the start of dawn.

Table 5*. Categorisation of the three daily time periods used during this study in the Addo Elephant National Park, South Africa. (Data obtained from www.timeanddate.org).*

		PERIOD START TIMES		
Seasons	**Months**	**Morning**	**Afternoon**	**Night**
Autumn	April 2019	05:46	12:16	18:45
	May 2019	06:06	12:13	18:19
Winter	June 2019	06:21	12:17	18:14
	July 2019	06:20	12:23	18:26
	August 2019	05:57	12:20	18:44
Spring	September 2019	05:18	12:11	19:03
	October 2019	04:36	12:02	19:27
	November 2019	04:03	12:01	20:00
Summer	December 2019	03:57	12:13	20:29
	January 2020	04:22	12:27	20:31
	February 2020	04:58	12:30	20:02
Autumn	March 2020	05:24	12:24	19:24
	April 2020	05:47	12:16	18:44
	May 2020	06:06	12:13	18:19

Pearson chi-square tests were used to compare the observed vs. expected number of records for categories such as age, age class, sex and presence or absence of tusks. Expected values were obtained by dividing the total number of individuals captured (n = 342) by the number of groups (or levels) within each categorical variable (3 for age, sex and tusks and 7 for age classes). As the structure of age, sex and tusklessness in the elephant population of AENP is unknown, hypothetical values for each level were assumed to be equal in ratio e.g., 33:33:33 (evenly distributed). Possible correlations between categorical variables were further analysed with contingency tables and correlation (Pearson's) analyses. Statistical analyses were performed using STATISTICA 7.0 (Statsoft) with a statistical significance set at $p < 0.05$.

The total number of camera trap days differed greatly among sites and seasons, some having no data at all and proved to be incomparable and complicated non-parametric analyses. The values had to be standardised by determining seasonal visitation frequencies per site in order to make them comparable. The seasonal visitation frequency (n/CTD) was calculated by dividing the total number of geophagic visits of elephants (n) with the camera trapping days (CTD), per season, per site (Table 6). The number of camera trap days were calculated from the time and date the camera was fully operational to the time and date when the last photograph was taken (i.e., starting a new sequence). The time and the date stamps on the photographs were used in each instance. When cameras were knocked over, the last photograph of the geophagy site in full view was used to end the sequence. In some cases, due to missing data, patterns of activity were discussed without statical analyses (Johnson 1999, Blake et al. 2011). Furthermore, correlation analyses were used to examine the relationship between the monthly use of licks and monthly rainfall, obtained from the South African Weather Service specifically for AENP.

4.3 Results

4.3.1 Elephant visitation patterns and frequencies

From 16 April 2019 to 7 May 2020, a total of 388 successful camera trap days were recorded across all six geophagy sites. However, trap effort was not equal neither across seasons nor sites: more trapping days were obtained for autumn than for winter, summer and summer considering that a few extra days for April and May of both 2019 and 2020 were included in the study. Combining data from all six sites, a total of 395 camera records were obtained throughout the study period, from which more than 86% (n = 342) corresponded to elephant geophagy visits. The remaining records could be attributed to six different mammal species. Hartebeest were the second most frequent visitors (n = 21), followed by kudu and zebra (both n = 11), black rhino (n = 6) and buffalo as well as eland (both n = 2).

Overall site B accounted for the most individual elephant visits compared to the other geophagy sites. Seasonally, Site C, was utilised the most during autumn (2.47/CTD), with Ca and Na identified as the elements in the soil of importance to the elephants, followed by spring (0.18/CTD) and winter (0.09/CTD). There were zero CTD recorded during summer. The soil at site D was rich in essential elements Ca, P and As, and was the only site with visitation records across all seasons, with the highest for autumn (0.23/CTD), followed by spring and summer (both 0.03/CTD) and then winter (0.2/CTD). Overall, Site D along with site A accounted for the lowest total visitation (both 0.05/CTD). Site E, where Mn, Ca, Na, Cu and Pb, were considered the attracting geophagic elements (*vide* Chapter 3), elephants utilised the site only during summer (0.39/CTD) and autumn (0.36/CTD). No elephants were recorded during spring despite the high amount of successful CTD (88.25 CTD) and no visits were recorded for winter as there were zero CTD. The highest visitation frequency for winter was accounted for by site F (0.52/CTD), which was the only site with Mg levels > 1 wt%. No elephants were recorded at site F during summer despite 90.67 successful camera trap days, while autumn and spring both accounted for the same visitation frequency (0.25/CTD).

Table 6. *Seasonal visitation frequencies (n/CTD) of elephants that practice geophagy at six different geophagy sites in Addo Elephant Park, South Africa. CTD, camera trap days; n, number of visits to geophagy site.*

	SPRING			**SUMMER**			**AUTUMN**			**WINTER**			**TOTAL**		
Site	***CTD***	***n***	***n/CTD***	***CTD***	***n***	***n/CTD***	***CTD***	***n***	***n/CTD***	***CTD***	***n***	***n/CTD***	***CTD***	***n***	***n/CTD***
A	60.11	3	0.05	14.08	1	0.07	2.32	-	-	91.99	5	0.05	168.5	9	0.05
B	29.57	47	1.59	61.52	78	1.27	33.39	58	1.74	-	-	-	124.48	183	1.47
C	71.23	13	0.18	-	-	-	6.48	16	2.47	21.25	2	0.09	98.96	31	0.31
D	90.99	3	0.03	70.64	2	0.03	38.44	9	0.23	92	2	0.02	292.07	16	0.05
E	88.25	-	-	51.54	20	0.39	44.03	16	0.36	-	-	-	183.82	36	0.20
F	88.93	22	0.25	90.67	-	-	77.44	19	0.25	49.91	26	0.52	306.95	67	0.22
TOTAL	**429.08**	**88.00**	**0.21**	**288.45**	**101.00**	**0.35**	**202.10**	**118.00**	**0.58**	**255.15**	**35.00**	**0.14**	**1174.78**	**342.00**	**0.29**

Collectively, the highest visitation records were obtained between 20:00 and 21:00 across all sites. The daily visits to geophagy sites per season (Fig. 17) show that the elephants visit geophagy sites mainly from 12:00 to 23:00 with the exception of summer. Interestingly, elephant visits to sites during the morning hours (04:00 - 07:00) were only recorded in summer, and not for any other season. According to the total number of visits by elephants, the hourly frequency of geophagy varied during the colder seasons (autumn and winter), with higher frequencies detected in the afternoon (14:00 and 16:00, respectively), and the warmer seasons (spring and summer), activity peaks occurred at night (20:00 and 22:00, respectively).

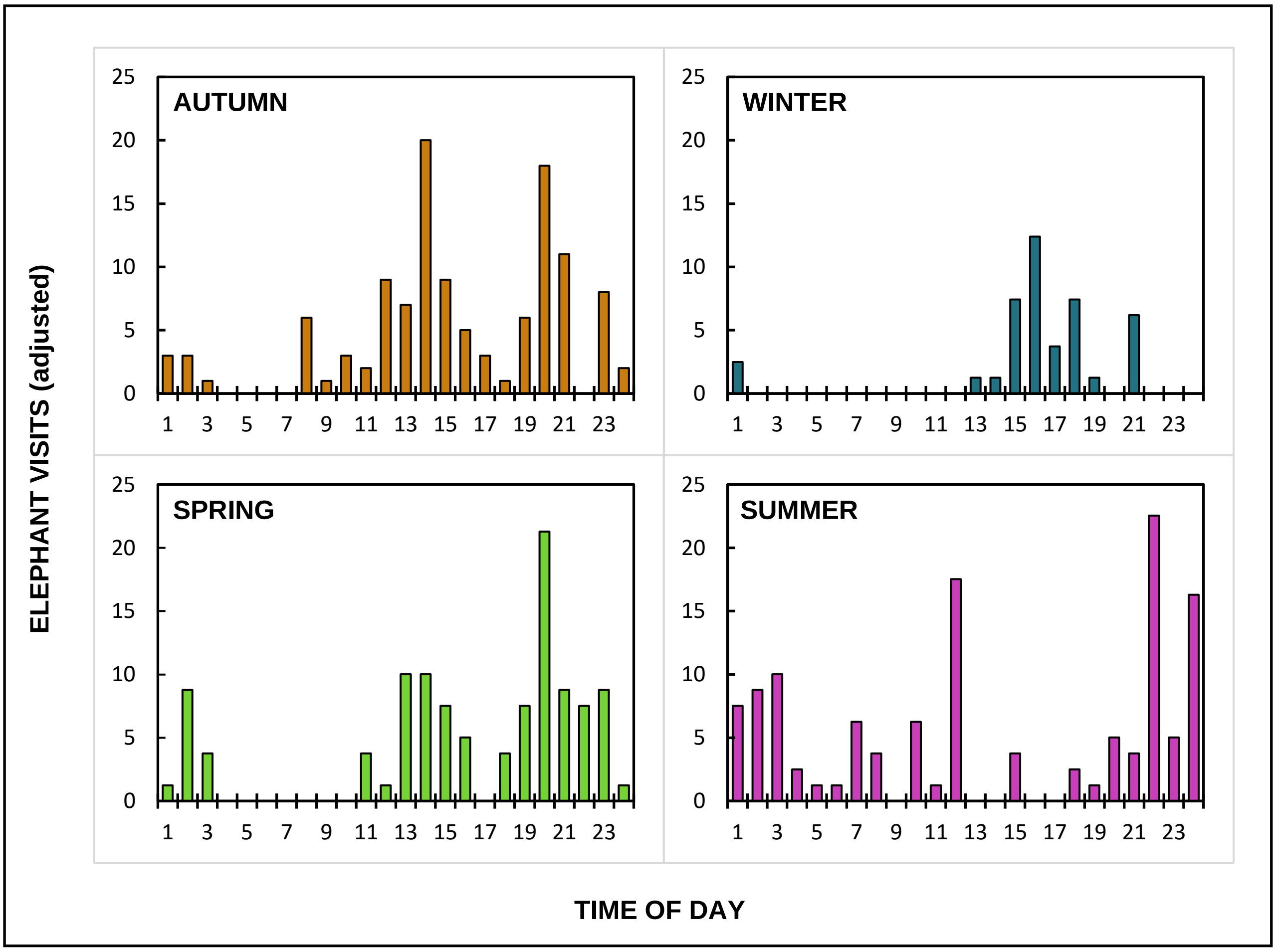

Figure 17. *Daily geophagic visits by elephants across all sites throughout the study period. The total number of elephant visits was standardised (adjusted) in proportion to the season with the highest number of trapping days.*

To determine a possible relationship, seasonal rainfall data (obtained for AENP from South African Weather Serivce) was plotted against the seasonal visitation frequency (n/CTD) (Fig. 18). The lowest visitation frequency was recorded during winter which correlates with the lowest precipitation levels observed. However, a linear regression analysis derived no significant correlation between seasonal rainfall and visitation frequencies ($r^2 = 0.112$, $r = 0.335$, $p = 0.58$).

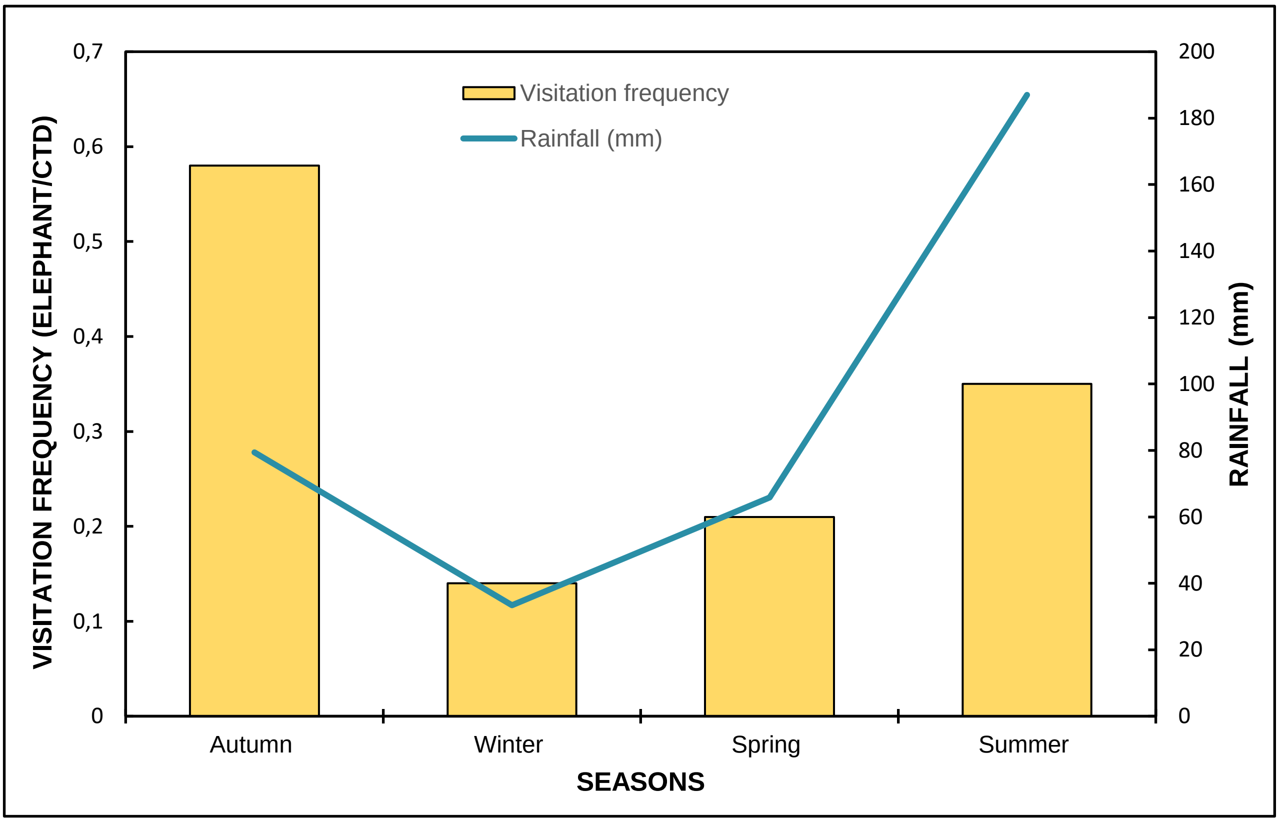

Figure 18. *Seasonal rainfall (mm) for the duration of the study compared to the seasonal visitation frequency of elephants (n/CTD). The total rainfall for the duration of the study was 445 mm. (Rainfall data obtained from the South African Weather Service for AENP). CTD, camera trap days; n, number of visits to geophagy site.*

4.3.2 Elephant geophagy by age and sex classes

The number of elephants showing geophagic activity (n = 342 individuals) was not evenly distributed among the three age groups ($\chi^2 = 75.49$, df = 2, $p < 0.001$, all sites and seasons combined, Fig. 18), since most of the licking observations corresponded to adults (n = 188), followed by juveniles (n = 91) and sub- and young adults (n = 63). These proportions did not differ significantly among seasons ($\chi^2 = 9.19$, df = 6, $p = 0.163$, all sites combined), thus showing a temporal consistency. However, they did differ among sites ($\chi^2 = 27.05$, df = 10, $p = 0.003$, all seasons combined), likely due to the absence of juveniles in site A or the high proportion of subadults in Site C.

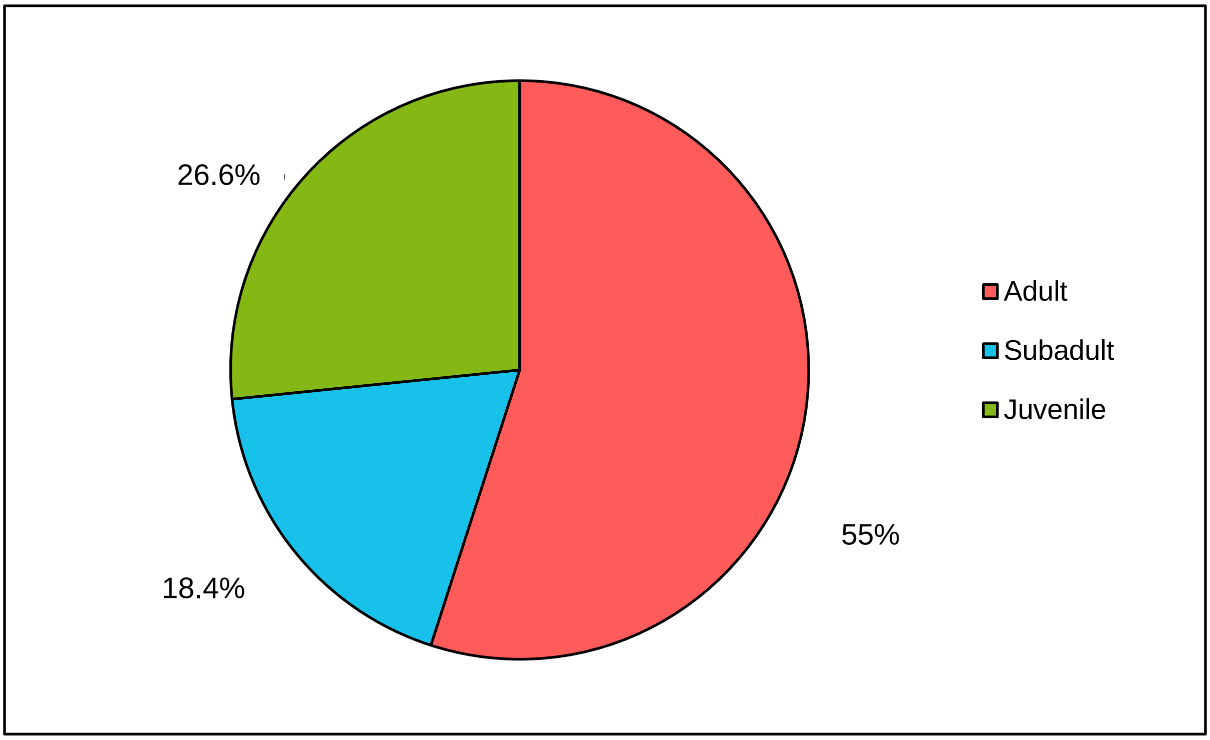

Figure 19. *Total proportion (observed values) of elephant age groups across all geophagy sites at Addo Elephant National Park, for the entire camera trapping duration from April 2019*

The observed sex ratio did not show significant differences compared to expected values which assumed equal distribution across the 3 different levels (χ^2 = 4, df = 2, p = 0.135). This might be attributed to the high number of elephants with unknown sex (n=100) and a slightly higher number of male observations (n = 130) compared to females (n = 112) (Fig. 20). Sex ratio values were stable throughout the seasons (χ^2 = 5.49, df = 6, p = 0.482), but they significantly differed across geophagy sites (χ^2 = 31.79, df = 10, p = <0.001), sites C and B accounted for the highest male visits (46% and 45% respectively), while site E and site A accounted for the most female visits (56% and 44% respectively).

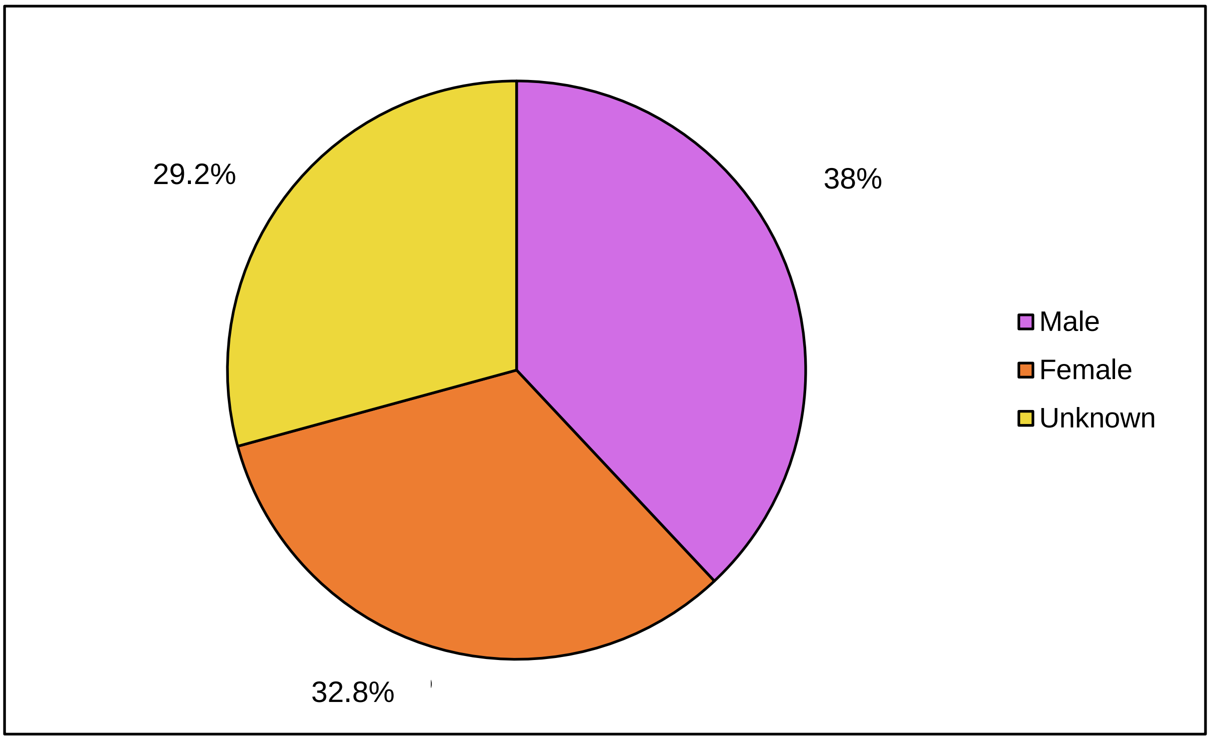

Figure 20. *Total proportion (observed values) of elephants utilising geophagy sites at Addo Elephant National according to sex, for the entire camera trapping duration from April 2019 to May 2020. Individuals that could not be sexes was marked as ‘unknown’.*

Finally, the presence or absence of animals with tusks proved to have significant differences compared to expected values ($\chi^2 = 38.89$, df = 10, $p < 0.001$). As seen in Figure 21, most of the observations corresponded to individuals with tusks (n = 167), followed by individuals without tusks (n = 98) and those out of sight (n = 77).

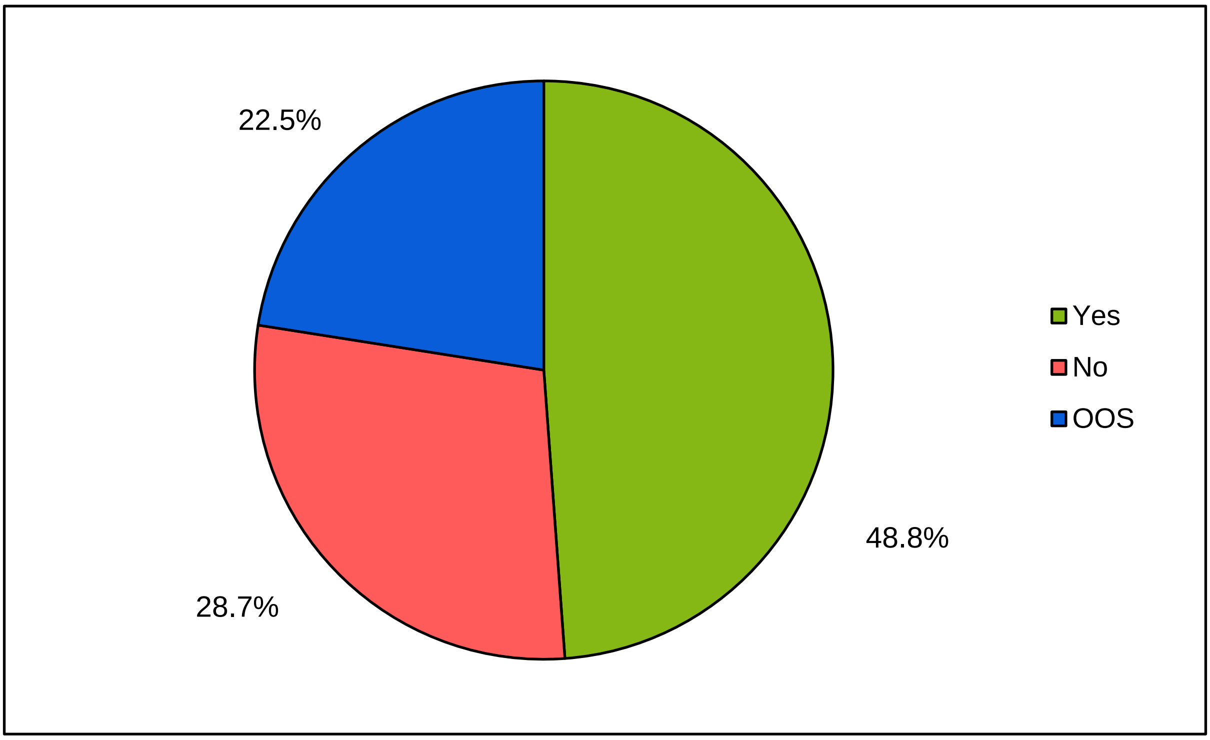

Figure 21. *Total proportion (observed values) of elephants utilising geophagy sites at Addo Elephant National, according to the presence or absence of tusks, for the entire camera trapping duration from April 2019 to May 2020. Where the presence or absence could not be determined, it was considered "out of sight" (OOS).*

4.4 Discussion

Data obtained from camera traps during this study provides information on visitation patterns and frequency unique to sex, age and the presence or absence of tusks in individuals. However, the potential for bias or skewed results due to missing data (inability to sex individuals or confirm the presence of tusks from photographs) should be considered. Site B, accounted for the highest visitation frequency across all sites. Geographically this site is the furthest south and located in the Colchester section of AENP. Site C, which had the second-highest visitation frequency, is also located in this section of the Park.

Seasonal variability in the utilisation of soil licks has been observed in several geophagy studies, mainly owing to two factors: seasonal variation and availability in diet as well as, physiological demands throughout different life stages (Atwood and Week 2003; Voigt et al. 2007). The AENP (AMC and Colchester sections) is considered to be predominantly covered by evergreen vegetation known as thicket (Whitehouse and Martin-Hall 2000; Vlok et al. 2003). In particular, the Colchester section is thought to have denser thicket vegetation coverage (77%) than the AMC (69%), considering that large herbivores were not able to access this section until the fence was removed (Tambling et al. 2013). It can therefore be assumed that food availability is higher in the Colchester section. Typical thicket species include spekboom, white milkwood, Cape plumbago, Karoo boer-bean and the common guarri, but elephants can feed on almost 150 different plant species throughout the year (Paley and Kerley 1998; Kerley and Landman 2006). More specifically, the elephant population in AENP, therefore, have a predominantly C_4 diet due to the high availability (approximately 40% plant cover) of crassulacean acid metabolism (CAM) plants (van der Merwe et al. 1988; Kerley and Landman 2006). In contrast, their diet differs greatly from other savannah elephant populations from Namibia, Botswana, Zambia, Malawi, and different parts of South Africa which mainly consists of C_3 plants and only small amounts of C_4 vegetation (van der Merwe et al. 1988). However, the Eastern Cape Province, experienced a multi-year drought period stretching from 2015 to 2020 greatly impacting vegetation (species) availability and quality (Archer et al. 2022). More specifically, during the time this study was conducted, the reported drought reached maximum intensity in 2019, followed by signs of possible recovery in 2020 (Archer et al. 2022). A study conducted previously in the Eastern Cape forests, found that some evergreen species had dead leaves or completely died as a result of a drought period (Geldenhuys 1993). It can therefore be assumed that the overall vegetation quality and availably across AENP might have been affected to some degree as a result. Precipitation patterns influence the availability of natural water sources and the productivity of vegetation nutrient levels in each area (Reichman and Van de Graff 1975).

Determining whether geophagy is driven by certain physiological demands such as pregnancy, lactation, and bone or tusk growth proves to be challenging for long-lived mammals such as elephants. Depending on factors such as population densities and resource availability, the age of sexual maturity (or average primiparous age) in elephant populations can range from seven to 22 years old (Laws et al. 1975). Elephants also do not have a distinct breeding season, and their reproductive success is dependent on habitat conditions, rainfall, and nutrient availability (Hall-Martin 1987). According to Moss (2001), however, the average calving interval for African elephants can range from three to nine years and is a good indicator of whether the population is experiencing nutritional stress or not. Irrespective of the high density of elephants in AENP, Gough and Kerley (2006) found an average calving interval of about three years and a 5.8% annual population growth rate. The mean annual rainfall for AENP used by Gough and Kerley (2006) was approximately 392 ± 111 mm from 1959 to 2003. Compared to the total rainfall observed during this study (445 mm) a similar positive correlation can be assumed and therefore a similar average calving interval can be expected.

It was predicted that elephant visitations would peak during daylight hours as it correlates with the time they spend foraging. Alternatively, it was predicted that peak visitations recorded after the sun had set would suggest that geophagy might be practiced when temperatures are lower, predators are least active and human movement in the Park is minimal. Collectively (after values had been adjusted to compensate for missing data) the highest visitation records observed were at night between 20:00 and 21:00 (n=44), and between 22:00 and 23:00 (n=30) across all sites. However, when divided seasonally, the highest visitation peaks are seen between 14:00 and 15:00 during autumn, 16:00 and 17:00 during winter, 20:00 and 21:00 during spring, and 22:00 and 23:00 during summer. Autumn accounted for the highest number of elephants (n=118) that utilised geophagy sites even though the number of successful camera trapping days were the lowest (202 CTD). The second highest visitation frequency was observed in summer, followed by spring and winter. It should, however be considered that missing camera trap data could have led to potential bias in seasonal results obtained especially winter. Although no significant correlations were found between rainfall and visitation frequencies, higher frequencies were seen during spring and autumn and both seasons accounted for higher precipitation levels than winter and summer. Suescún et al. (2016) documented a high loss of nutrient concentrations in soils after rainfall periods that ultimately affect soil fertility and nutrient expression. Elephants are known to adapt their foraging strategy during the wet seasons (Loarie et al. 2009; Owen-Smith and Chapota 2012), this adaptation could possibility include ingesting soil as supplementation for the nutrients lacking in vegetation. Taking all the above-mentioned factors into account, it is suggested that nutritional or elemental supplementation might be a possible (but also non-exclusive) driver of geophagy in the elephant population in AENP.

Elephants of all age groups and classes were observed utilising geophagy sites. However, as predicted, most of the utilisation counts belonged to adults. Lactating adult females were usually accompanied by their young, which could support why juveniles were the second most observed age group. A study conducted in China, on Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) found that lactating females did not engage in geophagy (Li et al. 2014). Therefore, lactating elephants observed eating soil in this study could still suggest that geophagy is driven by mineral and elemental supplementation to some extent due to physiological requirements. Elephant females and calves in South Africa’s Pilanesberg National Park were found to forage on similar plant species; however, calves were more selective of the new growths and higher quality parts of the plants (Woolley et al. 2011). By sampling what adults in the group eat, young elephants from the age of about one or two months progressively acquire forage knowledge from the older elephants in the group (Eisenberg 1981). This form of social learning between adults and young elephants could be true for forage as well as soil ingestion.

The proportion of males and females practicing geophagy did not show significant differences, although proportionally more males than for females (38% vs 33% respectively) where observed. Due to photograph limitations, individuals that could not be sexed (‘unknown’) could potentially impact results obtained. Under the assumption of no sexual differences in geophagy utilisation, this result would have been expected in a population with a female: male sex ratio close to 1:1, or slightly male-biased. However, the apparent lack of differences in the observed values became a striking result as the sex ratio for elephants of all ages in AENP is strongly female-biased, with a female: male ratio of 1.8:1 (Bissett 2021, pers comm*). Females usually form groups varying in size and will travel and forage together as such a unit. As a result, in terms of numbers alone, it would be expected that female records for geophagy should be higher. On the other hand, adult males generally travel solo or as part of a small fluid or bachelor's group (Holdø et al. 2002). Other studies documented female elephants spending more time eating soil due to reproductive demands and while lactating (Holdø et al. 2002; Sach et al. 2019). Similarly, it was predicted that similar results would be documented for females records in this study, however the opposite trend was observed possibility due to their greater intake need in males for elements such as Na for growth (Whitehouse 2002).

According to Stokke and du Toit (2000) and Shannon et al. (2006), due to males and females being different in body size, digestive anatomy and physiological requirements throughout different life stages, their diet and foraging strategies should differ on a finer scale. Female elephants are thought to feed preferentially on higher quality vegetation because of higher mass-specific nutritional demands compared to male elephants that forage for quantity rather than quality (Woolley et al. 2008). Male goats (*Capra hircus*) were found to have a diet consisting mainly of shrub species compared to females, likely because shrubs meet their high energy demands despite the lower nutritional quality thereof (Stronge et al. 1997). Even though elephants are considered to display a behavioural aversion to plants that contain a lot of carbon-based secondary plant metabolites (Schmitt 2017), seasonal variation in forage availability, quality and fluctuations in the secondary compounds is inevitable (Owen-

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Smith and Chapota 2012). These changes are expected across AENP especially during the study period as a response to the multi-year drought experienced (Archer et al. 2022). During the drier seasons, forage is the lowest in nutrient quality and availability, and has the highest levels of plant defence compounds (Schmitt et al. 2016). Ultimately megaherbivores, such as elephants, will gradually start to incorporate plants into their diet, which they had previously avoided (Schmitt et al. 2016). This could further support an increase in geophagic behaviour among species that would typically adjust their diet selection during dry seasons and feed on more chemically defended browse than grass (with fewer secondary chemical compounds) (Ward et al. 2020). The higher observations for male elephants could also be due to a greater need for “self-medication” to alleviate GI distress (Klaus et al. 1998; Pebsworth et al. 2019), in reaction to their foraging strategy. Woody plants, such as those found in the thicket biome are well defended by secondary metabolites (Herms and Mattson 1992), such as tannins (Robbins 1993). These compounds form part of a plant’s chemical defence that is known to generally interfere with fundamental biochemical processes in the consumers’ cells (Kohl et al. 2015). The most significant side effect of tannins, besides lowering the overall quality, is the reduction in protein absorption and digestibility in the gut (Schmidt 1989; Shimada 2006). Tannins are reported to have a negative correlation with digestibility for hindgut fermenters such as elephants compared to ruminant species (Oliver 1978). More severe symptoms for herbivores could include damage to the intestinal epithelium and acute toxicity (Blytt et al. 1988; Shimada 2006). A study conducted in Tanzania found that elephants that fed on tropical forest browse (leaves and bark), with high levels of secondary plant metabolites, consumed soil to assist in the detoxification and digestion thereof (Houston et al. 2001). Ingested clay minerals from soils stimulate mucous production, decreasing the permeability of the intestinal wall, and/or directly binding to plant secondary metabolites, like tannins, to aid in adsorption and excretion (Young 2010).

A study conducted on 174 females from AENP found that 98% of them were tuskless, while all-male elephants (n = 150) had tusks, suggesting that tusklessness is controlled by a sex-related gene (Whitehouse 2002). For this study, more elephants with tusks were observed utilising geophagy sights than bilaterally tuskless elephants, where most -but not all were bulls. These results however could possibly be skewed due to the limitation of not being able to determine if all individuals utilising geophagy sites had tusks ('OOS').

Considering that an ample amount of time passed since the study conducted by Whitehouse (2002), it is most likely that the genetic expression of tusks in females could have changed within the elephant population. On the other hand, it was seen from the camera trap images that in males, including older individuals, tusk size was smaller than expected, similar to the findings of Seydack et al. (2000), which made ageing individuals challenging. According to generic elephant ageing guides (Table 4), tusk presence, length, thickness, and circumference at the sockets play an important role in determining the age (Hanks 1972). Considering the energetic demand for tusk growth, the higher number of individuals observed utilising geophagy sites could suggest mineral and/or elemental selectivity to meet these demands. Greyling (2004) suggests that high amounts of calcium (8-9 g/day) are required to meet the demands of tusk growth in males, however, lactating cows with tusks would require even more. Furthermore, it should be noted that a portion of tusklessness recorded in this study belong to juveniles as tusk or tushes (if any) can only be seen between the age of one and two years old.

Elephants in AENP are considered to commonly practice geophagy from purposely selected locations. Geophagy in AENP might have different functions at different times for the elephant population as age and sex distributions at these sites differ. Findings suggest that soil eating is encouraged by the nutritional demands of certain physiological factors such as growth and lactation. Moreover, due to the foraging strategy of male elephants in particular, results also suggests that geophagy is practiced to aid in relieving GI stress caused by secondary plant metabolites.

CHAPTER 5

SPATIAL DISTRIBUTION IN RELATION TO GEOPHAGY SITES

5.1 Introduction

The increasing human population and global agricultural intensification has been severely reducing the available of African savannah elephants, ultimately forcing these populations into increasingly narrower regions that are typically limited by fences (Sach et al. 2020). As a result of these constraints, the pressure on habitats to meet their resource needs has intensified (Galanti et al. 2006). This might result in nutritional stress, necessitating changes in movement patterns and distribution attempts to obtain the required elements and maintain fitness (Galanti et al. 2006; Sach et al. 2020). Movement patterns are multidimensional with different types occurring at varying scales. Individuals could also respond to local environmental conditions differently. Predator avoidance, intra-specific competition, parasite avoidance, fences, rainfall and moonlight are all possible drivers of movement (Barnes et al. 2006; Purdon et al. 2018).

The size of an elephant's home range is an indicator of the availability of essential resources in many aspects, and core areas allow insight to the varying intensity certain areas are utilised within their home range (Osborn 2004). Home ranges can fluctuate in size from 15 to 3 700 km^2 depending on habitat, season, and population, but in protected areas, such ranges are nearly half in size (Douglas-Hamilton et al. 2005; de Beer and van Aarde 2008). Elephants are considered to have preferred core zones in their home ranges, where they spend the majority of their time (Douglas-Hamilton et al. 2005). Elephants move approximately 3-6 km every day and appear to be more nocturnal during dry seasons and more diurnal during rainfall seasons (Loarie et al. 2009). The distribution of water resources, food abundance, and mineral/elemental deposits are all important factors that elephants select at varying intensities throughout the year (Ferreira et al. 2017; Mills et al. 2018). Elephants require nutrients for a variety of biological activities, including organ and immune system function, reproductive requirements, energy metabolism and cellular growth (Ishiguro et al. 2018). Geochemistry ultimately influences the availability of minerals and elements in soils, and thus in plants and water (Prins and Langevelde 2008). Understanding an area's geochemistry, as well as the presence of geophagy sites, thus informs how the habitat is utilised (Blake et al. 2011). Visitation frequency of elephants at geophagy sites may vary due to mineral/elemental composition, distance, topographic features and/or predators (Lizcano and Cavelier 2000; Tobler et al. 2009; Rice 2010)

For decades, radio and satellite telemetry has been a significant aspect of many African elephant research and management efforts (Blake et al. 2001). Using GPS technology allows insight into the movement and spatial use of animals (Mills et al. 2018). Movement ecology can reveal species' ultimate and proximate causes and resource requirements and reveal patterns over time and space (Mills et al. 2018). Animals' movement patterns become more tortuous in regions with a substantial number of resources (Bartumeus 2009). This leads to efficient resource utilisation because the animals’ total displacement decreases and the amount of time spent consuming these resources increases (Turchin 1991). On the other hand, landscapes with dispersed resources showed straight and less complex movement patterns with substantial displacement (Roshier et al. 2008). Elephant conservation and management in protected areas require a thorough understanding of ranging behaviour and movement patterns.

The aim of this chapter was to document the spatial distribution of five individuals in relation to the identified geophagy sites. The total displacements for each elephant will be determined and the frequency with which the collared elephants visit the geophagy sites will be described. It is predicted that all collared elephants will include/visit at least one (or more) geophagy sites in their observed home range. The individual that included the most geophagy sites in their movement pattern is expected to have a greater total displacement than an individual with less geophagy sites incorporated. Alternatively, if none of the collared individuals have geophagy sites situated within to their home range, it can be deduced that these sites are not essential nutritional resources. In addition, it is predicted that the same geophagy sites will be utilised at similar frequencies indicating that specific mineralogical and geochemical compositions could be sought after by the population. Alternatively, if different geophagy sites are visited at varying frequencies, nutritional requirements could differ on an individual level and/or possible competition behaviour could be considered. Considering that vegetation quality lowers during dry/colder seasons (i.e., winter and autumn), it is predicted that geophagy site visits will be higher among the individuals to mitigate the nutritional shortages. Visits to geophagy sites during the dry seasons could also be driven by the need to alleviate GI stress and secondary plant metabolites in vegetation increase (Mwangi et al. 2004; Ayotte et al. 2006; Sienne et al. 2014).

By determining that five ‘random’ individuals from population consisting of about 500 individuals incorporate geophagy sites in their movement pattern, it can be assumed that these sites are a desired resource. The movement pattern of individuals is representative of the patterns seen throughout the population (Foley 2002).

5.2 Methodology

5.2.1 Elephant collaring

All GPS collar data (from April 2019 to May 2020) was provided by the AENP's Scientific Services. Three matriarchs from different family groups and two breeding adult bulls were collared (Fig. 22). The capturing and collaring process was done by SANParks veterinarians according to SANParks Standard Operating Procedure for the capture, transportation, and maintenance in holding facilities of wildlife (Bissett 2021, pers comm*). These five individuals were fitted with Vectronic's Vertex Plus elephant collars that were set to record one GPS fix hourly via IRIDIUM (bi-directional satellite communication). Each collar has 13+2 D-cell batteries with a long life of approximately four years. Unfortunately, no details on their age, history, or family groups were known for these five individuals.

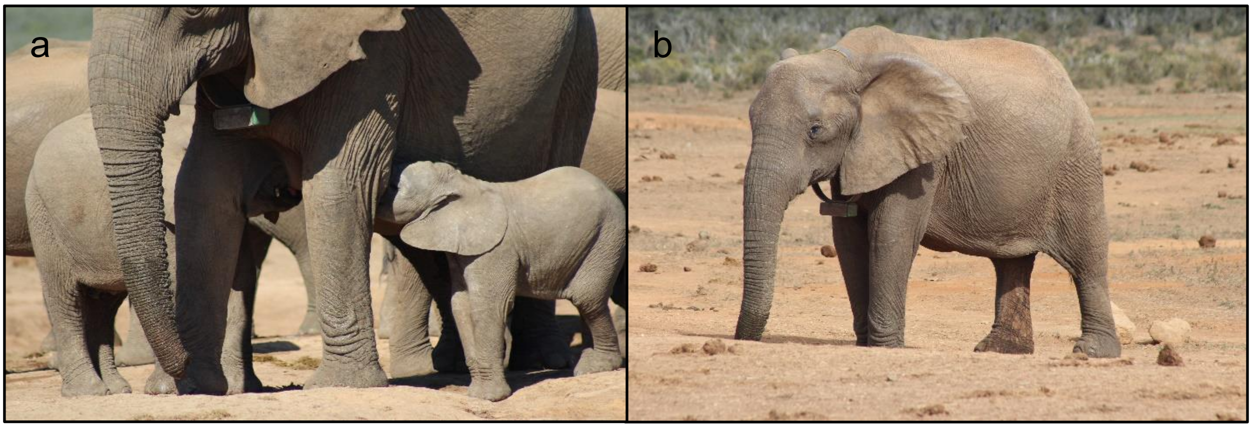

Figure 22. *Two of the five collared individuals in Addo Elephant National Park, South Africa. (a) matriarch named Bluebell and (b) matriarch named Mushara.*

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5.2.2 Data and statistical analyses

On some occasions due to satellite reception problems, terrain etc., certain hourly fixes/locations were not recorded. Unrealistic distance values obtained due to missing fixes were removed and the dataset was cleaned for further analysis. The Dilution of Precision (DOP) for GPS fixes ranged from 0 to ~10, indicating a relocation accuracy approximately within 0 - 20 m range (Jung et al. 2018). DOP is used to measure the accuracy of positional GPS fixes recorded relative to the geometry or positions of satellite receivers (D'Eon and Delparte 2005).

The GPS collar locations of all five elephants were mapped spatially against the locations of the identified geophagy sites. Firstly, kernel density estimations (KDE) per km^2 (Worton 1989) and core areas were calculated using ArcMap 10.8.1 software (Ferrel 2004). Time intervals between fixes (which were recorded hourly) were increased to using every 25 fixes (25 hours) instead to account for autocorrelation (Dray et al. 2010). Home ranges were calculated using ArcMap's Greater than tool to create the density raster layer with a 25-cell-by-cell input converted to a polygon and area (hectare) was determined per individual. Within the main camp section of the park is an encampment that covers an area of approximately 4 km^2, known as the Botanical Reserve, which is completely inaccessible to the elephants of the park. Therefore, it was subtracted from the total home range area for individuals (females) whose home range included the area.

Furthermore, fixes were processed in a geographical information system software (QGIS) where a projected coordinate system of WGS 84/ LO 25 was in order to account for the curvature of the Earth. Hourly fixes were used for fine-scale movement analyses (Graham et al. 2009; Selebatso et al. 2017; Wato et al. 2018;

Kroesen et al. 2020; Troup et al. 2020; Diaz et al. 2021). Around each site, a buffer zone (500 m radius) was constructed from the centre of each site (Poole et al. 2010). The buffer zone was divided in to 11 different intervals (Table 7).

Table 7. *Buffer increment within a 500 m radius set around geophagy sites used to process spatial data obtained from GPS collars for five elephants.*

Buffer Increment	Buffer Alias	Buffer Increment	Buffer Alias
< = 20	20	> 250 to < = 300	300
> 20 to < = 50	50	> 300 to < = 350	350
> 50 to < = 100	100	> 350 to < = 400	400
> 100 to < = 150	150	> 400 to < = 450	450
> 150 to < = 200	200	> 450 to < = 500	500
> 200 to < = 250	250		

Where GPS collar fixes intersected the above-mentioned buffer zones, locality maps were constructed which depicts a graduated colour scale from blue (closest to the centre of geophagy sites) to red (furthest). GPS collar fixes which did not intersect the above-mentioned buffer zones were excluded from the maps.

Linear distances between consecutive GPS points were estimated using a formula derived from the Pythagorean Theorem ($a^2 = b^2 + c^2$) applicable to any triangle squared. Given two geographical locations defined by latitude and longitude coordinates (Location 1: Lat_1 $Long_1$; Location 2: Lat_2 $Long_2$), the linear distance between them (D) can be estimated with the formula:

$$D = \sqrt{((\mathrm{Lat2} - \mathrm{Lat1}) \text{ x } 110941.85)2 + ((\mathrm{Long2} - \mathrm{Long1}) \text{ x } 111319.44 \text{ x } \mathrm{Cos}(\mathrm{Lat} * 2))2} \qquad \text{(equation 1)}$$

In this formula, the number 110941.85 represents the distance (in m) of an increase of one decimal degree in latitude, whereas 111319.44 represents the distance (in m) of an increase of one decimal degree in longitude at the Equator line. Given the spherical shape of Earth, one decimal degree in longitude represents different distances according to the latitude of the area. As AENP is situated far from the Equator (between -33.428 and -33.868 to the South of the Equator), the distance in longitude had to be corrected by the cosine of the latitude, the latter expressed in radians (Lat*).

The number of observed GPS fixes recorded within the buffer zone were compared the expected values for each individual using chi-square analyses. The expected values used were calculated by estimating the percentage of GPS fixes per individual multiplied by the number of fixes observed within the 500 m buffer zone. Contingency table analyses were used to compare between two categorical variables (e.g., between sites, buffer zones, seasons, individual) along with correlation (Pearson Chi-square) analyses. Statistical analyses were performed using STATISTICA 7.0 (Statsoft) with a statistical significance set at $p < 0.05$.

5.3 Results

After filtering, a combined total of 47 230 hourly GPS fixes were recorded for all five collared elephants between April 2019 and May 2020. Of the expected hourly fixes recorded within the buffer zone, 21% belong to Female 1, 17% to Female 2, 21% to Female 3, 21 % to Male 1 and 19% to Male 2. Total displacement between individuals varied, ranging from highest to lowest: Male 1 (3 366 km with a mean of 7.9 km per day); Female 1 (2 838 km with a mean of 6.7 km per day); Female 3 (2 792 km with a mean of 6.5 km per day); Male 2 (2 700 km with a mean of 6.4 km per day); Female 2 (2 252 km with a mean of 5.4 km per day).

Around each site a 500 m buffer zone was incorporated to determine how many of the total GPS fixes recorded indicated possible geophagy site visits. A combined total of 933 fixes for all five elephants fell within these buffer zones (Table 8). All the contingency table analyses show a significant relationship e.g., between individuals and geophagy sites (χ2 = 801.80, df = 20, p < 0.001); between geophagy sites and seasons (χ2 = 145.27, df = 15, p < 0.001) and between seasons and individuals (χ2 = 166.14, df = 12, p < 0.001).

Table 8. *Number of hourly GPS fixes recorded within a 500 m radius of each geophagy site, for each collared individual. The expected visitation values (italics) were calculated by estimating the % of total GPS fixes for each individual and the multiplying with total number of observed records within the buffer zones (933). The asterix (*) highlights the most visited site for each individual.*

	Female 1	**Female 2**	**Female 3**	**Male 1**	**Male 2**	**Total**
Site A	22	12	0	177*	73	**284**
Site B	0	42	1	32	93*	**168**
Site C	5	15	2	10	27	**59**
Site D	94*	53*	21	15	0	**183**
Site E	73	18	56*	20	0	**167**
Site F	13	2	1	56	0	**168**
Total	**207**	**142**	**81**	**310**	**193**	**933**
Expected	*196*	*163*	*196*	*197*	*181*	*933*

The distribution and home range of Female 1 relative to Park's boundaries is shown in Figure 23. She mainly utilised the northern section of the study area with a home range area covering approximately 11 319 ha in total. Overall, she visited five of the six sites (all except site B) throughout the study period (Fig. 24) with a total of 207 fixes recorded within the buffer zone. Site D however had the highest number of visits (46% of visits, n = 94) and site E the second highest (36% of visits, n = 73) (Table 8). Furthermore, a significant relationship was seen between the geophagy sites and buffer intervals ($\chi 2 = 74.43$, df = 36, $p < 0.001$). Seasonally she visited geophagy sites most during autumn (57% of visits, n = 118), followed by winter (21 % of visits, n = 44), spring (18% of visits, n = 38) and summer (3% of visits, n=7). The kernel density map (Fig. 23) however, show that four of the six sites were included in her home range area for the duration of the study. Site D and E are situated within core areas with a density interval ranging between 101-150 points per km^2. Although se visited site C, the site did not fall within her home range suggesting she deliberately travelled out of her home range to visit this site.

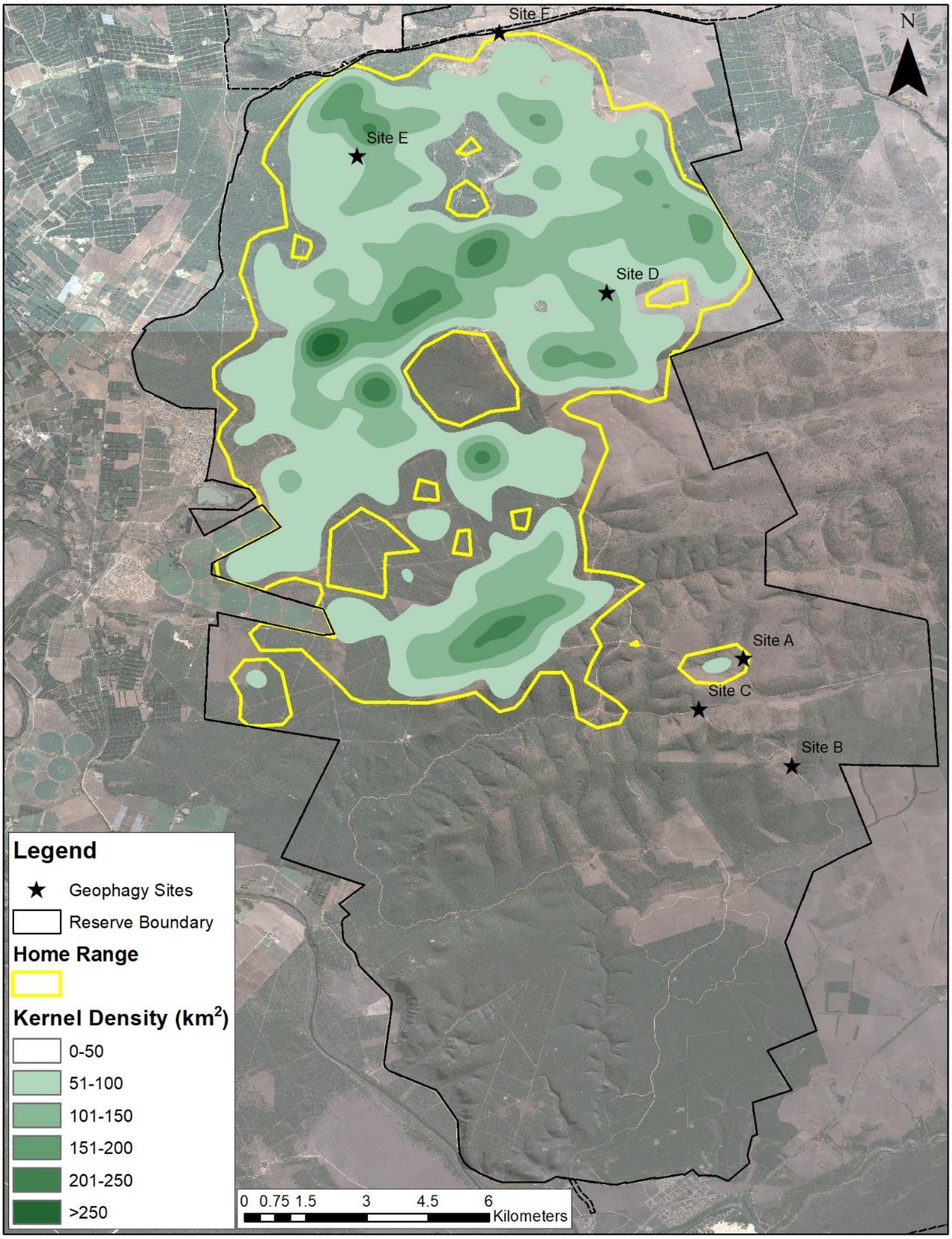

Figure 23. *Kernel density estimations (KDE) of distribution in relation to geophagy sites (A-F) of Female 1 in AENP. Increase in point density per km^2 is presented with a colour gradient to highlight core areas within the home range (yellow line).*

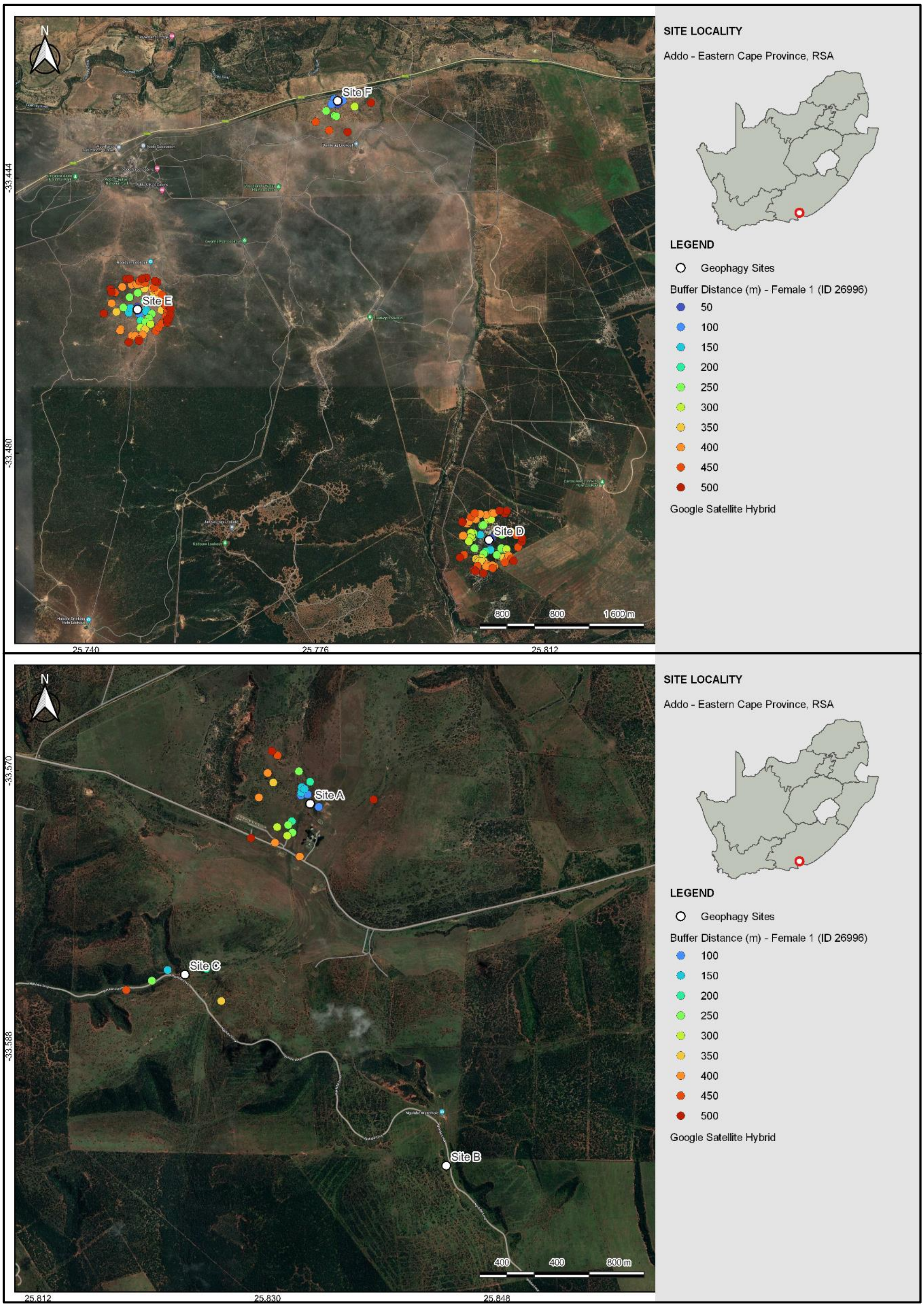

Figure 24. *GPS fixes for collared Female 1 detected within a 500 m radius from the centre of each geophagy site. Each fix is coloured from closest to the site (blue) to furthest from site (red) according to the different buffer distance intervals.*

The distribution and home range of Female 2 relative to Park's boundaries is shown in Figure 25. Her home range area covers approximately 8 975 ha in total. Female 2 visited each of the geophagy sites across the Park, during the study period with a total of 142 fixes recorded within the buffer zones (Fig. 26). Site D (37% of visits, n = 53), followed by site B (30% of the visits, n = 42) had the highest number of visits and site F (1% of the visits, n = 2) the lowest (Table 8). Furthermore, a significant relationship was seen between the geophagy sites and buffer intervals ($\chi2 = 112.70$, df = 50, $p < 0.001$). Seasonally she also visited geophagy sites most during autumn (48% of visits, n = 68), followed by winter (30% of visits, n = 43), spring (13% of visits, n = 19) and summer (8% of visits, n=12). According to the kernel density map (Fig 25), five of the six sites were included or lie on the border of her home range areas. None of these sites are however situated within high density core zones. Although she visited site F at least twice (Table 8), the site and a vast area around the site was not included in her home range.

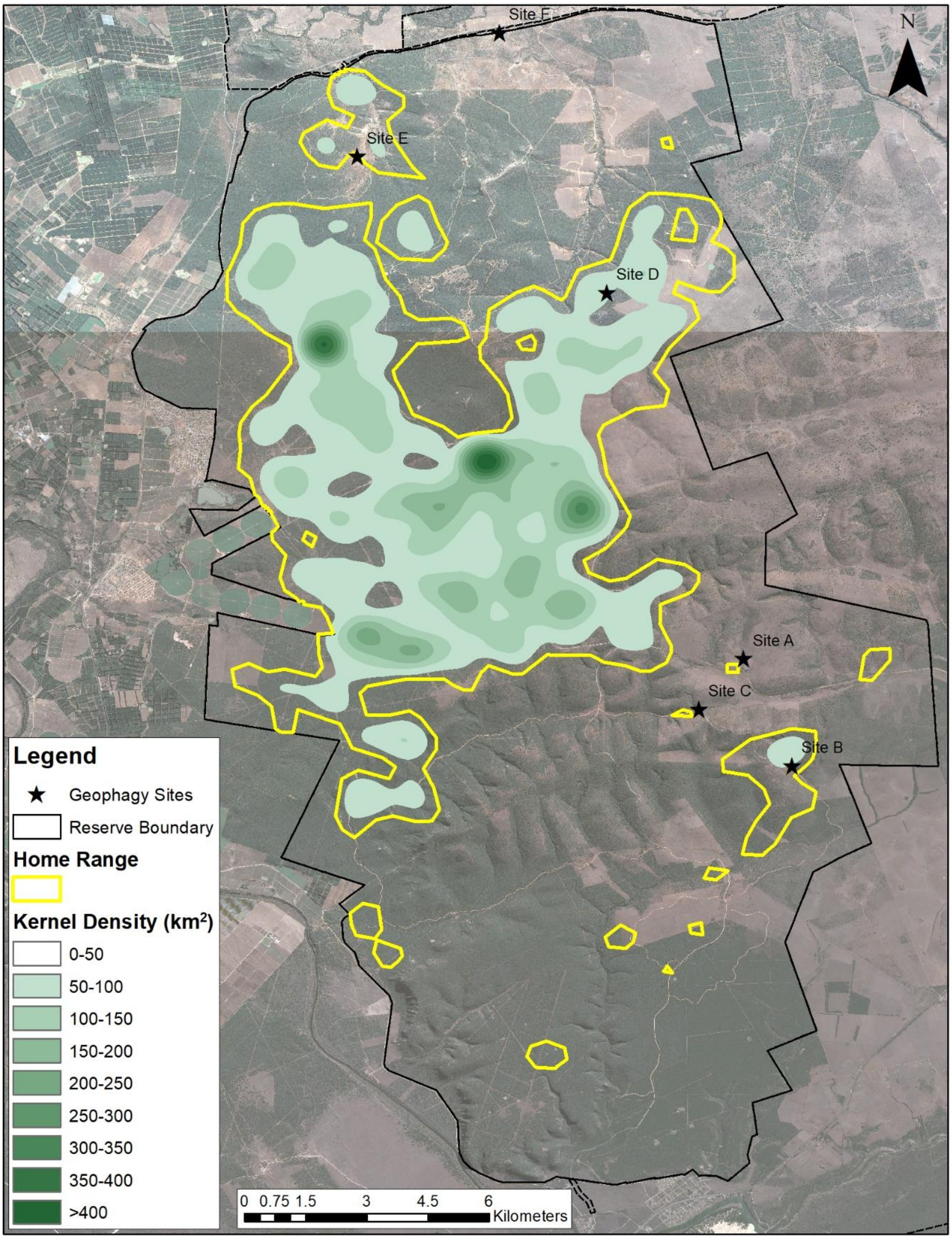

Figure 25. *Kernel density estimations (KDE) of distribution in relation to geophagy sites (A-F) of Female 2 in AENP. Increase in point density per km*^{2} *is presented with a colour gradient to highlight core areas within the home range (yellow line).*

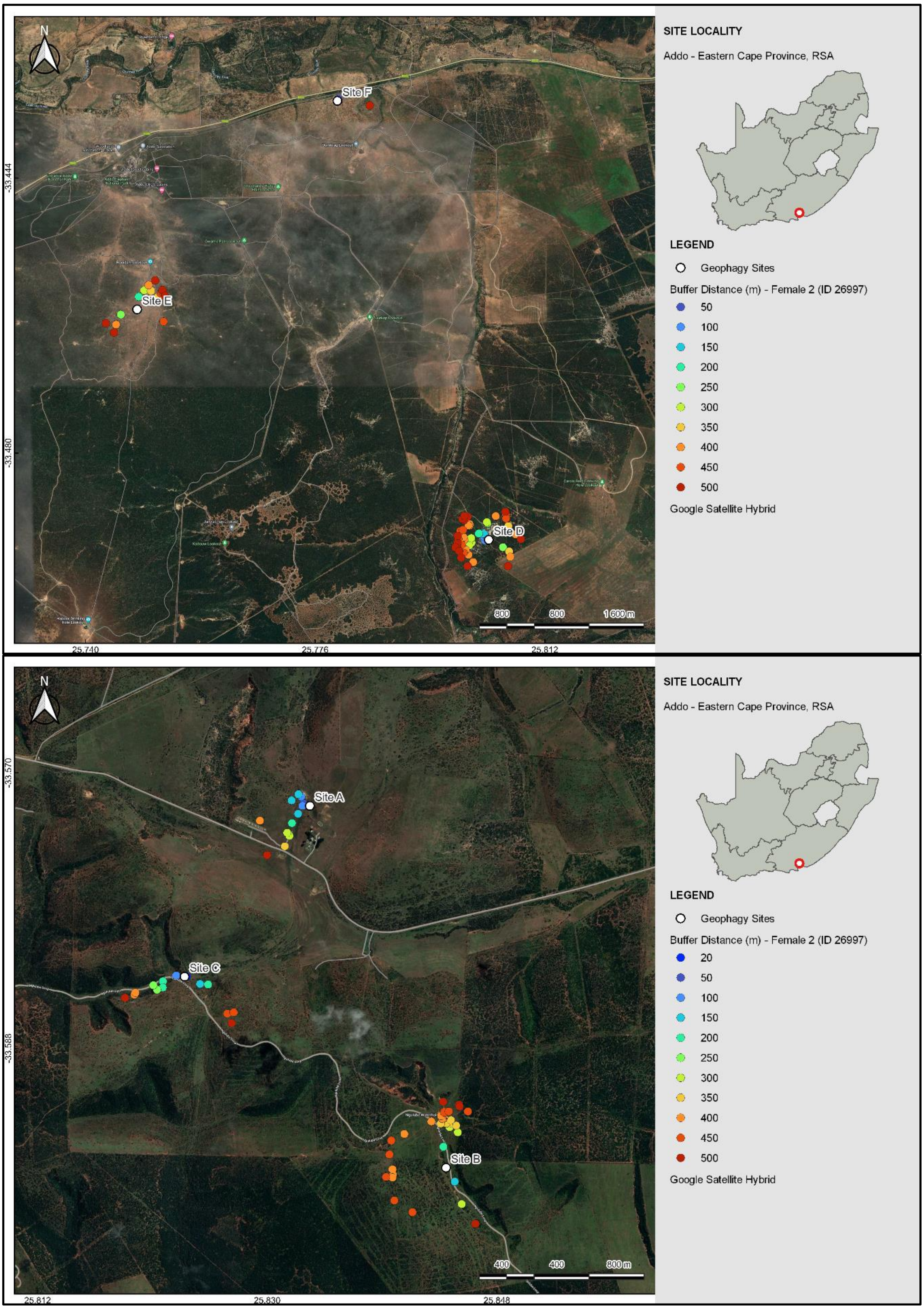

Figure 26. *GPS fixes for collared Female 2 detected within a 500 m radius from the centre of each geophagy site. Each fix is coloured from closest to the site (blue) to furthest from site (red) according to the different buffer distance intervals.*

The home range and core areas for Female 3 are presented in Figure 27. She mainly utilised the north-western section of the Park, and her home range covers an area of approximately 10 021 ha. Female 3 visited only five of the six geophagy sites (all except site A) during the study period with a total of 81 fixes recorded within the buffer zones (Fig. 28). Site E (69% of visits, n = 53), followed by site D (26% of visits, n = 21) had the highest number of visits (Table 8). For Female 3 however, a non-significant relationship is seen between the geophagy sites and different buffer intervals ($\chi 2 = 35.04$, df = 36, $p = 0.51$) Seasonally she also visited geophagy sites most frequently during autumn (72% of visits, n = 59), followed by winter (16% of visits, n = 13), spring (10% of visits, n = 8) and summer (1% of visits n=1). The kernel density map for Female 3 (Fig. 27), only include site E (her most visited site) in her home range, while site D lies on the border. As site B, C and F were visited at very low frequencies (< 2 hourly fixes recorded with a 500 m radius) and they are not included her home range boundaries. Similar to Female 2, although site F falls near her home range boundary, she only visited the site once.

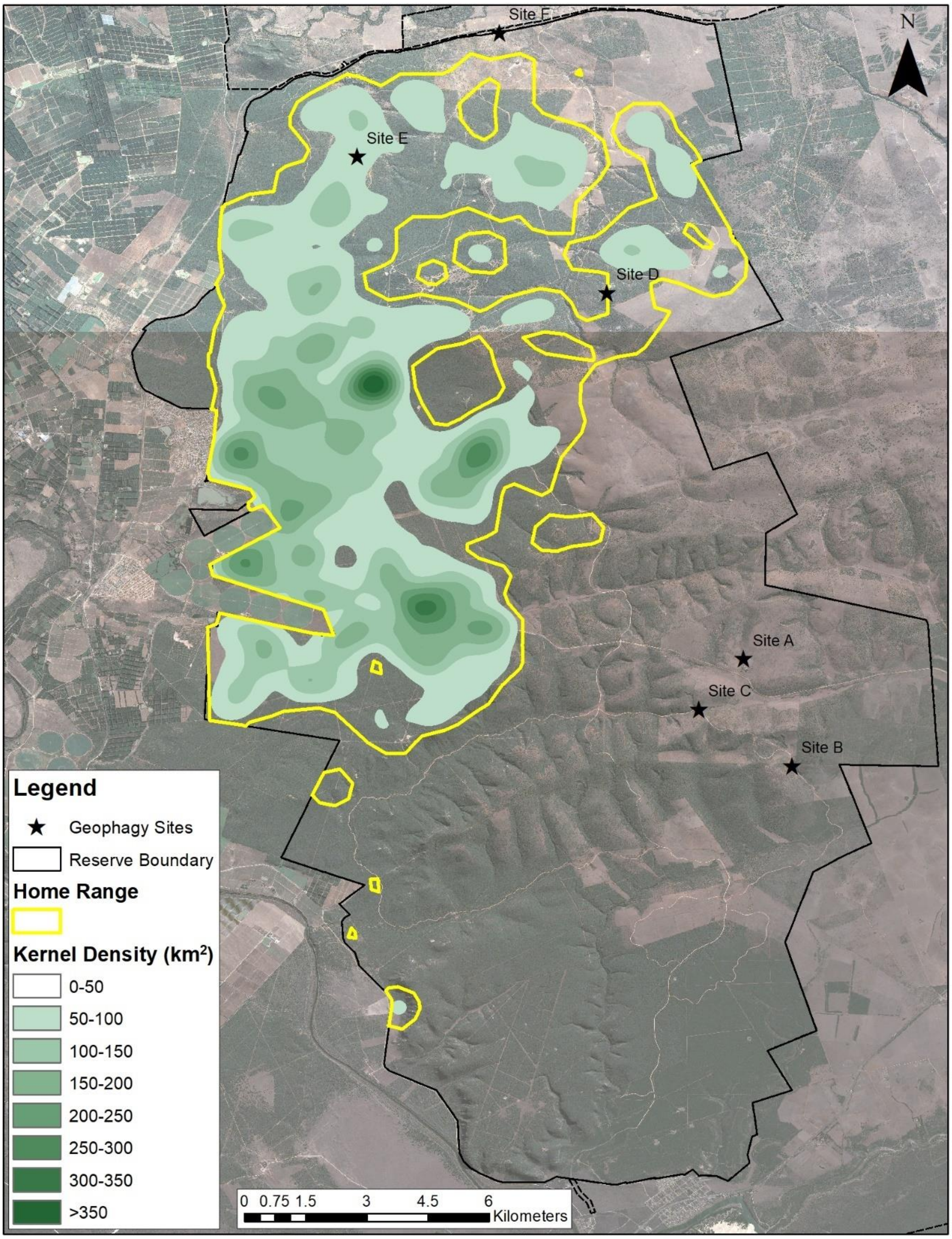

Figure 27. *Kernel density estimations (KDE) of distribution in relation to geophagy sites (A-F) of Female 3 in AENP. Increase in point density per km^2 is presented with a colour gradient to highlight core areas within the home range (yellow line).*

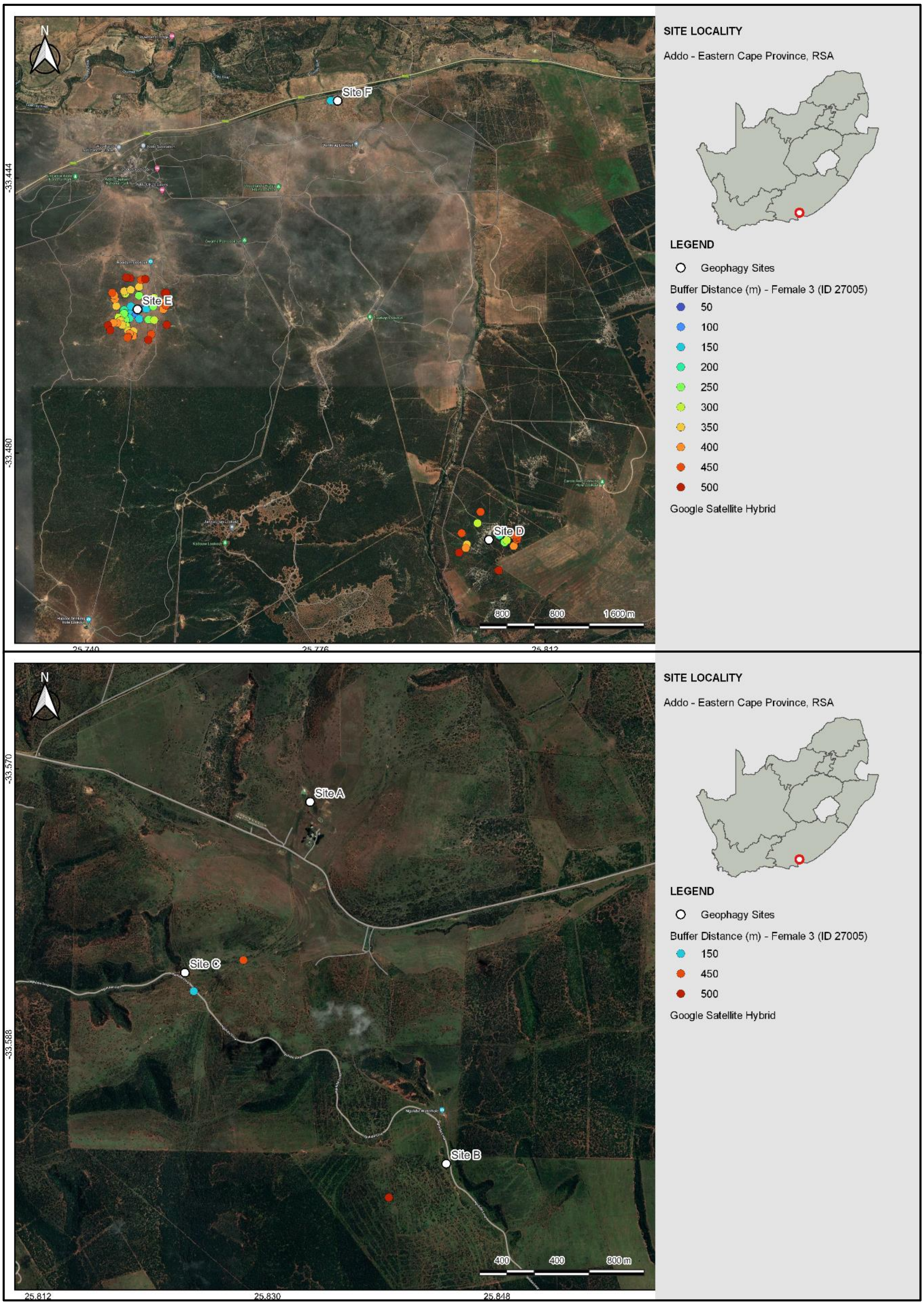

Figure 28. *GPS fixes for collared Female 3 detected within a 500 m radius from the centre of each geophagy site. Each fix is coloured from closest to the site (blue) to furthest from site (red) according to the different buffer distance intervals.*

The home range and core areas for Male 1 presented in Figure 29, displays a unique pattern compared to the three collared females. Male 1 spent most time along the fence boundary of the Park. In total, he has the smallest home range area of all collared elephants (2 800 ha) but with the highest total displacement of 3 366 km. Male 1 visited each of the geophagy sites across the Park, during the study period with a total of 310 fixes recorded within the buffer zone (Fig. 30). This was also the most fixes within the buffer zone recorded for all individuals. Site A (57% of visits, n = 177), followed by site F (18% of the visits, n = 56) had the highest number of visits, whereas site C (3% of the visits, n = 10) had the lowest (Table 8). Furthermore, a significant relationship was seen between the geophagy sites and buffer intervals ($\chi 2 = 135.56$, df = 50, $p < 0.001$). Seasonal data show that he visited geophagy sites most during autumn (51% of visits, n = 159), followed by summer (28% of visits, n = 88), winter (13% of visits, n = 39) and spring (8% of visits, n=24). According to the kernel density map (Fig. 29), only site F is included in his home range area.

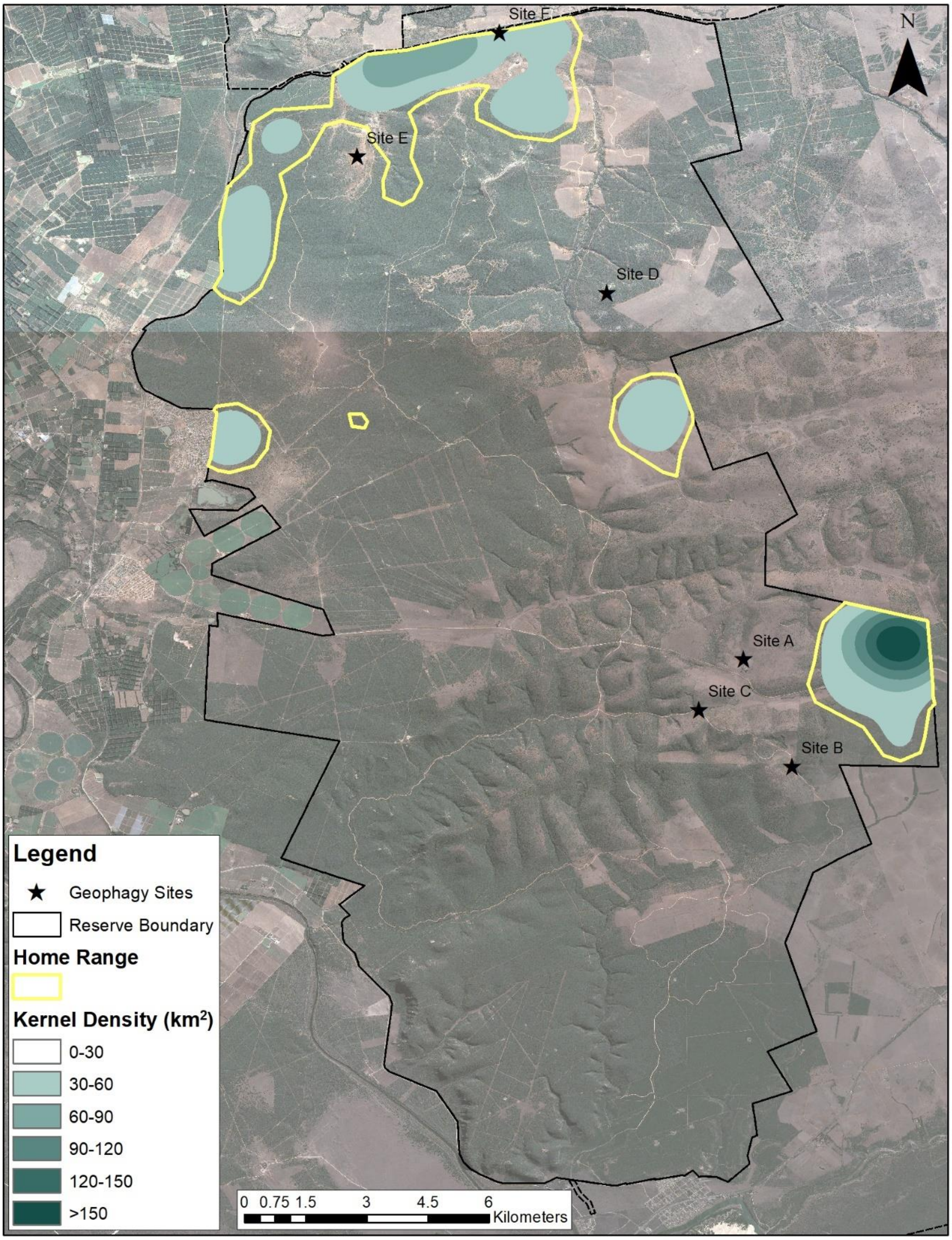

Figure 29. *Kernel density estimations (KDE) of distribution in relation to geophagy sites (A-F) of Male 1 in AENP. Increase in point density per km^2 is presented with a colour gradient to highlight core areas within the home range (yellow line).*

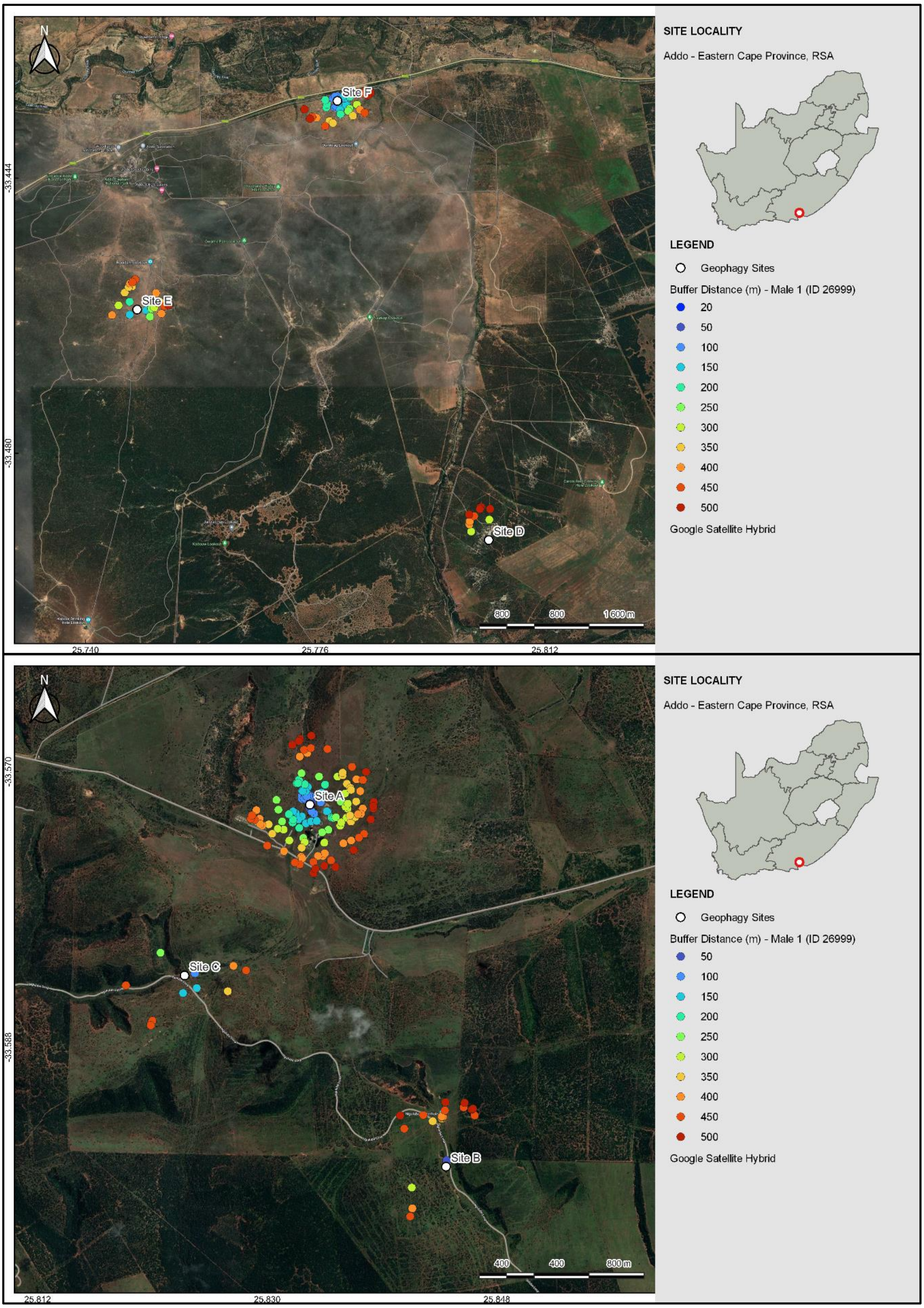

Figure 30. *GPS fixes for collared Male 1 detected within a 500 m radius from the centre of each geophagy site. Each fix is coloured from closest to the site (blue) to furthest from site (red) according to the different buffer distance intervals.*

The home range and core zones for Male 2 are presented in Figure 31. He mainly utilised the southern part of the park and had a home range area of 7 683 ha. Male 2 only visited three of the six geophagy sites (all except site D, E and F which are located in the northern section of the Park) during the study period with a total of 193 fixes recorded within the buffer zone (Fig. 32). Site B (48% of visits, n = 93) had the highest number of visits, whereas site C (13% of the visits, n = 27) had the lowest (Table 8). A significant relationship was seen between the geophagy sites and buffer intervals ($\chi2 = 91.04$, df = 20, $p < 0.001$). Seasonally a unique trend was seen, he visited geophagy sites most during spring (31% of visits, n = 60), followed by autumn (26% of visits, n = 51), winter (25% of visits, n = 49) and summer (17% of visits, n=33). From the kernel density map (Fig. 31), it can be seen that the three sites visited, are also included in his home range and are situated at core areas.

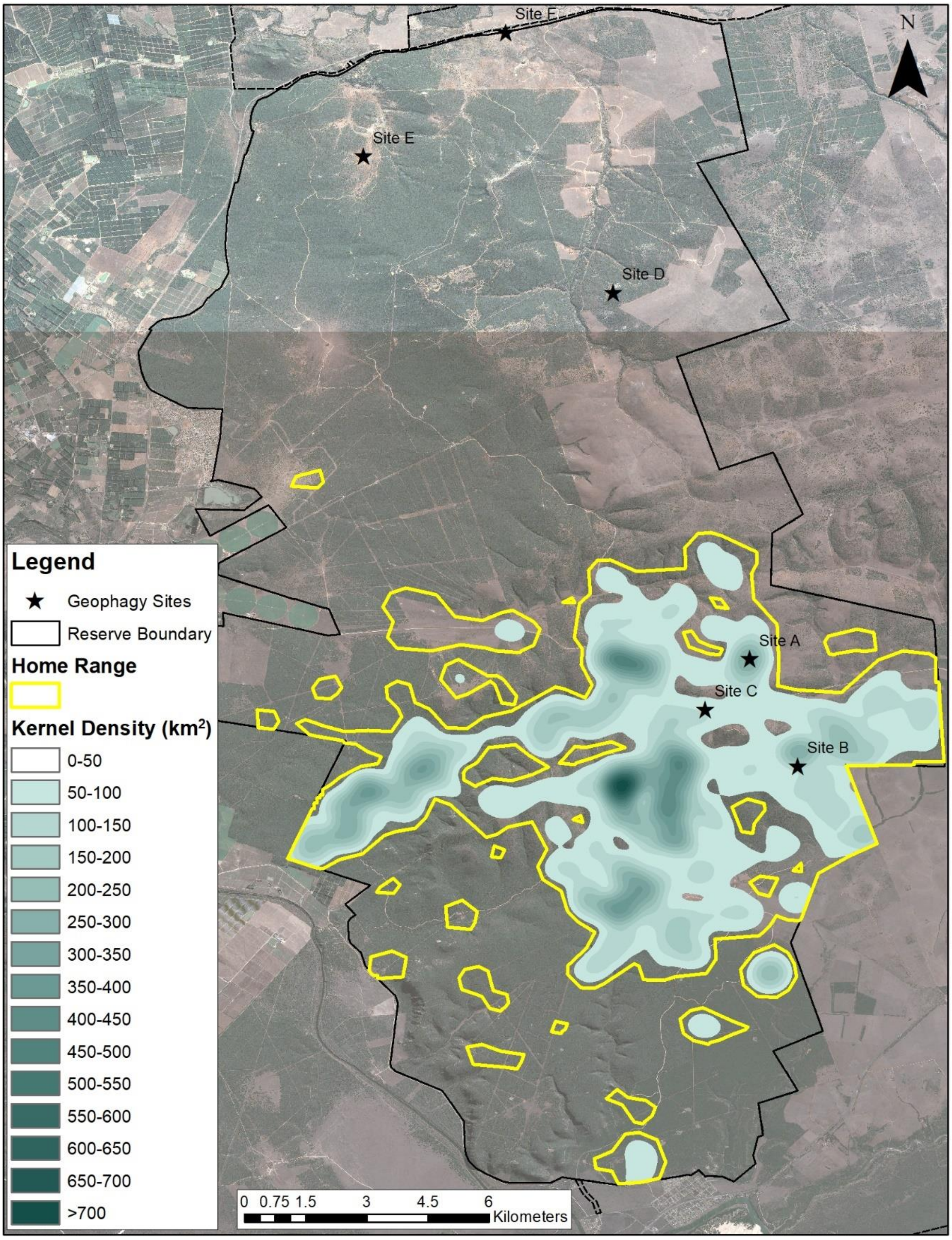

Figure 31. *Kernel density estimations (KDE) of distribution in relation to geophagy sites (A-F) of Male 2 in AENP. Increase in point density per km^2 is presented with a colour gradient to highlight core areas within the home range (yellow line).*

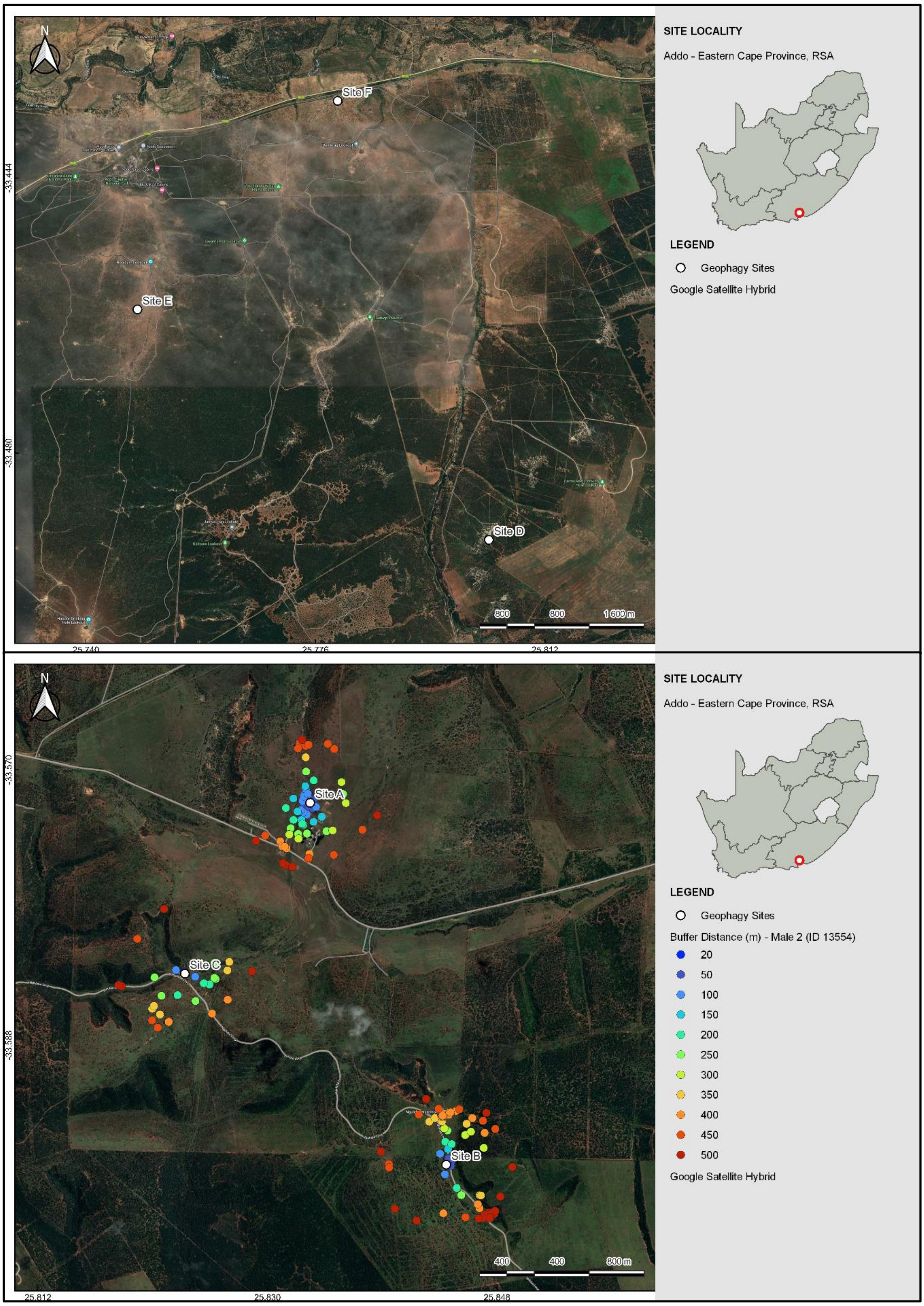

Figure 32. *GPS fixes for collared Male 2 detected within a 500 m radius from the centre of each geophagy site. Each fix is coloured from closest to the site (blue) to furthest from site (red) according to the different buffer distance intervals.*

Overall, a significant relationship was observed between season and specific site visitation (χ2 = 145.27, df = 15, p < 0.001). site A accounted for the most total visits for all elephants combined (n = 284), followed by site D (n = 183), site B (n = 168), site E (n = 167), site F (n = 72) and site C (n = 59). More specifically, during autumn and summer - site A accounted for the most visitations, during winter – site D was preferred and during spring – site B was preferred. Summer was also the only season where sites (D and F) were not visited at all by either of the collared elephants.

5.4 Discussion

Most environments have multiscale complexity in terms of time and space (Chave 2013). The degree of spatiotemporal environmental homogeneity could create predictable movement patterns in animals (Riotte-Lambert and Matthiopoulos 2019). The distribution and availability of resources, such as geophagy sites, affect the visitation frequency as well as movement patterns (Wiles and Weeks 1986). As expected, Male 1, which had the highest total displacement (3 366 km) and the lowest home range area (2 800 ha), included all six geophagy sites in his movement pattern. However, compared Female 2 (the only other individual to visit all six geophagy sites), the opposite is seen as she had the lowest displacement (2 252 km). According to Turchin (1991), an animals' total displacement will decrease and the amount of time spent consuming targeted resources will increase if the resources are efficiently utilised. Females are generally considered to remain in closer proximity to water and nutrient sources than males due to the demands of group living (Duffy et al. 2011; Sianga et al. 2017) Males are less dependent on water and are expected to have greater movement freedom as a result (Stokke and du Toit 2000). A study conducted on collared elephants in the Amboseli ecosystem on the Kenya/Tanzania border found that bulls had larger home ranges sizes compared to females (Ngene et al. 2017). It can be deduced that Female 2 was able to utilise resources, including geophagy sites, more efficiently to meet nutritional demands within a smaller area than Male 1. Although Male 2 had the second lowest displacement (2 700 km), it only differs with approximately 90 to 140 km compared to Female 3 and 1 respectively. The striking difference between the three individuals however, is that Male 2 only visited three of the six geophagy sites, whereas Female 1 and 3 visited five of the six sites. Nevertheless, the collared individuals included three or more geophagy sites in their movement pattern (more than what was predicted), suggesting that these nutritional hotspots are sought after and important resources for elephants.

Furthermore, visitation frequencies differed across geophagy sites for individuals. Female 1 and 2 were the only individuals that visited the same site, site D, the most. This was the geophagy site where calcite as mineral and Ca and P as essential elements, were identified as important (*vide* Chapter 3). This geophagy site also had the highest calcite (Ca) levels compared to all the other sites. Whereas Female 3 presented a greater preference for site E, which had higher K-feldspar compositions compared to other sites and where Mn, Ca, Na, Cu and Pb were considered the attracting essential elements (*vide* Chapter 3). Both sites D and E are located in the northern section of the park known as Addo Main Camp (AMC). Male 1 visited site A the most where calcite was identified as an important mineral as well as essential elements such as Mn, Ca, Na, P and As (*vide* Chapter 3). Male 2 visited site B the most where three minerals (ilmenite, K-feldspar and plagioclase) and essential elements Mn, Na and Cu were considered important (Chapter 3). Both sites A and B are located in the more southern section of the park (Colchester). Site C and

F were the only geophagy sites not preferred (did not have the highest visitation frequency) by any of the five collared individuals. Site C had elevated levels of calcite, K-feldspar and plagioclase and Na and Ca as essential elements (*vide* Chapter 3) and accounted for the lowest visitation frequency overall. Considering that the geochemical and mineralogical make-up of the site may show similarities to preferred sites, the surrounding area was not as actively utilised compared to the other sites. Only for Male 2 site C was situated within a core area. The elephants were most likely able to satisfy their geophagic needs at geophagy sites within their home range than having to travel further to site C. On the other hand, Site F had elevated Fe and Mg concentrations (higher at the feeding area compared to the control, *vide* Chapter 3). It was predicted that concentrations at higher levels would highlight sought-after elements, however as Site F was not preferred by individuals it can be deduced that the need or supplementation thereof is not as important as other elements such as Na, Ca and Mn. Mn is poorly absorbed from diet and Mn-deficiencies could lead to skeletal abnormalities and slow bone growth (Cherian 2020). These essential elements (Na, Ca and Mn) are important for certain physiological demands such as bone and tusk growth in elephants (McCullagh 1969; Sach et al. 2020) and reproductive demand in females (Ensley et al. 1994; Dierenfeld 2008; Leshchinsky 2015).

As predicted the variation of geophagy site composition and utilisation possibly suggests that nutritional supplementation and/or deficiencies and behavioural aspects come in to play at an individual level. Considering that elephants can feed on approximately 150 different plant species in AENP (Paley and Kerley 1998; Kerley and Landman 2006), each collared individuals’ preferences might result in different nutritional shortcomings and needs as suggested by the utilisation difference among them. As proximate environmental conditions vary, it is beneficial that elephants are able to show behavioural flexibility and movement plasticity (Purdon et al. 2018). The striking differences between the two collared males alone also suggests idiosyncratic behaviour playing a role in movement patterns. According to Beirne et al. (2021), there is growing acknowledgement of the need of quantifying the role of, and variance associated with, individual movement patterns. However, considering that only two collared male individuals are compared, differences in patterns and home ranges are likely to appear and could be attributed to environmental and/or behavioural differences. Male 2 did not utilise the northern section of the Park for the duration of the study. This might be due to the general nature for males to disperse across the habitat to avoid breeding and resources competition (Macri et al. 2002; Evans 2006). Furthermore, bulls are considered to also avoid certain areas inhabited by female groups to avoid competition (Stokke and du Toit 2002). This could also support why Male 2 remained in the southern part of the Park, as the northern section (in terms of geophagy site visits) was predominantly utilised by females. Spatial and social segregation was observed by elephants on northern Botswana (Stokke and du Toit 2000). Male 1 on the other hand included all geophagy sites, opposed to only three for Male 2. He might have had a higher propensity to travel further to explore, which is a useful trait when new or better resources are sought-after (Spinage 1994; Osborn 2004). A study conducted by Leggett (2006) in north western Namibia, concluded that adult bulls might travel far distances in search for females in oestrus during male musth periods.

Overall, for the five individuals combined, site A accounted for the most visitations. The higher frequencies overall could be due to a permanent man-made waterhole located near the geophagy site also attracting the elephants to the area.

However, if this waterhole near site A was responsible for high visitation records, then it would be expected that site A would account for the highest visitation frequencies across all seasons as well. This is only true for autumn and summer, but for spring and winter the visitation frequency ranked third and fourth highest respectively. It can be deduced that the waterhole situated in close proximity to site A was non-exclusively responsible for the visits.

Significant seasonal differences in visitation frequencies were also observed between individuals and between geophagy sites. Seasonal changes in movement across habitats and therefor geophagy site utilisation, is usually in response to diet and physiological (especially reproductive) changes (Blake et al. 2011). Habitat utilisation patterns are considered to be intentional and depended on characteristics throughout a heterogenous landscape (Thapa et al. 2019). For this study, it was predicted that higher visitations during winter and autumn would suggest mineral supplementation as vegetation availability and quality decreases (Semel et al. 2019), especially during the local drought experienced (Archer et al. 2022). Not only is the nutritional quality of vegetation affected, but during dry seasons the secondary plant metabolites increase (Mwangi et al. 2004; Schmitt et al. 2016; Ward et al. 2020), driving geophagy behaviour to alleviate GI distress (Krishnamani and Mahaney 2000; Ayotte et al. 2006; Shannon et al. 2006; Sienne et al. 2014). Highest site visitations during the dry/colder months were observed for the three collared females where visits peaked in autumn followed by winter. For Male 1, autumn accounted for the most visits but is followed by summer instead. The visitation for Male 2 however, peaked in spring and is closely followed by autumn. These observations therefore mainly support the possibility for nutritional supplementation and/or alleviation of GI stress. A study conducted in Hwange National Park, Zimbabwe, similarly found higher geophagy site utilisation during the dry seasons, specifically for Na supplementation (Holdø et al. 2002).

The collar data obtained by the five collated elephants of AENP provide insight into the spatial distribution in relation the geophagy sites only. The visitation frequency and patterns suggest that the elephants in AENP incorporated geophagy sites in their movement patterns and home ranges. A study conducted by Klaus-Hügi et al. (2000) on the movement patterns of Bongos (*Tragelaphus eurycerus*) in relation to natural lick sites in Dzanga National Park, Central African Republic, found that they also intentionally and directly converged to these sites. According to Klaus and Schmid (1998), soils are not ingested at random within an elephant's home range, but rather from specific spatially defined locations. Taking this into consideration and that AENP currently has approximately 490 elephants, it can be expected that, most individuals would visit at least one geophagy site in a similar time frame. Although movement patterns are influenced by multidimensional factors such as water, vegetation, predators, slopes etc, very few studies include geophagy sites as a contributing factor of movement patterns. Geophagy behaviour is considered to have important implications for conservation and management (Milewski 2000).

CHAPTER 6

GENERAL CONCLUSIONS

6.1 Summary and general conclusions

Situated within the onshore Algoa Basin of the Eastern Cape, South Africa, the AENP is underlain with a unique and complex geological foundation (Muir et al. 2015). The Park is underlain by Enon-, Kirkwood- Sundays River- and Alexandria Formation rich in clays, mudstone, siltstone and sandstone with dominant calcic and ferric luvisol soils (Anonymous 2017). As a result, the AENP has very diverse vegetation types throughout the Park, specifically succulent thickets within the study area (Landman et al. 2007; Kakembo et al. 2015). The vegetation of any given area and the ability of these plants to incorporate the minerals and elements thereof underpins the relationship between animals and their food supply (Joy et al. 2015). There are many factors that can have an effect on the mineral and elemental uptake and accumulation in plants and can differ seasonally, topographically, among different species of browse and graze and due to rainfall (Prins and Langevelde 2008). Movement patterns in elephants are predominantly determined by nutritional resources (Kerley and Landman 2006; Loarie et al. 2009). A shortage of essential nutrients throughout an animal's life stages is universally accepted as the most likely motivation of geophagic behaviour (e.g., Klaus et al. 1998; Young et al. 2011; Kalumanga et al. 2016; Pebsworth et al. 2019). Another possible driver for geophagy is the protection or alleviation of certain GI disorders (Chandrajith et al. 2009; Pebsworth et al. 2011).

The geochemical and mineralogical composition varied among sites and with various minerals and elements in higher concentration at the feeding sites compared to the soil. Considering minerals and major elements for all six geophagy sites (subsampled data combined), each site had highest quartz (therefor SiO_2) concentrations as predicted, except for site D which had significantly higher calcite (CaO) concentrations. Plagioclase (made up of a Na-Ca ration) concentrations were the second highest identified across all sites, again with site D as the exception as quartz (SiO_2) accounted for the second highest concentrations. Considering trace elements for all six geophagy sites (subsampled data combined), the highest levels detected for site A, B, C, E and F was Zr (as expected) followed by Ba, for site D was Sr followed by Ba. Due to the mineralogical and geochemical difference for site D compared to the other sites, it surprising that site B was the most frequently utilised geophagy lick site. More specifically site B had the highest Zr concentrations across all sites but is considered a non-essential and non-toxic element (Ghosh et al. 1992; Sach et al. 2020). The mineral/elemental concentrations (and combinations thereof) between and within sites suggests that Na and Ca might non-exclusively, be the driving elements of geophagy in the AENP elephant population.

In general, Na is considered essential because it balances body fluids, regulates tissue pH and osmotic pressure, and helps muscles and nerves function (Klein and Thing 1989). Na is highly sought after by females, particularly during pregnancy and nursing (Michell 1995). Furthermore, Na is one of the active ingredients used medically as an antacid that relieves GI discomfort and controls diarrhoea (Krishnamani and Mahaney 2000). Similarly, site B which was utilised most by the elephants, had elevated ilmenite concentrations which is a Fe-containing mineral. Additionally known for acting as antacids to lessen digestive tract acidity are elements like Fe and Ca (Wilson 2003; Limpitlaw 2010). Elephants require a high intake of Ca for intensive tusk growth and during lactation. Deficiency of Ca in an elephant's diet, including Ca deficiency in maternal milk fed to juveniles, could lead to metabolic bone disease and other bone growth defects (Ensley et al. 1994; Leshchinsky 2015).

Although the results suggest seasonal variation in visitation frequencies, the potential bias introduced by missing data should be considered. Autumn accounted for the highest number of elephant visits across all sites per season, even though the number of successful camera trapping days were the lowest. As predicted, increase in geophagic activity across drier/colder seasons could be due to fluctuations in vegetation quality and plant availability. This was expected after the intense drought period experience for 2019 (Archer et al. 2022). During drought and dry seasons, the amount of secondary plant metabolites in browse increases (Schmitt el al. 2016; Ward et al. 2020).

The highest visitation frequency across all sites peaks between 14:00 and 15:00 during autumn, 16:00 and 17:00 during winter, 20:00 and 21:00 during spring, and 22:00 and 23:00 during summer. Overall combined, the highest visitation peaks are documented between 20:00 and 21:00. Alternatively, it was predicted that visitation peaks after dusk (nights) could suggest predator and tourist avoidance and preferring to ingest soil after foraging when temperatures are lower and energy expenditure is less. Additionally, it could suggest that geophagy is practiced at night to mitigate secondary plant metabolites ingested while foraging during the day. AENP experienced varying rainfall throughout the study period with a high peak in summer. A study conducted by Suescún et al. (2016) found that high concentrations of nutrient loss due to rainfall influenced soil fertility in the area. However, no significant correlation was determined between seasonal precipitation levels and geophagic visitation frequency of elephants obtained via camera traps.

Adults made up almost 55% of the total visits, followed by subadults and juveniles. Furthermore, more males were recorded utilising geophagy sites than females however, the high number of individuals that could not be sexed from the photographs (referred to as ‘unknown’) could lead to skewed results. Given the high nutritional demand in females for reproduction, pregnancy and lactation, the opposite results were expected, more so because of the 1:8:1 ratio of females to males in the AENP elephant population. The higher observation for males utilising geophagy sites could be due to their larger body size and therefor greater need for certain elements for tusk and bone growth (McCullagh 1969). The need for males to ingest soil might also be to alleviate GI distress due to their bulk foraging strategy. (Shannon et al. 2006). Furthermore, more elephants with tusks were recorded utilising geophagy sites than elephants without tusks. Due to not being able to determine from the photographs whether certain individuals had tusks or not (referred to as 'out of sight'), the results could be skewed. However, the higher number of elephants with tusk utilising the geophagy sites was expected and could also be explained by the high nutritional demand for tusk growth (McCullagh 1969; Dierenfeld 2008).

Geophagy sites are fixed in time and space from a nutritional resource perspective, and most likely play a role in an elephant's movement choice. By analysing the movement patterns of the five collared elephants (two bulls and three matriarchs), it can be deduced that multiple geophagy sites are incorporated in their movement patterns and home ranges. This study found that the three females had larger KDE home ranges (8 975-11 319 ha) than males (2 800-7 683 ha), which is opposite to other studies (e.g., Leggett 2006; Ngene et al. 2017). However, the total displacement between individuals found that Male 1 travelled approximately 520 - 1 100 km further than any other individual while and spent more time along the fence boundary of the Park.

The visitation frequencies obtained using camera trap data found that site B was more utilised. Whereas, the GPS data obtained from collared elephants combined found more frequent visits to site A and the surrounding area. Considering that geophagy site A is situated near a waterhole, it could non-exclusively account for high visits. This highlights the difference in methods to report on geophagy activity.

On an individual level, different geophagy sites were more utilised than others. Site D (which is distinctively rich in calcite) was visited more than other sites by Female 1 and 2 and was also situated within their core areas. Female 3 mostly visited site E which was also situated within her core area. Male 1 mostly visited site A, however the geophagy site was not included in his home range. Male 2, on the other hand, showed a preference for site B which was also situated within his home range and core area. The preferred sites for collared elephants similarly indicate that Na and Ca as well as Mn are main drivers for geophagy. These essential elements (Na, Ca and Mn) are important for certain physiological demands such as bone and tusk growth in elephants (McCullagh 1969; Sach et al. 2020) and reproductive demand for females (Ensley et al. 1994; Dierenfeld 2008; Leshchinsky 2015).

In its entirety, this study found that elephants engage in geophagy for a number of reasons that are nonexclusive, including the protection and nutrient supplementation hypotheses. Elephants in AENP are considered to frequently practice geophagy from purposely selected locations and that Na, Ca and Mn are drivers of geophagic behaviour. Geophagy in AENP might have different functions at different times for the elephant population, as age and sex distributions at these sites differed and utilisation pattern differed across preferred sites. Geophagy sites located in a habitat as a potential variable or factor should be included for movement patterns or habitat utilisation studies and could provide valuable insight for conservation and management strategies.

6.2 Future studies

To my knowledge, this is the first interdisciplinary geophagy study conducted on African savannah elephants to this extent in South Africa. I found that information on nutritional requirements and digestive physiology for wild elephants is scarce and mainly based on domestic equid models. Furthermore, other published geophagy studies on African and Asian elephants barely include complete geochemical and mineralogical analysis of the lick sites, with more recent laboratory techniques and equipment. Very few include findings on geophagic behaviour for an extended period of time, utilisation patterns and population dynamics which makes comparability challenging.

Considering the extent of missing camera trap data obtained, future studies conducted should consider setting up two cameras at a geophagy site, where one might act as a back-up. Furthermore, video footage might add valuable insight in the social behaviour and sequences at these geophagy sites and assist with individual identification. I also think that cafeteria studies in a controlled environment would also provide useful data on the selectiveness for specific minerals/elements. To better understand why different groups in various habitats are observed engaging in geophagy, more thorough behavioural studies are recommended.

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Appendix A

***Table A1**. Mineralogical (X-Ray Diffractometry) analysis and composition (weight %) of primary and secondary minerals present in all soil sampled for sites A-F in Addo Elephant National Park, South Africa*

		XRD CHEMICAL COMPOSITION (WT. %)									
		Calcite	**Clinopyroxene**	**Dolomite**	**Gypsum**	**Ilmenite**	**K-feldspar**	**Muscovite**	**Plagioclase**	**Quartz**	Total
Site A	Feeding Site	4	-	-	-	-	-	13	12	71	100
	1 m away	-	-	8	12	-	-	15	10	55	100
	Control	2	-	-	11	9	-	13	12	53	100
Site B	Feeding Site	-	-	-	-	6	7		15	72	100
	1 m away	-	-	3	-	3	7	7	20	60	100
	Control	-	-	4	-	-	5	7	13	71	100
Site C	Feeding Site	3	-	-	-	3	7	7	14	66	100
	1 m away	2	-	-	-	3	6	7	13	69	100
	Control	2	-	-	-	3	6	10	11	68	100
Site D	Feeding Site	50	-	-	-	-	-	11	13	26	100
	1 m away	37	-	-	-	-	-	12	17	34	100
	Control	25	-	-	-	-	-	11	29	35	100
Site E	Feeding Site	-	-	-	9	-	10	13	19	49	100
	1 m away	-	-	-	11	-	12	15	15	47	100
	Control	2	-	-	9	-		15	19	55	100
Site F	Feeding Site	-	5	-	-	-	7	8	19	61	100
	1 m away	-	4	-	-	-	7	8	18	63	100
	Control	-	5	-	-	-	7	10	13	65	100

Semiquantitative amounts of each mineral is considered: dominant >50%, abundant 20-50%, minor 10-19%, accessory 2-9%, trace <2%, and if “- “not present.

Table A2. *Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site A in Addo Elephant National Park, South Africa.*

SITE A		**FEEDING SITE**	**1 m AWAY**	**CONTROL**
XRF Major elements (wt. %)	SiO_2	69.16	68.31	69.17
	TiO_2	0.88	0.75	0.80
	Al_2O_3	12.57	15.04	14.75
	*Fe_2O_3	5.45	6.08	5.83
	*MgO	0.49	0.75	0.59
	*MnO	0.04	0.04	0.03
	*CaO	1.36	0.42	0.53
	*Na_2O	0.41	0.33	0.29
	*K_2O	1.43	1.56	1.49
	*P_2O_5	0.08	0.04	0.06
	Loss on ignition	5.81	5.26	5.72
	Total	**97.68**	**98.57**	**99.26**
XRF Trace elements (mg/kg)	Sc	14	21	15
	*V	130	146	143
	Cr	105	108	108
	Co	22	27	26
	Ni	33	41	41
	*Cu	8	12	11
	*Zn	37	40	37
	*As	18	17	17
	Rb	89	104	100
	Sr	69	58	53
	Y	27	30	28
	Zr	457	315	376
	Nb	12	11	11
	Ba	303	315	306
	*Pb	11	16	15
	Th	11	11	11

* Considered an essential element for biological functions (Sach et al. 2020)

***Table A3**. Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site B in Addo Elephant National Park, South Africa.*

SITE B		**FEEDING SITE**	**1 m AWAY**	**CONTROL**
XRF **Major elements** **(%)**	SiO_2	85.43	85.93	84.11
	TiO_2	1.82	2.06	2.09
	Al_2O_3	3.85	5.58	5.31
	*Fe_2O_3	2.67	3.22	3.24
	*MgO	0.07	0.13	0.10
	*MnO	0.05	0.04	0.04
	*CaO	0.19	0.31	0.19
	*Na_2O	1.04	0.97	0.99
	*K_2O	0.52	0.66	0.62
	*P_2O_5	0.03	0.03	0.03
	Loss on ignition	2.40	2.14	1.89
	Total	**98.07**	**101.07**	**98.63**
XRF **Trace elements** **(mg/kg)**	Sc	8	6	6
	*V	121	132	130
	Cr	57	75	73
	Co	11	11	12
	Ni	10	10	9
	*Cu	5	5	4
	*Zn	17	21	19
	*As	5	5	5
	Rb	32	37	38
	Sr	69	66	66
	Y	20	22	22
	Zr	2061	2179	2020
	Nb	23	24	24
	Ba	159	177	181
	*Pb	8	12	13
	Th	12	12	15

* Considered an essential element for biological functions (Sach et al. 2020)

***Table A4**. Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site C in Addo Elephant National Park, South Africa.*

SITE C		**FEEDING SITE**	**1 m AWAY**	**CONTROL**
XRF Major elements (%)	SiO_2	86.22	88.63	80.95
	TiO_2	1.27	1.37	1.53
	Al_2O_3	4.77	4.86	6.59
	*Fe_2O_3	2.09	2.11	3.00
	*MgO	0.16	0.10	0.26
	*MnO	0.03	0.03	0.04
	*CaO	1.89	0.84	1.02
	*Na_2O	1.11	1.36	0.95
	*K_2O	0.67	0.68	0.89
	*P_2O_5	0.02	0.02	0.03
	Loss on ignition	2.64	1.66	2.76
	Total	**100.86**	**101.66**	**97.99**
XRF Trace elements (mg/kg)	Sc	6	4	8
	*V	63	66	100
	Cr	48	49	72
	Co	6	7	10
	Ni	11	9	13
	*Cu	<4	7	8
	*Zn	12	15	21
	*As	6	5	7
	Rb	33	32	49
	Sr	86	83	85
	Y	18	16	26
	Zr	1055	1088	1214
	Nb	14	15	18
	Ba	195	205	245
	*Pb	5	4	10
	Th	8	9	13

* Considered an essential element for biological functions (Sach et al. 2020)

Table A5. *Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site D in Addo Elephant National Park, South Africa.*

SITE D		**FEEDING SITE**	**1 m AWAY**	**CONTROL**
XRF Major elements (%)	SiO_2	34.46	47.81	56.32
	TiO_2	0.10	0.17	0.22
	Al_2O_3	3.09	4.66	5.86
	*Fe_2O_3	0.90	1.50	1.67
	*MgO	0.61	0.62	0.64
	*MnO	0.02	0.02	0.04
	*CaO	31.36	22.34	16.66
	*Na_2O	0.27	0.41	0.53
	*K_2O	0.51	0.77	1.00
	*P_2O_5	0.05	0.03	0.04
	Loss on ignition	26.62	19.45	14.53
	Total	**98.00**	**97.78**	**97.52**
XRF Trace elements (mg/kg)	Sc	6	10	10
	*V	10	21	33
	Cr	11	14	19
	Co	<3	<3	<3
	Ni	11	18	15
	*Cu	<4	<4	<4
	*Zn	12	17	21
	*As	13	12	11
	Rb	21	29	38
	Sr	189	179	196
	Y	12	12	14
	Zr	75	97	120
	Nb	3	4	5
	Ba	132	164	197
	*Pb	<2	<2	<2
	Th	8	8	9

* Considered an essential element for biological functions (Sach et al. 2020)

***Table A6**. Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site E in Addo Elephant National Park, South Africa*

SITE E		FEEDING SITE	1 m AWAY	CONTROL
XRF Major elements (%)	SiO_2	71.38	68.27	70.06
	TiO_2	0.64	0.69	0.79
	Al_2O_3	12.32	15.88	15.20
	*Fe_2O_3	4.23	5.64	4.51
	*MgO	0.65	0.91	1.03
	*MnO	0.04	0.03	0.03
	*CaO	0.42	0.31	0.32
	*Na_2O	0.90	0.65	0.64
	*K_2O	2.11	2.71	2.35
	*P_2O_5	0.07	0.08	0.07
	Loss on ignition	4.70	5.66	5.08
	Total	**97.45**	**100.82**	**100.08**
XRF Trace elements (mg/kg)	Sc	11	18	15
	*V	97	120	109
	Cr	57	52	50
	Co	19	24	20
	Ni	25	32	26
	*Cu	17	17	14
	*Zn	51	62	52
	*As	9	10	13
	Rb	102	126	107
	Sr	104	87	93
	Y	27	28	27
	Zr	447	331	384
	Nb	11	12	11
	Ba	358	383	362
	*Pb	16	18	9
	Th	13	14	13

* Considered an essential element for biological functions (Sach et al. 2020)

Table A7. *Soil chemistry (X-Ray Fluorescence) of major (in oxide form, weight %) and trace (mg/kg) elements of geophagic soil at site F in Addo Elephant National Park, South Africa.*

SITE F		**FEEDING SITE**	**1 m AWAY**	**CONTROL**
XRF Major elements (%)	SiO_2	84.82	83.83	82.91
	TiO_2	0.57	0.53	0.53
	Al_2O_3	7.42	7.66	7.82
	*Fe_2O_3	3.02	2.35	2.91
	*MgO	1.14	0.43	0.51
	*MnO	0.05	0.10	0.09
	*CaO	0.35	0.46	0.41
	*Na_2O	1.08	1.24	0.87
	*K_2O	1.38	1.39	1.54
	*P_2O_5	0.16	0.13	0.14
	Loss on ignition	1.84	2.29	3.04
	Total	**101.83**	**100.41**	**100.78**
XRF Trace elements (mg/kg)	Sc	5	6	9
	*V	47	46	56
	Cr	34	40	51
	Co	12	11	13
	Ni	14	17	17
	*Cu	9	11	13
	*Zn	26	27	38
	*As	8	9	3
	Rb	49	52	63
	Sr	92	121	88
	Y	20	20	20
	Zr	404	439	377
	Nb	9	9	8
	Ba	300	370	345
	*Pb	3	<2	13
	Th	10	9	11

* Considered an essential element for biological functions (Sach et al. 2020)

***Table A8**. Results of analysis of variance using one-way ANOVAs for normally distributed variables or Kruskal-Wallis (KW) ANOVA (for non-normally distributed variables).*

		Site A	**Site B**	**Site C**	**Site D**	**Site E**	**Site F**	***p***		
Minerals	Quartz	59.67 ± 9.87	67.67 ± 6.66	63.00 ± 2.00	31.67 ± 4.93	50.33 ± 4.16	67.67 ± 1.53	**0.000**	***	
	Calcite	2.00 ± 2.00	0.00 ± 0.00	0.00 ± 0.00	37.33 ± 12.5	0.67 ± 1.15	2.33 ± 0.58	**0.019**	*	KW
	Plagioclase	11.33 ± 1.15	16.00 ± 3.61	16.67 ± 3.21	19.67 ± 8.33	17.67 ± 2.31	12.67 ± 1.53	**0.202**	NS	
	Mica	13.67 ± 1.15	4.67 ± 4.04	8.67 ± 1.15	11.33 ± 0.58	14.33 ± 1.15	8.00 ± 1.73	**0.000**	***	
	Gypsum	7.67 ± 6.66	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	9.67 ± 1.15	0.00 ± 0.00	**0.025**	*	KW
	Dolomite	2.67 ± 4.62	2.33 ± 2.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	**0.192**	NS	KW
	Ilmenite	3.00 ± 5.20	3.00 ± 3.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.00 ± 0.00	**0.091**	NS	KW
	K-feldspar	0.00 ± 0.00	6.33 ± 1.15	7.00 ± 0.00	0.00 ± 0.00	7.33 ± 6.43	6.33 ± 0.58	**0.009**	**	
	Clinopyroxene	0.00 ± 0.00	0.00 ± 0.00	4.67 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	**0.005**	**	KW
Major elements	SiO_2	68.88 ± 0.49	85.16 ± 0.94	83.85 ± 0.96	46.2 ± 11.02	69.9 ± 1.56	85.27 ± 3.93	**0.000**	***	
	TiO_2	0.81 ± 0.07	1.99 ± 0.15	0.54 ± 0.02	0.16 ± 0.06	0.71 ± 0.08	1.39 ± 0.13	**0.000**	***	
	Al_2O_3	14.12 ± 1.35	4.91 ± 0.93	7.63 ± 0.20	4.54 ± 1.39	14.47 ± 1.89	5.41 ± 1.03	**0.000**	***	
	Fe_2O_3	5.79 ± 0.32	3.04 ± 0.32	2.76 ± 0.36	1.36 ± 0.4	4.79 ± 0.75	2.40 ± 0.52	**0.000**	***	
	MgO	0.61 ± 0.13	0.10 ± 0.03	0.69 ± 0.39	0.62 ± 0.02	0.86 ± 0.19	0.17 ± 0.08	**0.002**	**	
	MnO	0.04 ± 0.01	0.04 ± 0.01	0.08 ± 0.03	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	**0.045**	*	KW
	CaO	0.77 ± 0.51	0.23 ± 0.07	0.41 ± 0.06	23.45 ± 7.41	0.35 ± 0.06	1.25 ± 0.56	**0.009**	**	KW
	Na_2O	0.34 ± 0.06	1.00 ± 0.04	1.06 ± 0.19	0.4 ± 0.13	0.73 ± 0.15	1.14 ± 0.21	**0.000**	***	
	K_2O	1.49 ± 0.07	0.6 ± 0.07	1.44 ± 0.09	0.76 ± 0.25	2.39 ± 0.30	0.75 ± 0.12	**0.000**	***	
	P_2O_5	0.06 ± 0.02	0.03 ± 0.00	0.14 ± 0.02	0.04 ± 0.01	0.07 ± 0.01	0.02 ± 0.01	**0.000**	***	
Trace elements	Sc	16.67 ± 3.79	6.67 ± 1.15	6.67 ± 2.08	8.67 ± 2.31	14.67 ± 3.51	6.00 ± 2.00	**0.001**	***	
	V	139.67 ± 8.5	127.67 ± 5.86	49.67 ± 5.51	21.33 ± 11.5	108.67 ± 11.5	76.33 ± 20.55	**0.000**	***	
	Cr	107.00 ± 1.73	68.33 ± 9.87	41.67 ± 8.62	14.67 ± 4.04	53.00 ± 3.61	56.33 ± 13.58	**0.000**	***	
	Co	25.00 ± 2.65	11.33 ± 0.58	12.00 ± 1.00	3.00 ± 0.00	21.00 ± 2.65	7.67 ± 2.08	**0.000**	***	
	Ni	38.33 ± 4.62	9.67 ± 0.58	16.00 ± 1.73	14.67 ± 3.51	27.67 ± 3.79	11.00 ± 2.00	**0.000**	***	
	Cu	10.33 ± 2.08	4.67 ± 0.58	11.00 ± 2.00	4.00 ± 0.00	16.00 ± 1.73	6.33 ± 2.08	**0.000**	***	
	Zn	38.00 ± 1.73	19.00 ± 2.00	30.33 ± 6.66	16.67 ± 4.51	55.00 ± 6.08	16.00 ± 4.58	**0.000**	***	
	As	17.33 ± 0.58	5.00 ± 0.00	6.67 ± 3.21	12.00 ± 1.00	10.67 ± 2.08	6.00 ± 1.00	**0.000**	***	
	Rb	97.67 ± 7.77	35.67 ± 3.21	54.67 ± 7.37	29.33 ± 8.50	111.67 ± 12.66	38.00 ± 9.54	**0.000**	***	
	Sr	60.00 ± 8.19	67.00 ± 1.73	100.33 ± 18.01	188 ± 8.54	94.67 ± 8.62	84.67 ± 1.53	**0.000**	***	
	Y	28.33 ± 1.53	21.33 ± 1.15	20.00 ± 0.00	12.67 ± 1.15	27.33 ± 0.58	20.00 ± 5.29	**0.000**	***	
	Zr	382.67 ± 71.23	2086.67 ± 82.55	406.67 ± 31.09	97.33 ± 22.5	387.33 ± 58.07	1119 ± 83.91	**0.011**	*	KW
	Nb	11.33 ± 0.58	23.67 ± 0.58	8.67 ± 0.58	4.00 ± 1.00	11.33 ± 0.58	15.67 ± 2.08	**0.000**	***	
	Ba	308.00 ± 6.24	172.33 ± 11.72	338.33 ± 35.47	164.33 ± 32.50	367.67 ± 13.43	215.00 ± 26.46	**0.000**	***	
	Pb	14.00 ± 2.65	11.00 ± 2.65	6.00 ± 6.08	2.00 ± 0.00	14.33 ± 4.73	6.33 ± 3.21	**0.009**	**	
	Th	11.00 ± 0.00	13.00 ± 1.73	10.00 ± 1.00	8.33 ± 0.58	13.33 ± 0.58	10.00 ± 2.65	**0.006**	**	

***Figure A1**. Exposed soil layer at site D with scattered shell fragments. (Taken by Kristen Darker).*