Behavioural aspects of enzootic geophagy amongst large mammal herbivores

by

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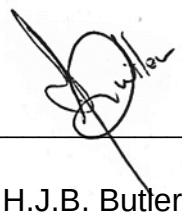
Declaration

I declare that the thesis submitted by me, H.J.B. Butler, in fulfilment of the requirements for the degree in Doctor of Philosophy 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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H.J.B. Butler Date

Abstract

Geophagy – the deliberate ingestion of soils by animals – is an unlikely yet widespread occurrence. Soil has low nutritional value, wears teeth, impedes digestion by impaction within the digestive tract, and, from an ecological view, congregation of animals at 'lick' sites may increase interspecific competition intensity and frequency of encounters with predators. In addition, it increases the risk of disease transmission. The widespread occurrence of geophagy in both herbivorous and carnivorous mammals, as well as insectivores, rodents, primates (including humans), and even birds and reptiles are thus a conundrum that must surely reflect that the benefits of soil consumption outweigh the many costs thereof. But the benefits are, for the most part, unresolved for large mammalian herbivores, thus current knowledge is insufficient to facilitate a detailed understanding of the trade-off. Suggested reasons for animals to practice geophagy are mainly divided into two concepts, either that soil consumption contributes mineral supplementation to the diet, or that clay in the digestive tract has detoxification properties, for example aiding in the precipitation of potentially harmful plant secondary compounds and/or intestinal parasites. Thus far, geophagy in natural settings has been limited largely to studies on single species, often single populations of those species, leading to varied interpretations. An objective source of data that encompasses variations in geophagy that occur across species and habitats is lacking.

In this study, geophagy amongst large mammal herbivore assemblages was approached across four habitat types in southern African savannas. These habitats are, in descending order of aridity, the Kalahari, Nama Karoo, Grassveld, and Bushveld habitats. A study of the physico-chemical, mineralogical, and geochemical properties of 'lick' sites frequently visited by herbivores, including laboratory analyses of elemental composition using XRD and XRF analyses, revealed few commonalities across habitats. Physical properties varied even within habitats, such that factors like soil colour - which has been suggested as a stimulus for geophagy, and cation exchange capacity (CEC), which did not differ between

ingested and non-ingested soils, appeared to be unimportant to herbivores. A high Ca content was observed in geophagic soils in arid habitats, implying possible supplementation of this mineral, but varying quantities of essential elements like Fe, Mg, K, Mn, P, Cr, Co, Zn, and Mo likely also play a role because they better explain the variance in frequency of soil consumption across habitats than Ca alone. In the Bushveld habitat, however, occurrence of kaolinite, a mineral commonly found in antacid medication, indicates that here soil consumption served more to relieve gastric disorders than to act as a mineral supplement. In a second study, these geochemical properties of soil were compared with similar assays applied to argillaceous dung pellets sampled in the vicinity of lick sites. These results showed lower-than-expected concentrations of some essential elements like Ca, Cr, Mg, Mo and Na, in dung pellets, but higher-than-expected levels of Co, Cu and K, suggesting that while herbivores are able to absorb some minerals from soil, others are precipitated. A negative relationship between parasite faecal egg load and soil concentration further supported the protection hypothesis of geophagic soil.

Relative frequency of geophagy across mammalian herbivore species, habitats, and seasons was evaluated based on recordings of site visits using camera traps. These data were based on 27 261 images representing 27 970 trap hours (1 222 trap days) across the sites and seasons, and included information for 24 herbivore species. In general, relative frequencies were higher in habitats dominated by grasses than in the Bushveld, a mixed tree/grass savanna, and the Nama Karoo, comprising a complex mixture of grass and dwarf karroid shrubs. However, this pattern varied across seasons depending on the habits of the dominant species in each. Browsers utilised geophagy sites more frequently in summer months, whereas grazers were more commonly encountered during autumn and winter. Interestingly, in the Bushveld, browsers practiced geophagy more often during autumn, and grazers more often during the spring. This “switch” suggests that phenological patterns in the vegetation – which are vastly different for woody plants that dominate the Bushveld compared with grasses that dominate elsewhere – play a role as a stimulus for soil consumption, with

animals turning to this resource when the nutritional value of their staple foods (browse or grass) declines. These observations support the supplementation hypothesis of geophagy. All species, irrespective of habitat and season, visited geophagy sites almost exclusively during daylight hours, minimizing the risk of predation by nocturnal apex predators like lion (*Panthera leo*). But activity times at different sites varied across species: generally low levels of temporal niche overlap between species suggest that competition for foraging at lick sites is mitigated by temporal niche partitioning.

Overall, this study presents quantitative data for geophagy and related aspects over a wider array of mammalian herbivores and habitats than most other investigations on geophagy. The results emphasized that geophagy is a regular, non-trivial dietary behaviour amongst large mammalian herbivores. They also highlight that soil consumption serves as both nutritional supplementation and protection, but that the relative intensities of these two mechanisms vary across habitats (and across seasons), as well as serving differently-adapted species (such as browsers and grazers) differently. Further studies tracking simultaneous changes in availability and nutritional quality of plant foods with the frequency of geophagy will give more context-dependent predictive insights into this behaviour. Similarly, in vitro and in vivo experimentation is still needed to fully understand the physiological implications of soil consumption. Since these are not feasible for most wildlife species, proxy-based approaches using dung pellet analyses, as presented in this study, hold some promise for investigation of benefits and banes of geophagy.

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Chapter 1: Introduction

Herbivores require nutrients to sustain all physiological functions on a daily basis. These nutrients can come from a variety of sources and can be obtained from water, energy, protein, vitamins, and minerals (McDowell 1985). Minerals, naturally occurring inorganic compounds that can break down into simpler structures or elements via chemical processes, are required for normal life sustaining processes although only some are essential to support adequate growth, reproduction and general heath throughout the life cycle. Of the 90 naturally occurring elements only 26 are known to be essential for animal life (McDonald et al. 2011). Eleven of these can be classified as major elements and are present in the animal's body in large quantities while the remaining 15 can be regarded as minor or trace elements as these are required in very small amounts for optimum bodily functions (McDowell 2003; McDonald et al. 2011; Cherian 2020).

Herbivores attain the bulk of their nutritional needs through the plant material they ingest. Since animals cannot synthesize minerals, the long-term maintenance of bodily mineral reserves is necessarily obtained from their diet (McDowell 2003). However, the species and composition of plants, growth stage and maturity of the plant, the type of soil, as well as climate and seasonal conditions are important factors that influence the mineral intake of such animals (McDonald et al. 2011). Furthermore, the capacity of forage to provide an adequate supply of minerals to herbivores depend on the mineral content of the plant as well as the bioavailability of minerals to the animal (Spears 1994). Bioavailability is the proportion of a nutrient that is absorbed, transported for cellular assimilation and converted to a biologically active form to be utilised physiologically (O'Dell 1984).

Conversely, plants obtain trace elements from the soil in which they grow. The forming of soil, and ultimately the amount of any element in the soil, is consequently associated with the geochemistry of the underlying rock from which the soil is formed. The underlying geology is therefore the definitive source of trace elements to herbivorous animals. In support of this,

many natural occurring mineral deficiencies livestock are associated with specific regions and are directly linked to geology and soil chemistry of such areas (McDonald et al. 2011).

Optimal foraging theory as described by Stephens and Krebs (1986), predicts that animals should apply foraging tactics whereby they balance maximum energy (nutritional) gains while reducing energetic losses associated with resource acquisition. This can be accomplished by adjusting diet composition for essential nutrients (Emlen 1966; MacArthur and Pianka 1966) and therefore, selecting food with above-threshold levels of minerals (Ceacero et al. 2009). Several studies indicated that animals have the ability to detect some minerals in the contents of food sources and thereby modify their feeding behaviour (Weeks and Kirkpatrick 1976; McNaughton 1988; 1990) or regulate their consumption according to their nutritional need of specifically calcium (Ca) to phosphorus (P) ratio to some extent (Chládek and Zapletal 2007; Villalba et al. 2008). According to McNaughton (1988; 1990) the migration patterns observed in African ungulates is based primarily on the availability of primarily sodium (Na) but he also speculates on the influence that chemical elements including aluminium (Al), Ca, iron (Fe), magnesium (Mg) and P might have on such behaviour. This process of nutritional perception of animals as defined by Richter (1943) has been refuted by opposing results that animals cannot detect the nutritional value of food sources (Muller et al. 1977; McDowell 1985; 1996) when applied to minerals other than Na and P. However, several studies indicated that minerals including Ca, Fe, Mg and zinc (Zn) in forage might be pursued by ungulates during feeding (Seagle and McNaughton 1992). This selection of certain elements by herbivores was demonstrated during free-choice feeding experiments (Barrows 1977) and in support of this, Mahaney and Krishnamani (2003) emphasize that animals have an innate ability to explore and taste the chemically hostile environment in which they live. With reference to geophagy, Pebsworth et al. (2012) and Pebsworth et al. (2021) demonstrated that animals have preferences to certain soils that they consume deliberately which indicates that they can discriminate differences in soil composition.

The concept of optimal foraging theory is however more nuanced than merely the selection of specific food sources. In this context, optimizing means balancing maximum energy (nutritional) gains while reducing energetic losses associated with resource acquisition. Many authors, including Calef and Lortie (1975), Salter and Pluth (1980), Kreulen (1985), Mahaney and Krishnamani (2003), Bravo et al. (2012), Pebsworth et al. (2019), to name a few, have reported on the deliberate consumption of soil among herbivores animals. The intentional ingesting of soil, geophagy, is a widespread behaviour among many animals and has been documented for various animal species including humans. Regarding animals, literature on geophagy has been reported on animal groups including reptiles (Sokol 1971; Marlow and Tollestrup 1982; Beyer et al. 1994; Esque and Peters 1994; Rich and Talent 2009), birds (Diamond et al.1999; Gilardi et al. 1999; Downs et al. 2019), marsupials (Best et al. 2013), nonhuman primates (Hladik 1977; Oates 1978; Mahaney 1987; Davies and Baillie 1988; Krishnamani et al. 2000; Mahaney et al. 1995; Pebsworth et al. 2019), and humans (Abrahams and Parsons 1996, Young et al. 2008, Young 2010, Young 2011, Young et al. 2011). Literature on geophagy amongst mammals (Table 1.1) clearly indicate that this behaviour is not limited to herbivores only, but is a phenomenon that also occur amongst carnivores, insectivores and even rodents.

Enzootic geophagy has been observed in many parts of the world and in climates ranging from temperate, to dry, wet, arctic and montane areas (Kreulen and Jager 1984). However, it appears to be particularly common in sub-Saharan Africa (Kutalek et al. 2010). Although numerous incidents of geophagy have been reported, detailed geophysical descriptions of geophagy sites are not always disclosed. Geophagy sites can be located on mountains (Schaller 1967), exposed cliff faces, or riverbanks (Diamond 1999; Mee et al. 2005) while the preferred soil types can vary from dry soils to clay and mud (Slabach et al. 2015). Geophagy sites generally occur in areas barren of vegetation where surficial geology has been exposed by either erosion (Klaus et al. 1998; Lee et al. 2010) or anthropogenic clearings like roads (Matinata and Perrella 2020). Reports were also made of the utilisation of termitaria

Table 1.1. *List of mammals, excluding nonhuman primates, of currently available accounts that practise geophagy.*

Order Family ***Genus and species***	**Common name**	**Reference**
Order Artiodactyla		
Family Bovidae		
Aepyceros melampus	Impala	Stephenson et al. 2011
Alcelaphus buselaphus	Hartebeest	Parris 1976
Alcelaphus buselaphus major	Western hartebeest	Ajayi and Ogunjobi 2015
Antilope cervicapra	Blackbuck	Groves and Leslie 2011
Bison bison	Bison	Tracy and McNaughton 1995
Bos gaurus	Gaur	Groves and Leslie 2011
		Zangmo et al. 2018
Bos indicus	Cattle	Mills and Milewski 2007
Bos mutus	Yak	Groves and Leslie 2011
Bos primigenius	Caucasian aurochs	Panichev et al. 2014
Budorcas taxicolor	Golden takin/mishmi takin	Nowak 1999
		Groves and Leslie 2011
Budorcas tibetana	Sichuan takin	Groves and Leslie 2011
Budorcas whitei	Bhutan takin	Groves and Leslie 2011
Capra caucasica	Tur	Groves and Leslie 2011
		Panichev et al. 2014
Capra cylindricornis	Daghestan tur	Groves and Leslie 2011
Capra hircus	Goat	Mills and Milewski 2007
Capra sibirica	Siberian ibex	Groves and Leslie 2011
Cephalophus nigrifrons	Black-fronted duiker	Groves and Leslie 2011
Cephalophus rufilatus	Red-flanked duiker	Groves and Leslie 2011
Connochaetes taurinus	Blue wildebeest	Parris 1976
Gazella christii	Gujarat chinkara	Groves and Leslie 2011
Hippotragus niger	Southern sable antelope	Groves and Leslie 2011
		Stephenson et al. 2011
		Baptista et al. 2013
Kobus kob kob	Buffon's kob	Groves and Leslie 2011
		Ajayi and Ogunjobi 2015
Oreamnos americanus	N. American mountain goat	Nowak 1999
		Ayotte et al. 2008
		Groves and Leslie 2011
		Kroesen et al. 2020
Oreotragus oreotragus	Cape Klipspringer	Groves and Leslie 2011

(Table 1.1 continue)

Order

Family

Genus and species	**Common name**	**Reference**
Oryx dammah	Scimitar-horned oryx	Groves and Leslie 2011
Oryx gazella	Gemsbok	Paris 1976
Ourebia montana	Sudan oribi	Groves and Leslie 2011
Ovis canadensis	Bighorn sheep	Holl and Bleich 1987
		Groves and Leslie 2011
Ovis dalli	Dall's sheep/ (stone's sheep)	Ayotte et al. 2008
		Groves and Leslie 2011
Philantomba congica	Western blue duiker	Groves and Leslie 2011
Rupicapra r. caucasica	Caucasian chamois	Panichev et al. 2013
Sylvicapra grimmia	Grey duiker	Nowak 1999
		Groves and Leslie 2011
		Stephenson et al. 2011
Syncerus caffer	Cape buffalo	Mills and Milewski 2007
		Groves and Leslie 2011
		Stephenson et al. 2011
Tragelaphus angasii	Nyala	Stephenson et al. 2011
Tragelaphus eurycerus	Bongo	Klaus-Hügi et al. 1999
		Groves and Leslie 2011
Tragelaphus scriptus	Bushbuck	Mills and Milewski 2007
		Stephenson et al. 2011
		Ajayi and Ogunjobi 2015
Tragelaphus strepsiceros	Greater kudu	Stephenson et al. 2011
Redunca fulvorufula	Mountain reedbuck	Stephenson et al. 2011
Family Camelidae		
Camelus bactrianus	Bactrian camel	Franklin 2011
Family Cervidae		
Axis axis	Axis deer	Moe 1993
Alces alces	Moose	Klaus-Hügi et al. 1999
		Ayotte et al. 2008
		Stepanova et al. 2017
Dama dama	Feral fallow deer	Best et al. 2013
Cervus canadensis	Elk	Jokinen et al. 2016
Cervus elaphus	Elk/wapiti	Ayotte et al. 2008
		Panichev et al. 2014
	Sika deer	Li et al. 2018
Cervus duvauceli	Barasingha	Moe 1993
Cervus unicolor	Sambar deer	Matsubayashi et al. 2007

(Table 1.1 continue)

Order

Family

Genus and species	**Common name**	**Reference**
		Matsuda et al. 2014
Mazama americana	Red-brocket deer	Montenegro 2004
		Tobler 2008
		Tobler et al. 2009
		Blake et al. 2011
		Griffiths et al. 2020
Mazama gouazoubira	Grey-brocket deer	Tobler et al. 2009
		Griffiths et al. 2020
Mazama rufina	Little red brocket	Mattioli 2011
Muntiacus muntjak	Muntjac/barking deer	Moe 1993
Odocoileus hemionus	Mule deer	Knight and Mudge 1967
		Jokinen et al. 2016
Odocoileus virginianus	White-tailed deer	Knight and Mudge 1967
		Wiles and Weeks 1986
		Atwood and Weeks 2002
		Jokinen et al. 2016
Rangifer tarandus groenlandicu	Caribou	Heard and Williams 1990
Family Giraffidae		
Giraffa camelopardalis	Giraffe	Skinner and Mitchell 2011
Okapia johnstoni	Okapi	Skinner and Mitchell 2011
Family Suidae		
Babyrousa babyrussa	Barbirusa	Clayton and MacDonald 1999
Hylochoerus meinertzhageni	Giant forest hogg	Nowak 1999
Phacochoerus aethiopicus	Cape warthog	Henshaw and Ayeni 1971
Sus barbatus	Bearded pig	Matsuda et al. 2014
Sus scrofa	Wild boar	Moe 1993
Family Tayassuidae		
Catagorus wagneri	Chacoan peccary	Taber et al. 2011
Pecari tajacu	Collared peccary	Montenegro 2004
		Tobler 2008
		Tobler et al. 2009
		Blake et al. 2011
		Griffiths et al. 2020
Tayassu pecari	White-lipped peccary	Emmons and Stark 1979
		Montenegro 2004

(Table 1.1 continue)

Order Family ***Genus and species***	**Common name**	**Reference**
		Tobler 2008
		Tobler et al. 2009
		Blake et al. 2011
Family Tragulidae		
Hyemoschus aquaticus	Water chevrotain	Meijaard 2011
Order Carnivora		
Family Felidae		
Panthera tigris tigris	Bengal tiger	Schaller 1967
		Moe 1993
Felis chaus	Jungle cat	Moe 1993
Puma concolor	Puma	Blake et al. 2011
Leopardus pardalis	Ocelot	Blake et al. 2011
Leopardus wiedii	Margay	Blake et al. 2011
Family Herpestidae		
Herpestes edwardsii	Indian grey mongoose	Moe 1993
Herpestes auropunctatus	Small indian mongoose	Moe 1993
Family Procyonidae		
Nasua nasua	Ring-tailed coati	Blake et al. 2011
		Griffiths et al. 2020
Procyon cancrivorus	Crab-eating raccoon	Blake et al. 2011
		Griffiths et al. 2020
Family Ursidae		
Ursus arctos	Brown bear	Seryodkin et al. 2016
Ursus arctos horribilis	Grizzly bear	Mattson et al. 1999
Family Viverridae		
Aonyx sp	Otter	Matsuda et al. 2014
Paradoxurus hermaphroditus	Palm civet	Moe 1993
Vierricula indica	Lesser oriental civet	Moe 1993
Order Chiroptera		
Family Phyllostomidae		
Artibeus obscurus	Dark fruit-eating bat	Voigt et al. 2008.
Carollia perspicillata	Seba's short-tailed bat	Voigt et al. 2008.
Order Cingulata		
Family Dasypodidae		
Dasypus novemcinctus	Nine-banded armadillo	Blake et al. 2011
		Griffiths et al. 2020
Priodontes maximus	Giant armadillo	Blake et al. 2011

(Table 1.1 continue)

Order

Family

Genus and species	**Common name**	**Reference**
Order Didelphimorphia		
Family Didelphidae		
Didelphis marsupialis	Common opossum	Blake et al. 2011
Order Diprotodontia		
Family Macropodidae		
Macropus giganteus	Eastern grey kangaroo	Best et al. 2013
Table 1.1. (Continued)		
Macropus robustus robustus	Eastern wallaroos	Best et al. 2013
Macropus rufogriseus	Red-necked wallabies	Best et al. 2013
Wallabia bicolor	Swamp wallabies	Best et al. 2013
Order Perissodactyla		
Family Equidae		
Equus asinus	Feral donkeys	Freeland and Choquenot 1990 Mills and Milewski 2007
Equus caballus	Horse	Salter and Pluth 1980 Rubenstein 2011
Equus quagga	Plains zebra	Stephenson et al. 2011
Equus zebra zebra	Cape mountain zebra	Penzhorn 1982 Stephenson et al. 2011
Family Rhinocerotidae		
Diceros bicornis	Black rhinoceros	Ayeni 1979
Dicerorhinus sumatrensis	Sumatra rhinoceros	Dinerstein 2011
Ceratotherium s. simum	Southern white rhinoceros	Stephenson et al. 2011
Rhinoceros sondaicus	Javan rhinoceros	Dinerstein 2011
Rhinoceros unicornis	Greater one-horned rhinoceros	Moe 1993 Dinerstein 2011
Family Tapiridae		
Tapirus pinchaque	Mountain tapir	Medici 2011
Tapirus terrestris	Lowland tapir	Montenegro 2004 Mills and Milewski 2007 Tobler 2008 Tobler et al. 2009 Blake et al. 2011 Medici 2011 Link et al. 2012 Griffiths et al. 2020

(Table 1.1 continue)

Order Family ***Genus and species***	**Common name**	**Reference**
Order Pholidota		
Family Manidae		
Manis temminckii	Ground pangolin	Gaubert 2011
Order Pilosa		
Family Choloepodidae		
Choloepus didactylus	Linnaeus's two-toed sloth	Griffiths et al. 2020
Family Megalonychidae		
Choloepus hoffmanni	Hoffmann's two-toed sloth	Blake et al. 2011
Family Myrmecophagidae		
Tamandua tetradactyla	Southern tamandua	Blake et al. 2011
Order Proboscidea		
Family Elephantidae		
Loxodonta africana	African elephant	Houston et al. 2001 Holdø et al. 2002 Mills and Milewski 2007 Kalumanga et al. 2016
Loxodonta cyclotis	African forest elephant	Klaus et al. 1998 Wittemyer 2011
Elephas maximus	Asian elephants	Chandrajith et al. 2009 Matsuda et al. 2014
Order Rodentia		
Family Caviidae		
Hydrochoerus hydrochaeris	Capybara	Mills and Milewski 2007
Family Cuniculidae		
Agouti paca	Paca	Montenegro 2004
Cuniculus paca	Lowland paca	Blake et al. 2011 Link et al. 2012 Griffiths et al. 2020
Family Dasyproctidae		
Dasyprocta fuliginosa	Black agouti	Montenegro 2004 Blake et al. 2011 Griffiths et al. 2020
Myoprocta pratti	Green acouchi	Blake et al. 2011
Family Echimyidae		
Proechimys sp.	Spiny rat	Montenegro 2004 Blake et al. 2011

(Table 1.1 continue)

Order Family ***Genus and species***	**Common name**	**Reference**
Echimys saturnus	Dark spiny tree-rat	Blake et al. 2011
Family Erethizontidae		
Coendou prehensilis	Brazilian porcupine	Montenegro 2004 Blake et al. 2011
Family Hystricidae		
Hystrix brachyura	Malayan porcupine	Matsuda et al. 2014 Griffiths et al. 2020
Family Sciuridae		
Sciurus igniventris	N. Amazon red squirrel	Blake et al. 2011
Order Tubulidentata		
Family Orycteropodidae		
Orycteropus afer	Aardvark	Taylor 2011

(Baptista et al. 2013; Kalumanga et al. 2016) and even mud nests of insects (Hunter 1984) for the purpose of soil consumption.

Several functions have been attributed to geophagy across vertebrate taxa. The variations in the utilisation of soil locality and soil type can be explained by species-specific periods of mineral imbalances and deficiencies but might also be as a result of variation in nutrient availability in dietary forage (Jones and Hanson 1985; Kreulen 1985; Knight et al. 1988; Eksteen and Bornman 1990; Ayotte et al. 2008). Geophagy may also maintain homeostasis between major minerals in the physiology of herbivores with a change in availability and nutrition of forage during the early wet season, dry season or in early spring (Langman 1978; Fraser and Reardon 1980; Kreulen 1985; Moe 1993). Studies have also emphasised that minerals in lick soils may support the seasonal demands of calving (Tankersley and Gasaway 1983) as well as the following period of lactation (Fraser and Reardon 1980; Tankersley and Gasaway 1983; Moe 1993; Holdø et al. 2002). Minerals in lick soils also contribute in the growing process of antlers (Fraser and Reardon 1980) as well as horns, tusks and skeletal bones (Henshaw and Ayeni 1971).

However, the deficiencies and/or change in nutritional value of forage might not be the only reason why herbivores ingest soil. Soil may also be consumed as a method to alleviate gastrointestinal ailments (Vermeer and Ferrell 1985; Mahaney et al. 1993; 1996) and geophagic soil can replenish the loss of minerals during times of diarrhoea (Herbert and Cowan 1971). Furthermore, lick soil can prevent or remedy forestomach acidosis (Davies and Baillie 1988) as well as metabolic acidosis (Kreulen 1985; Knight et al. 1988; Melendez et al. 2007), a status defined by a decrease in bicarbonate and pH levels in the blood of ruminants (Hernández et al. 2014).

Soil, especially that with a high clay content, is reported to adsorb secondary plant metabolites like tannins and alkaloids (Kreulen 1985; Knight et al. 1988; Johns and Duquette 1991; Gilardi et al. 1999; Ta et al. 2018; Dornan and McCabe 2020) which can decrease protein digestion in vertebrate herbivores (Barbehenn and Constabel 2011; Dornan and McCabe 2020). Clay can also adsorb other damaging compounds and bacteria (Ta et al. 2018) and strengthen the epithelium of the gastrointestinal tract as protection against secondary plant metabolites as well as other pathogens and harmful chemicals (Mahaney et al. 1993; Gilardi et al. 1999). Geophagic clay can also attract and destroy the cell membrane of bacterial cells (Papaioannou et al. 2005). According to Ketch et al. (2001) the reason behind the behaviour of geophagy might even be to sustain the microbial fauna in the alimentary canal and thereby support digestive properties. Geophagy may also lead to the reduction or ultimately the elimination of intestinal endoparasites (Kreulen 1985; Klaus et al. 1998; Knezevich 1998; Krishnamani and Mahaney 2000; Papaioannou et al. 2005).

Apart from nutritional and medicinal benefits, geophagy provides mechanical support for birds and reptiles in the digestion process during the maceration of ingested food particles (Dib et al. 2001; Brightsmith and Muñoz-Najar 2004; Downs et al. 2019) but no literature that support the same benefit for other herbivore species could be found. However, the principle of parsimony might explain the deliberate ingestion of soil. According to Krishnamani and Mahaney (2000) the eating of soil might suppress hunger during famine times and that the

smell of wet soil, enhanced by clay, salts or lime, or even organic matter may stimulate geophagy in primates and may also taste good (Krishnamani and Mahaney 2000). Ultimately, geophagy may only be a behavioural tradition with no real nutritional significance (Mahaney et al. 1990) or might even have no proximate purpose at all (Krishnamani and Mahaney 2000). However, a hypothesis for zero benefit is very unlikely given the many risks and costs associated with geophagy.

Apart from the benefits that geophagy provide, several costs towards the deliberate ingestion of soil were identified. The search for and travel over long distances to geophagy sites is subjected to an investment of energy (Wiles and Weeks 1986; Klein and Thing 1989; Stephenson et al. 2011) which could have been directed towards other activities such as foraging (Wiles and Weeks 1986; Klein and Thing 1989). Repeated use of geophagy sites may also create a piosphere effect, whereby animals congregate at these sites regularly (much like they do at waterholes), which in turn attracts predators and therefore increases predation risk (Henshaw and Ayeni 1971; Moe 1993; Rawson and Bach 2011; Fack et al. 2020). Aggregations of high numbers of animals that visit geophagy sites also increase the likelihood of transmission of disease and parasites (Henshaw and Ayeni 1971; Abrahams and Parsons 1996; Pebsworth et al. 2012) and animals that ingest soil may also be exposed to the uptake of toxicological contaminants in the soil (Rich and Talent 2009; Kutalek et al. 2010). Soil from geophagy sites with a high sand fraction might also lead to excessive tooth wear (Barker 2005; Martinelli et al. 2013). Prolonged or regular consumption of soil may also cause a blockage of the alimentary canal, a condition commonly referred to as sand impaction. The prevalence of sand impaction depends on the frequency of visits to geophagy sites, the amount of soil that is ingested during visits as well as the rate at which soil passes through the alimentary canal to be excreted. Several cases of sand impaction have been reported for different animal species including ostriches (*Struthio camelus*) in Botswana (Mushi et al. 1998), a one-month-old alpaca (*Lama pacos*) in Canada (Abutarbush and Petrie 2006), a giraffe calf (*Giraffa camelopardalis*) in Nigeria (Jegede et al. 2016), postpartum dairy cows in

Florida, United States of America (Melendez et al. 2007) as well as in horses (*Equus caballus*) in Finland (Niinistö and Sykes 2021).

That the occurrence of geophagy is almost certainly a non-random event that carries with it definite benefits to the animal is emphasized by the large amounts of time certain animals spend on this behaviour. For example, in a study on the geophagic behaviour of elephants (*Loxodonta africana*) in Hwange National Park (Zimbabwe), Holdø et al. (2002) reported that female elephants spent a higher percentage of their time in utilising licks sites than drinking water or even feeding. Furthermore, in comparison with male elephants, females spent a greater portion of their activity budget on the consumption of soil than males (Holdø et al. 2002). Although many researchers mentioned the differences in seasonal visitations to geophagy sites between male and female animals (example Fraser and Reardon 1980; Tankersley and Gasaway 1983; Moe 1993; Atwood and Weeks 2003; Ayotte et al. 2008; Ping et al. 2010; Pebsworth et al. 2012, Jokinen et al. 2016; Li et al. 2018; Griffiths et al. 2020), aspects on geophagy of non-primate large mammalian herbivores are limited to only a few species of mainly Cervidae and all such studies were confined to the northern hemisphere.

In a review of geophagy amongst primates, Pebsworth et al. (2019) showed a pattern in the geographical distribution of the occurrence of geophagy. This review showed that almost a third (32.4%) of the accounts were from Asia, a quarter (25.0%) from the Neotropics, almost a quarter (24.3%) were from Africa, and the rest (18.3%) were records from Madagascar (Pebsworth et al. 2019). For large mammalian herbivores, demonstrating a similar pattern from the available literature is difficult, since most studies do not mention the precise location of the behaviour. Nevertheless, at a very broad spatial scale, the most frequent occurrence of geophagy amongst herbivores appears to be sub-Saharan Africa (Fig. 1.1). This may be because of the large diversity of herbivores in Africa, but also the diversity of habitats that can be exploited by these animals.

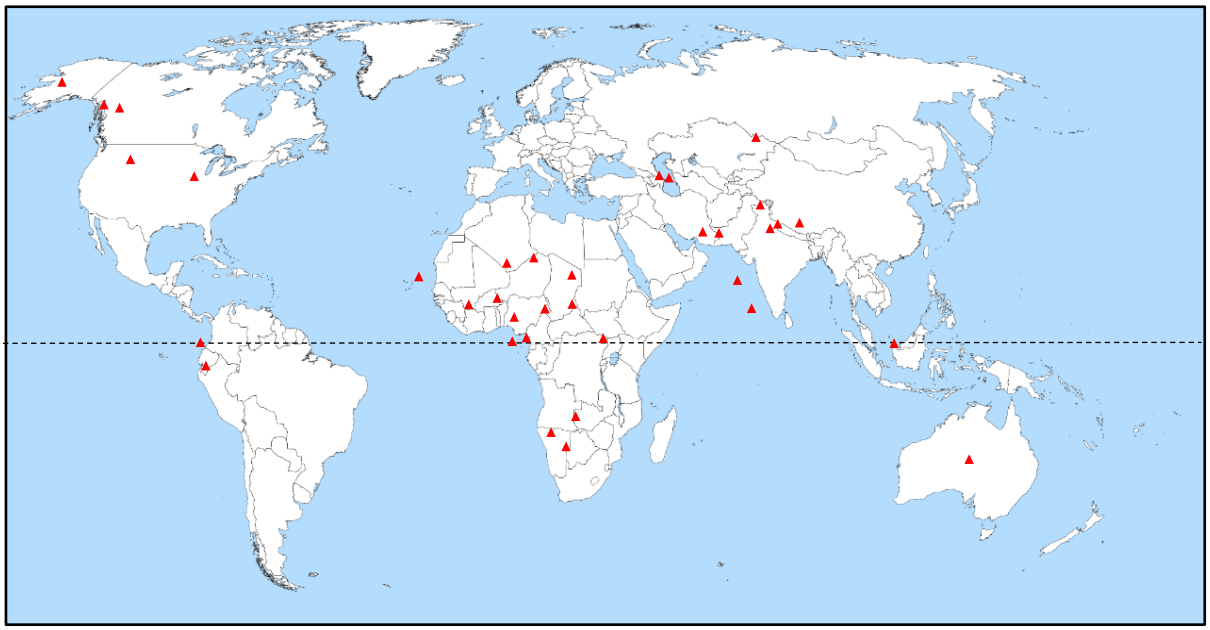

Figure 1.1*. Global distribution of mammals listed in Table 1.1. that practise geophagy and where the localities were disclosed.*

The lack of detailed information about variations in the occurrence of geophagy across herbivore species, seasons, habitats, and even between individuals of different sex and age classes, makes it difficult to resolve the factors that underly this behaviour. In southern Africa, the extensive occurrence of wildlife across different types of protected areas offers the opportunity to fill this knowledge gap. According to Statistics South Africa (2021) officially protected land in South Africa accounted for 11 280 684 ha (112 807 km^2) which is larger than countries such as Portugal and Denmark. This area represents 4.1% of mainland South Africa and is expanded in all provinces and in all biomes across South Africa. Nature reserves made up 44.5% of the total protected areas while the 19 National Parks contribute 37.4% to the protected area estate of South Africa (Statistics South Africa 2021). Apart from officially protected areas, the private sector also contributes to the protection and preservation of not only wildlife species, but also ecosystems (Parker et al. 2020). However, all these areas of conservation are enclosed and can be described as island parks which limit migration of animals over large areas. Animals are therefore confined and are dependent on forage in relatively small areas. In order to coexist in restricted areas large herbivore mammals must

exploit all possible resources including mineral licks for nutrition. Furthermore, to minimise competition for food, resource partitioning among African ruminants make coexistence possible (Estes 1991).

An investigation into the behavioural aspects of geophagy in different habitats, where animals compete not only for forage but also for soil minerals, will elucidate both the biophysical factors that stimulate this behaviour, as well as the role of geophagy in resource partitioning and multispecies coexistence. The goal of this study was to investigate and compare the frequency occurrence of geophagy amongst different large herbivore species distributed over a spatio-seasonal gradient. This includes a comparison across four different habitat types within the central interior of southern Africa, namely (in descending levels of aridity) Kalahari, Nama Karoo, Grassveld, and Bushveld.

By examining of the “what”, “who” and “when” conundrum of geophagia on a broader scale, might elucidate on the “why” of this ubiquitous behaviour among large mammalian herbivores. The first objective of this study was to try and answer the “what” question by determine whether Na, or possibly a different suite of elements, may elicit geophagy by large mammalian herbivores in diverse habitats in southern Africa. This includes a comprehensive description of the physiochemical, mineralogy and geochemistry of known, and newly discovered geophagic soil in these habitats. This was done by means of laboratory analyses of the soil including X-Ray Diffraction (XRD) and X-Ray Fluorescence (XRF). Argillaceous dung pellets of different Bovidae species that were found at the geophagy sites, were also included in the XRD AND XRF analyses.

A second objective was to answer the “who” and “when” questions by generating a statistically robust dataset of animals representing browsers, intermediate-feeders and grazers, of various body sizes, different age and sex classes in different habitats over four seasons that practice geophagia. This was done by means of camera trap photography which proof to be an efficient for mammal inventories. The use of heat-motion sensors camera traps in diverse habitats over all seasons, allows for the monitoring of geophagy site visitation on

taxonomic, spatial, and temporal scales in a way that previous studies could not achieve. This will fill the existing knowledge gap on geophagy amongst large mammalian herbivores, at least partially.

With seasonal changes in nutritional value of plants, and the consequent seasonal change in food selection by herbivores, it is expected that seasonal changes in frequency of geophagy will occur. It is expected that the presence of chemical elements and minerals, which are essential for maintaining homeostasis for optimum bodily functions on a daily basis, will be present in geophagic soil. Indeed, if geophagy act primarily as a way to supplement nutritional requirements, then one might expect higher rates to occur during limiting periods like the dry season. Differences in frequency of geophagy between males and females during times of different physiological states, might also be indicative of mineral supplementation required during specific times of the year including pregnancy, parturition and lactation. On the other hand, lack of seasonal change may indicate factors other than supplementation. Differences between food sources on a diet niche scale ranging from browsers to grazers, might evoke different stimuli for geophagia other than mineral supplementation, and therefore a different pattern in geophagia is expected.

1.1 Dissertation outline

In Chapter 1 an introduction was presented about the rationales behind geophagy, with a list of mammals that have been reported on to consume soil. Knowledge gaps in our understanding of geophagy was also identified. Chapter 2 will provide a description of all four study areas as well as detailed information on each geophagy site under investigation in the study areas. This includes information on the location, climate, a list of mammalian herbivores that occur in the areas, as well as a brief description of the geological setting of each study site. Chapter 3 will focus on geochemical analyses of geophagic soil chemical elements as well as minerals that might be the driving force behind geophagy at each lick site. Principal component analyses (PCA) were used to identify possible chemical elements and minerals to answer the question of “what” animals ingest when they practice geophagy. Chapter 4

presents analyses of argillaceous dung pellets including minerals and nutritional elements that might be of importance to consumers in geophagic soil. The prevalence of parasite eggs in the dung pellets are also discussed. In Chapter 5 the comprehensive data set of 25 827 camera trap images of 27 261 large mammalian herbivores representing 24 species that were recorded over a six years (1 222 trap days and 27 970 trap hours) period was analysed. Visitation rates were compared using a general linear model (LM) and to compare patterns of peak activity time, and of temporal niche overlap, across habitats and seasons, two-factor crossed-design LMs were used. Visitation frequency of females with males were compared using a generalized linear mixed model (GLMM) with a binomial distribution and logit link function. Chapter 6 summarises the dissertation and pose questions for future research on geophagy among large mammalian herbivores.

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Chapter 2: Study areas and study sites

Fieldwork was carried out in protected wildlife areas of two countries, Botswana and the Republic of South Africa, at the southern tip of the African continent. Four diverse study areas, one in Botswana and three in South Africa, were included. Approval for this study was granted by the Animals Ethics committee of the University of the Free State (No. UFS-AED2011/02). Research permits were obtained for all four study areas before fieldwork commenced. This included a research permit (EWT 8/36/4 XII.33) for the Kalahari Wildlife Management Area (Kgalagadi district No.12), north of Mabuasehube Game Reserve in Botswana, as well as Tussen-die-Riviere Game Reserve (permit number 01/13010) and Willem Pretorius Game Reserve (permit number 01/24081), both in the Free State Province, and Loskop Dam Nature Reserve (permit butler1203.1), Mpumalanga Province of South Africa. As shown in Fig. 2.1 the areas represent different ecoregions namely the Kalahari Xeric Savanna, Nama Karoo, Highveld Grassland and southern African Bushveld (Olson et al. 2001), all within the broad summer rainfall zone of the interior (Chase and Meadows 2007).

2.1 Kalahari Wildlife Management Area

2.1.1 General overview

The Kalahari Wildlife Management Area (Kgalagadi district No.12), covering an area of 88 100 ha, is situated directly north of the Mabuasehube Game Reserve which, in turn, forms part of Botswana's much larger (3 725 600 ha) Kgalagadi Transfrontier Park (Fig. 2.2). Previously (1986) the Wildlife Management Areas in Botswana were established to support wildlife-based economic activities and to secure migratory corridors linking the south-western Kalahari to the north-eastern Central Kalahari Game Reserve (Twyman 2001). Amalgamated with the former Kalahari Gemsbok National Park of South Africa in 2000 (Thondhlana et al. 2011), the international Kgalagadi Transfrontier Park accounts for an area of 4 013 700 ha where animals can roam freely without any restrictions by fences.

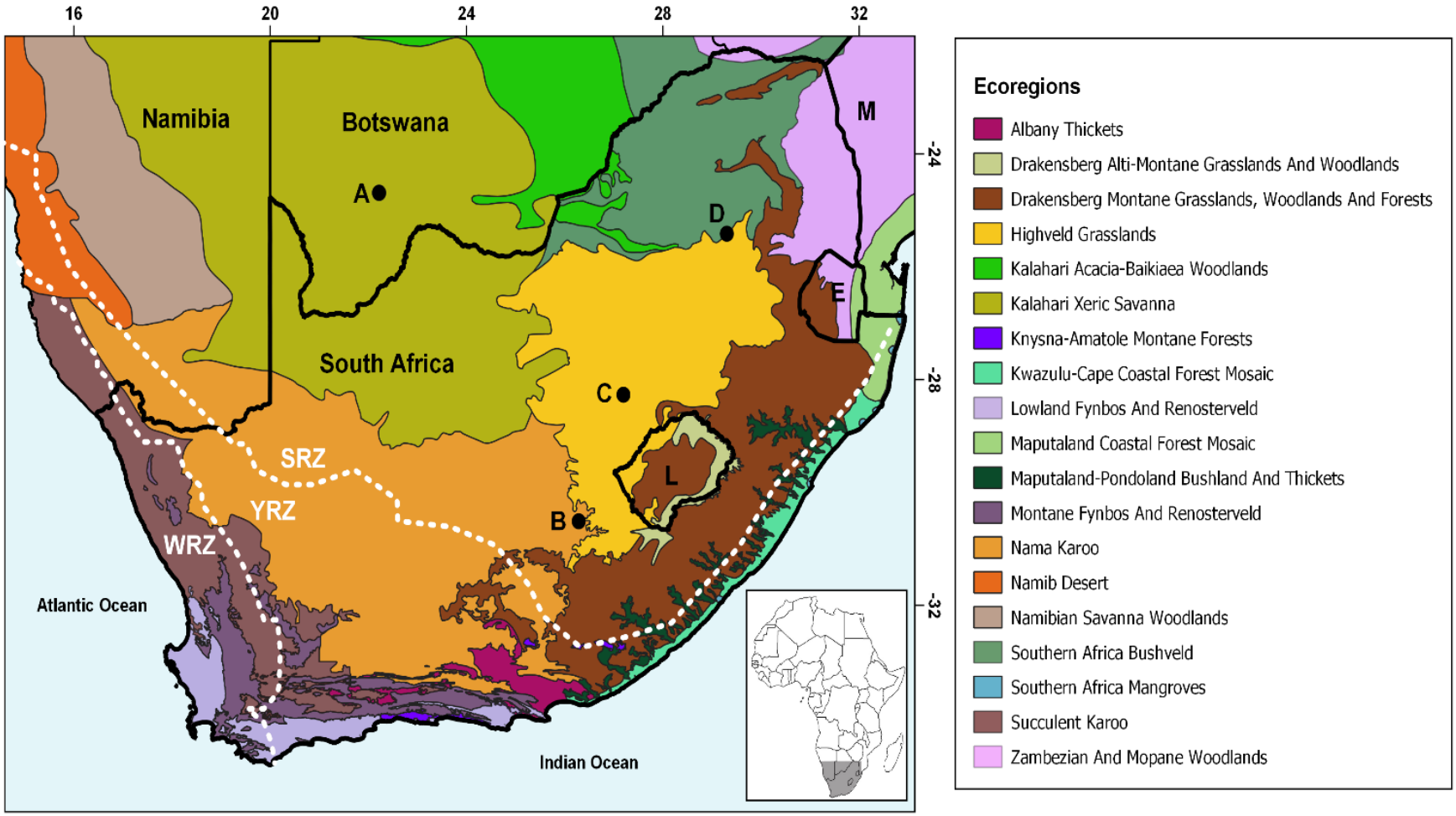

Figure 2.1. *Location of study areas in Botswana and South Africa relative to the classification of ecoregions as described by Olson et al. (2001). Dashed white lines demarcate the different rainfall zones as defined by Chase and Meadows (2007). SRZ, WRZ and YRZ indicate summer, winter and year-round rainfall zones respectively. Study sites: A, Jack's Pan in the Kalahari Wildlife Management Area; B, Tussen-die-Riviere Game Reserve; C, Willem Pretorius Game Reserve; D, Loskop Dam Nature Reserve. E., Eswatini (formerly known as Swaziland); L, Lesotho; M, Mozambique.*

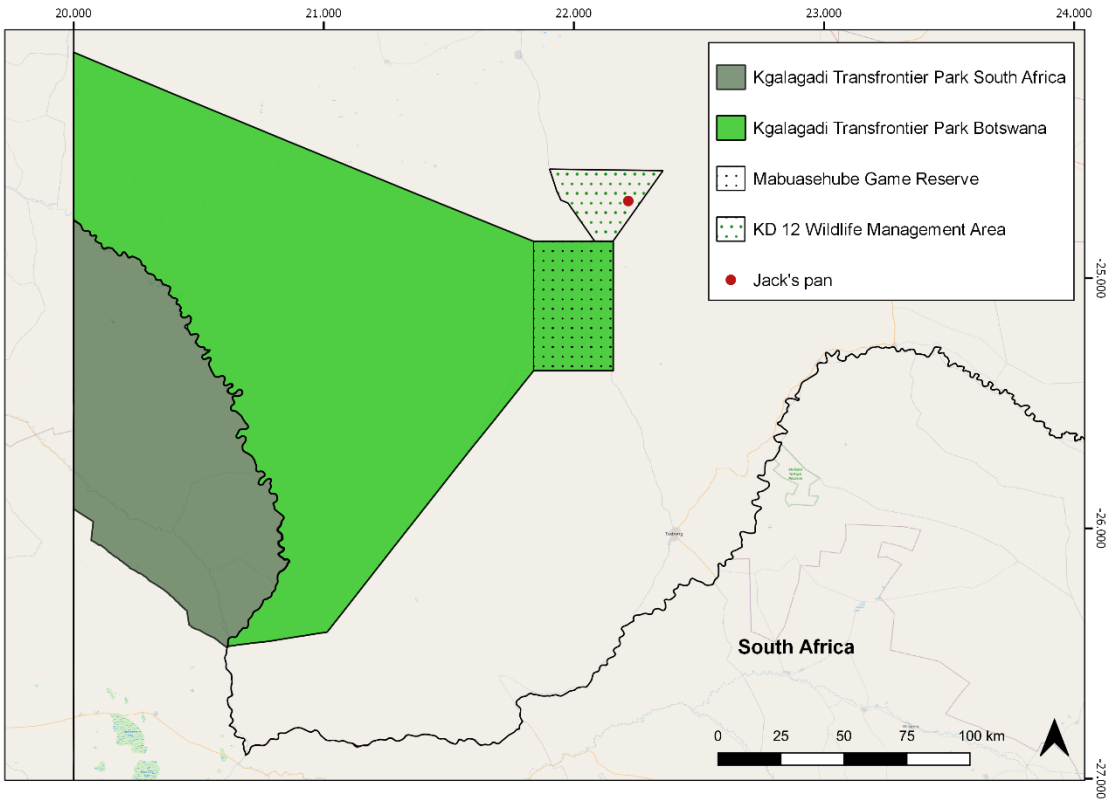

***Figure 2.2**. Location of the study site, Jack's Pan (red circle) in the Kgalagadi district No.12 Wildlife management area and adjacent to Mabuasehube Game Reserve of the south-western Kalahari Desert (Botswana).*

The Kalahari is a vast, sand-covered plain with no noticeable variation in topography and relatively very few rocky outcrops (Parris 1984). Numerous pans, varying from small depressions to relative deep catchment areas roughly 15 m below the surrounding sandy surface, are scattered throughout the region (Parris 1984). Such pans usually have a well-developed dune on the leeward side (Parris and Child 1973). Jack's Pan, one of the largest pans in the study area, served as the main research site. Located at -24.690643º, 22.222403º (*vide* Fig. 2.2) at an altitude of 1 061 m above sea-level, it is situated approximately 18 km north of the Mabuasehube Game Reserve (Fig. 2.2) where borehole water is almost permanently available to wildlife.

In general, the Kalahari arid savanna experiences a short summer rainfall pattern with annual precipitation ranging from 170 to 400 mm (Jeltsch et al. 1997) and daily temperature

from -10 to 45 °C (Van Rooyen et al. 1990). Three distinct seasons, hot and wet (January - April), cold and dry (May - August) and hot and dry (September - December), are also implicated (Mills and Retief 1984; Van Rooyen and Van Rooyen 1998). As shown in Fig. 2.3 this is substantiated by the climatological data obtained from the Bosobogolo Rest Camp, approximately 62 km south-west of the Kalahari study area.

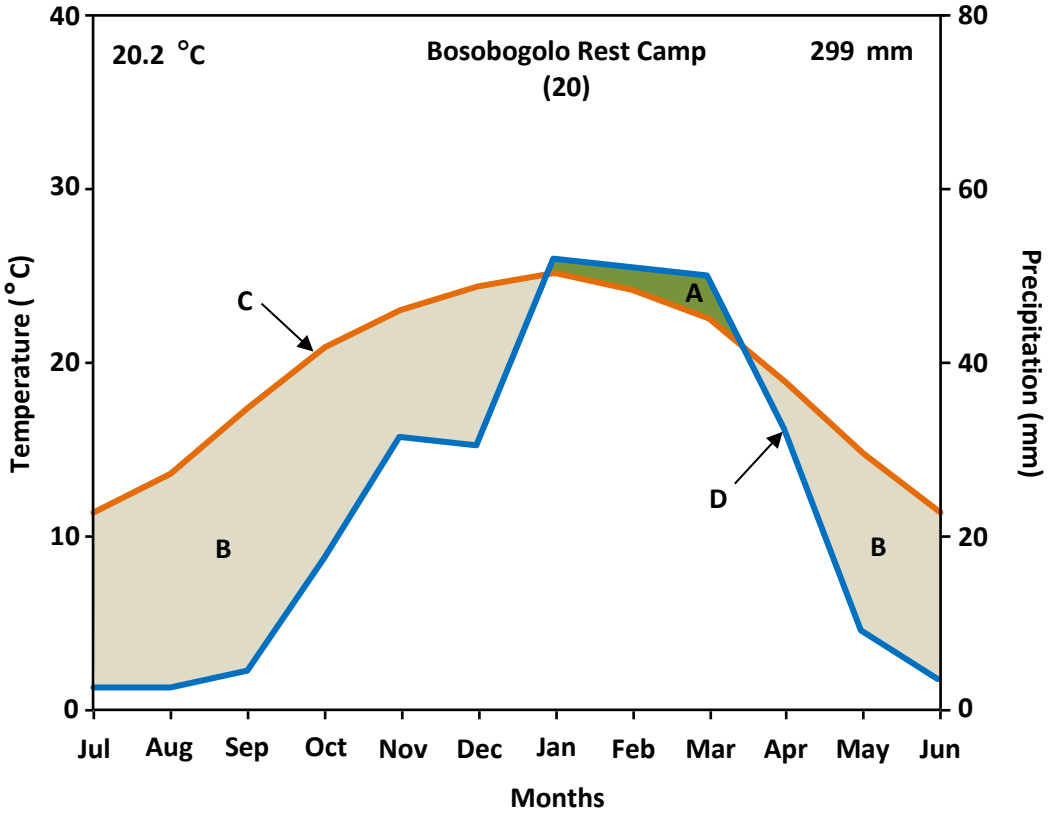

Figure 2.3. *Climatogram of Bosobogolo Rest Camp in the Kgalagadi Transfrontier Park according to the method of Walter and Lieth (1967). Number in brackets indicates total years of observation. Mean annual temperature and precipitation are shown indicated in the top left and right corners, respectively. A, wet season; B, dry season; C, average monthly temperature; D, average monthly precipitation. (Data source: Climate-data.org at https://en.climate-data.org/africa/botswana/kgalagadi-district/bosobogolo-campsite).*

The harsh climate of the Kalahari arid savanna, also classified as Sandveld (Bekker and De Wit 1991), has a profound influence on plant communities. Due to superficial aeolian sand deposits throughout the region, the vegetation is relatively homogeneous with thorn trees

such as blackthorn (*Senegalia mellifera*), camel thorn (*Vachellia erioloba*), sweet thorn (*V. karroo*), Kalahari-sand acacia (*V. luederitzii*), umbrella thorn (*V. tortilis*) and buffalo thorn (*Ziziphus mucronate*) as well as the shepherd tree (*Boscia albitrunca*) being dominant (Bekker and De Wit 1991). The grass layer gives the impression of grassland (Low and Rebelo 1996) but varies extensively in coverage. Prominent grasses include Kalahari sour grass (*Schmidtia kalihariensis*), bushman grass *(Stipagrostis ciliate, S. obtuse, S. uniplumis)*, love-grass (*Eragrostis lehmanniana*) species (Bekker and De Wit 1991; Low and Rebelo 1996). The centre of scattered pans and depressions were either bare or covered by *Eragrostis*, *Panicum* and *Sporobolus* species. Jack's Pan, specifically, is fringed by dense thickets of three- thorn (*Rhigozum trichotomum*), a spreading spiny shrub hardly ever utilised by browsing wildlife.

Apart from kudu (*Tragelaphus strepsiceros*), seven species of antelope, the blue wildebeest (*Connochaetes taurinus*), common duiker (*Sylvicapra grimmia*), eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*), springbok (*Antidorcas marsupialis*) and steenbok (*Raphicerus campestris*), are indigenous to the south-western Kalahari (Knight 1995). With no restrictions by fences, the animals can move freely between the Kgalagadi Transfrontier Park, including the Mabuasehube Game Reserve, and Botswana Wildlife Management Areas. According to Bergström and Skarpe (1999), however, wildlife tends to aggregate around pan areas, especially those furthest away from human settlements.

Population estimates of wildlife in the area were obtained from data of aerial censuses conducted by the Botswana Department of Wildlife and National Parks in 2012. Prior to that, the last wildlife survey was carried out in 2005 (Anonymous 2012). Although no blue wildebeest, kudu or springbok were reported for the Mabuasehube Game Reserve (Table 2.1), all three species were observed during field studies in the reserve as well as at Jack's Pan. Although no predators are listed in the data of aerial censuses conducted by the Botswana Department of Wildlife and National Parks in 2012, large predators including lion (*Panthera*

Table 2.1. *Population surveys of large mammalian herbivores in the south-western Kalahari conducted by the Botswana Department of Wildlife and National Parks in 2012 according to Anonymous (2012). KTP, Kgalagadi Transfrontier Park; KWMA, Kalahari Wildlife Management Area*.

Large herbivore species		KTP	KWMA
Blue wildebeest	*Connochaetes taurinus*	9 527	
Common duiker	*Sylvicapra grimmia*	5 272	55
Eland	*Taurotragus oryx*	18 041	27
Gemsbok	*Oryx gazella*	90 777	1 568
Giraffe	*Giraffa camelopardalis*	272	
Greater kudu	*Tragelaphus strepsiceros*	3 021	
Red hartebeest	*Alcelaphus buselaphus*	40 347	534
Springbok	*Antidorcas marsupialis*	29 704	
Steenbok	*Raphicerus campestris*	18 537	277
Warthog	*Phacochoerus africanus*	812	

leo), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), brown hyaena (*Hyaena brunnea*) as well as smaller predators such as black-backed jackal (*Lupulella mesomelas,* previously *Canis mesomelas*) and bat-eared fox (*Otocyon megalotis*) were observed during field studies.

2.1.2 Geology

The Kalahari Wildlife Management area falls within the Kaapvaal Craton (Key and Ayres 2000). The Kalahari is basically a plateau which was formed at least 65 million years ago after the breakup of Gondwana (Thomas and Shaw 1991). The edges of the plateau were uplifted and as the continent moved northwards, the basin which formed was filled with fluvial and dune sediments which mainly consisted of sands, interbedded with calcrete and silcrete (Wang et al. 2007). However, according to Haddon and McCarthy (2005) the Kalahari basin has a particularly low elevation in certain areas suggesting that downward displacement of the interior of the basin was the driving force behind the Kalahari Group sedimentation rather than

adjacent uplift of the plateau edges. These sediments overlie older consolidated rocks which are mainly Karoo sandstones, capped by Karoo volcanic rocks but also Precambrian rocks consisting of Neoarchaean and Proterozoic sedimentary basins, which are also sometimes capped with volcanic rocks, basement-type crystalline rocks and dolomites (Upton et al. 2018).

The geology of Botswana has been affected by extensive tectonic activity, while recent uplift of ancient erosion surfaces forms the current high plateau topography, superimposed on ancient regional structural trends while some regions within the basin also comprise weathered material (Haddon 2000; McFarlane and Eckardt 2004). According to the geology description of Botswana by Carney et al. (1994), the Transvaal Supergroup forms the bedrock geology of the study site in the south-western part of Botswana.

2.1.3 Soil identification

Soil at all the different geophagy sites in all study areas were classified according to the soil database for southern Africa (SORTERSAF, ver. 2.1) as described by Batjes (2002). Data in the form of shapefiles were downloaded and geospatial data were analysed and soil maps of dominant soil types were compiled with an open-source geographic information system (GIS) platform application QGIS 3.20.3 Odense.

According to the soil database for southern Africa (SORTERSAF, ver. 2.1) as described by Batjes (2002), the dominant soil (BW 75) at Jack's Pan in the KD 12 Wildlife Management area can be classified as Arenosols. This soil type can be described as undifferentiated soils in areas of sandy deposits of coarse texture, consisting of albic (white) material, and develops as a result of in situ weathering of quartz-rich parent material but might also form in recently deposited sand like dunes in deserts (Jones et al. 2013). These soils, dominant in Africa, are among the most widespread soil types in the world (Jones et al. 2013). Based on the SORTERSAF database, the main soil unit composition (65%) of the soil at the study site consist of Ferralic Arenosols (ARo) (Fig. 2.4) but also comprises 15% Haplic Arenosols (Arh), 10% Luvic Arenosols (ARl) and 10% Haplic Calcisols (CLh).

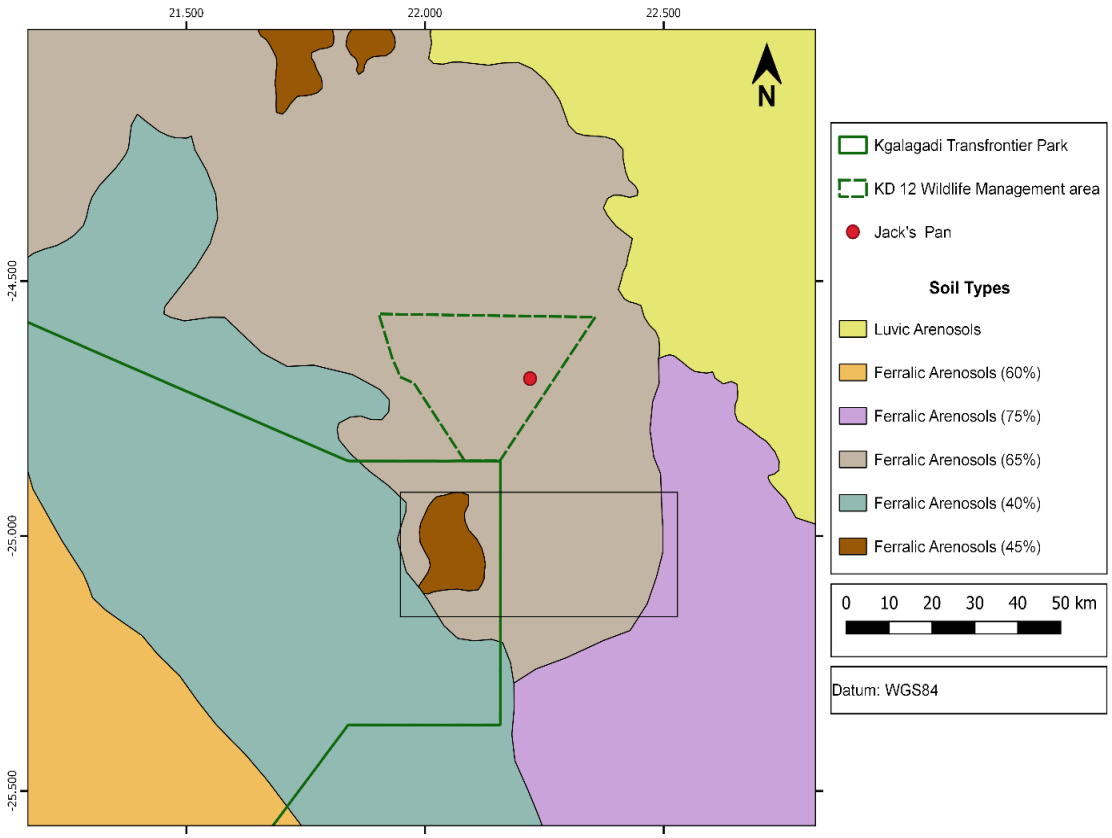

Figure 2.4. *Classification of dominant soil types according to the soil database (SORTERSAF, ver. 2.1) for southern Africa (Batjes 2002) at Jack's Pan in the Kalahari. Wildlife Management area.*

2.1.4 Description of Geophagy site

Jacks' Pan can be described as an elongated almost kidney shaped clay pan (Fig. 2.5 A) which covers an area 1.14 km^2 (113.63 ha) and has a circumference of 5.514 km. At an altitude of 1 062 m above sea level, the pan is orientated from north-east to south-west lengthwise with a maximum length of 4.33 km. No vegetation occurs on the pan. The pan varies in width (maximum 1.33 km; minimum 0.57 km) and the pan floor is slightly raised across the middle section. This raised area in the middle forms two separate deeper ends, one on the south-east and one on the north-west of the pan where water accumulates during the brief rainy season. It is in both these lower lying areas where animals established geophagy sites (Fig. 2.5 B and C).

Field observations indicated that animals do not consume soil on Jack's Pan in an indiscriminate way (pers.obs.). Numerous geophagy pits, are excavated over the entire low-lying areas of the pan. During the time of the study a total of 164 geophagy pits of different sizes were counted on the pan. These geophagy pits are clustered in close proximity of each other (Fig. 2.6 A) and visited on a frequent basis to such an extent that the surrounding areas of frequently used geophagy pits are trampled to fine sand and foot paths are formed (Fig. 2.6 B) which link these deeper excavated pits (pers.obs.). Animals, which prefer soil that is moist, maintained geophagy pits on a continuous basis, and loose dry soil which accumulated into the geophagy pits is constantly scraped out with the hooves of the front legs (Fig. 2.7 A). As animals excavate the geophagy pits, which can become up to 2 m in length and 1.5 m wide, it sometimes becomes so deep (> 60 cm) that the entire head of an animal is below the surface of the pan while soil is consumed (Fig. 2.7 B). The preference for soft moist soil is evident in the orientation of the deeper almost cave like excavation (Fig. 2.8 A) of all the pits which always face in a north-westerly direction with the minimum exposure to direct sunlight (pers.obs). However, whenever these geophagy pits fill with rainwater during the sporadic rainy season, such pits are abandoned and a new pit is excavated adjacent to the old one (Fig. 2.8 B).

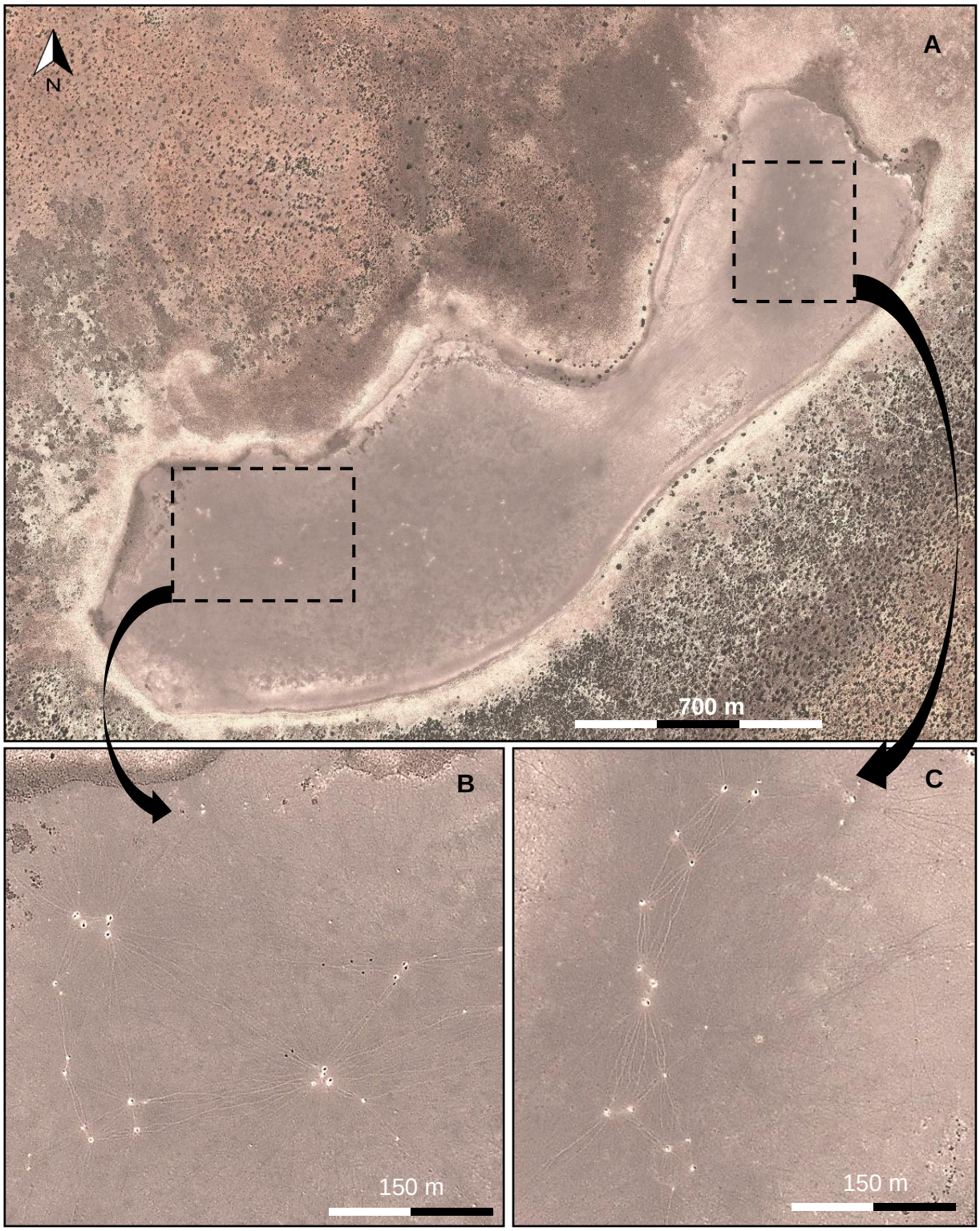

Figure 2.5. *An aerial view (modified from Google Earth™ 2021) of Jack's Pan (A) in the Kalahari Wildlife Management area (Botswana) and enlarged areas (B and C) with clustered geophagy pits (lighter shaded dots).*

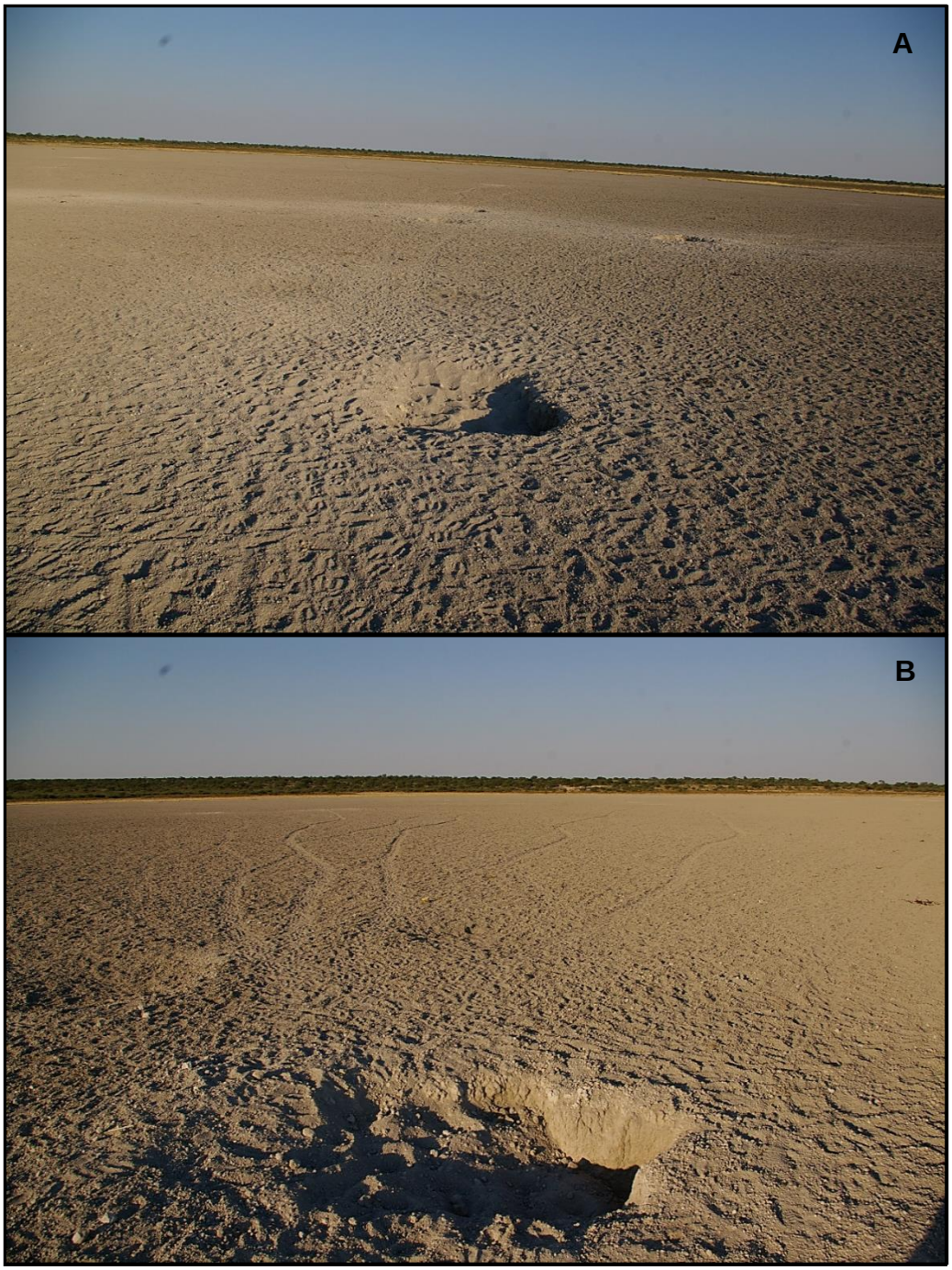

***Figure 2.6**. Clustered geophagy pits (A) with trampled surrounding areas (A and B) and footpaths between geophagy pits (B) at Jack's Pan in the Kalahari Wildlife Management area. (Source: HJB Butler©).*

***Figure 2.7**. Loose soil is constantly removed from geophagy pits at Jack's Pan in the Kalahari Wildlife Management area with the hooves (A) up to depths where the entire head of the animal disappeared (B). (Source: HJB Butler©)*

***Figure 2.8**. A typical excavated geophagy pit at Jack's Pan orientated with the minimum exposure to direct sunlight (A). Abandoned waterfilled geophagy pits and a fresh started pit next to it. (Source: HJB Butler©).*

2.2 Tussen-die-Riviere Game Reserve

2.2.1 General overview

Tussen-die-Riviere Game Reserve is situated approximately 23 km east of the town of Bethulie, (-30.42 to -30.58°; 26.05° to 26.33°) in the Free State Province, South Africa. Wedged between the Caledon and Gariep rivers, the western boundary of the reserve is formed by the confluence of the two rivers (Fig. 2.9). The reserve was established in 1967 and proclaimed as a nature reserve in 1972 (Vrahimis 1991) and resorts under the custodianship of the Free State Department of Economic, Small Business Development, Tourism and Environmental Affairs (DESTEA).

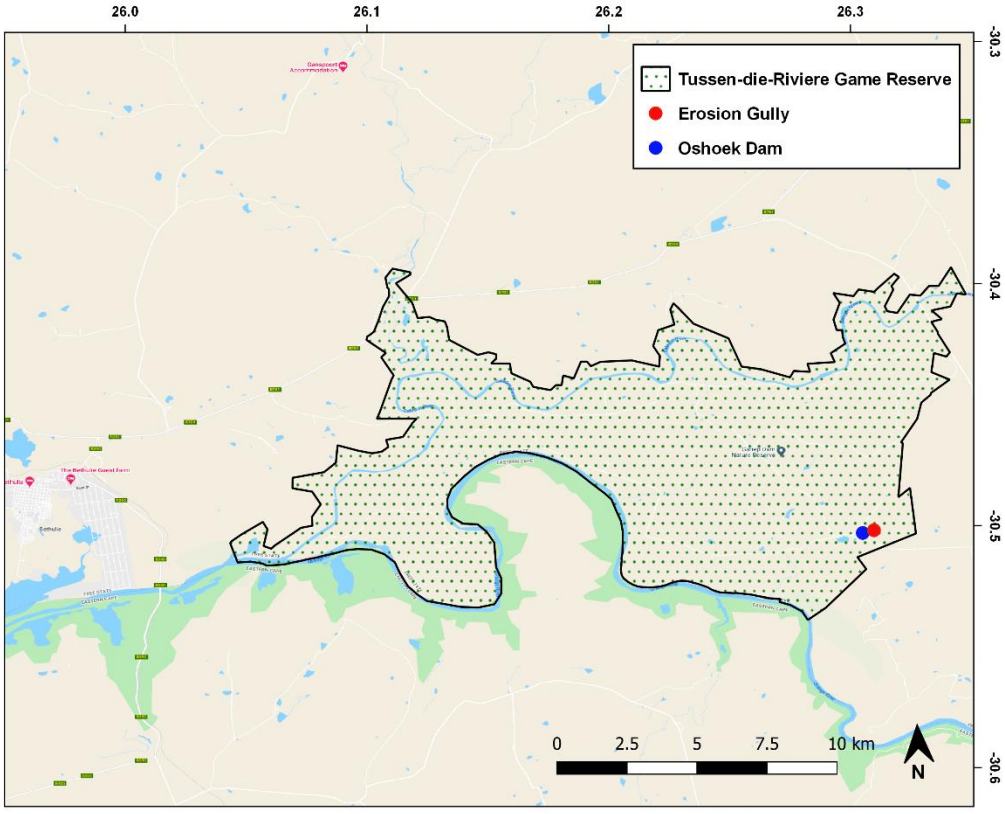

Figure 2.9. *Location of study sites in Tussen-die-Riviere Game Reserve, Free State Province, South Africa.*

Geomorphologically, Tussen-die-Riviere Game Reserve falls in the Highveld physiographic region in which the nearly horizontal beds of the Karoo System determine most

of the landscape (Wegner 1973). Although the flat surface of the area gives the appearance of a low relief plain, it is largely a structural phenomenon caused by dolerite dykes and sills, the latter often capping the mesas and dolerite hills or “koppies” (Wegner 1973). Covering an area of 23 000 ha with altitudes varying from 1 150 to 1 480 m above sea level (Watson 2006), the landscape generally consists of open plains interrupted by low hills and river valleys.

Long-term meteorological data (1999 - 2018) for the region were obtained from the nearest weather station at Gariep Dam airport, 73 km west of the Tussen-die-Riviere Game Reserve study site. Summer rainfall is experienced from November to April with peaks at the beginning of the year (Fig. 2.10). Overall, however, mean annual precipitation is relatively low (404 mm). Notwithstanding a mean annual temperature of 19.2 °C, frost is quite common. Absolute minimum (-9.3 °C) and maximum (38.3 °C) temperatures occur in July and January respectively.

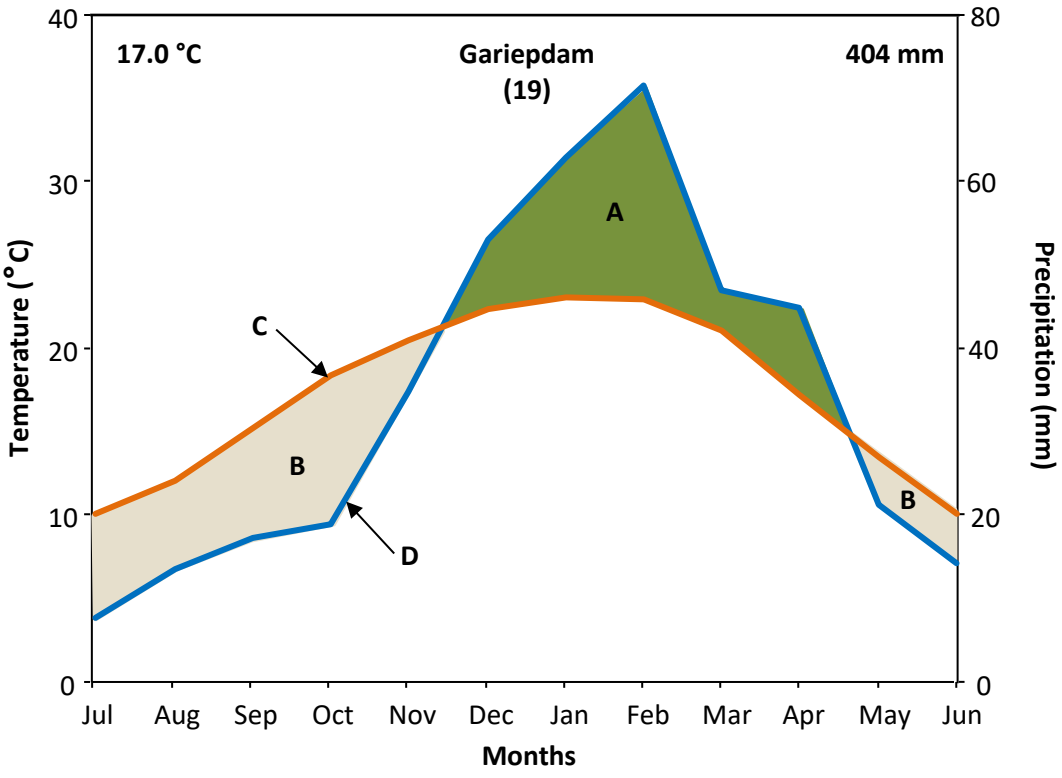

Figure 2.10*. Climatogram of Gariep Dam using the method of Walter and Lieth (1967). Number in brackets indicates total years of observation. Mean annual temperature and precipitation are shown in the top left and right corners, respectively. A, wet season; B, dry season; C, average monthly temperature; D, average monthly precipitation (Data source: South African Weather Service).*

The vegetation of Tussen-die-Riviere Game Reserve is characterised by a complex mixture of grass and shrubs, classified by Mucina and Rutherford (2006) as Xhariep Karroid Grassland interspersed with small patches of dwarf karroid shrubs such as *Chrysocoma ciliate*, *Eriocephalus ericoides*, and *E. spinescens*. Although no tall trees were listed, sweet thorn and buffalo thorn do occur close to the study site. Both Low and Rebelo (1996) and Olson et al. (2001) categorised the region as Nama Karoo where three-awn (*Aristida adscensionis*, *A. canescens*, *A. congesta*, *A. diffusa*) and love-grass species (*Eragrostis chloromelas*, *E. curvula*, *E. lehmanniana*, *E. obtusa*), amongst others, are common.

Originally Tussen-die-Riviere Game Reserve was utilised exclusively as a hunting venue, but by the turn of the century it was also managed as a conservation area after the successful introduction of several ungulate species (Watson 2006). No large carnivores were introduced as all indigenous small to medium-sized carnivores like caracal (*Caracal caracal*) in the ecosystem remained undisturbed (Avenant and Cavallini 2007). To prevent excessive population explosions a strategic culling programme of ungulate game species was subsequently implemented. As a result, the overall population of game species has been kept relatively stable over several decades (Table 2.2).

2.2.2 Geology

According to the geological description of South Africa by Johnson et al. (2006), Tussen-die-Riviere Game Reserve is underlain by the Tarkastad Subgroup (upper portion of the Beaufort Group, Karoo Supergroup). The Tarkastad Subgroup is an arenaceous unit comprised of 90 to 95% sandstone and 5 to 10% mudstone. It is further subdivided by the lower Katberg Formation (sandstone-rich) and upper Burgersdorp Formation (mudstone-rich) (Johnson et al. 2006). Light brownish grey or greenish grey in colour scattered pebbles, up to 15 cm in diameter, are

Table 2.2. *Population surveys of large mammalian herbivores in Tussen-die-Riviere Game Reserve conducted by DESTEA officials during the annual censuses between 2011and 2014.*

Large herbivore species		2011	2012	2014
African buffalo	*Syncerus caffer*	113	100	130
Black rhino	*Diceros bicornis*	1	2	1
Black wildebeest	*Connochaetes gnou*	400	362	542
Blesbok	*Damaliscus pygargus phillipsi*	205	251	343
Common duiker	*Sylvicapra grimmia*	37	63	69
Common reedbuck	*Redunca arundinum*	32	31	28
Eland	*Taurotragus oryx*	450	500	539
Gemsbok	*Oryx gazella*	287	303	372
Impala	*Aepyceros melampus*	188	201	200
Greater kudu	*Tragelaphus strepsiceros*	431	337	422
Mountain reedbuck	*Redunca fulvorufula*	272	210	200
Plains zebra	*Equus quagga*	254	295	369
Red hartebeest	*Alcelaphus buselaphus*	545	518	517
Springbok	*Antidorcas marsupialis*	1 344	1 174	1 651
Steenbok	*Raphicerus campestris*	34	44	52
Warthog	*Phacochoerus africanus*	1 415	1 252	1 442

present in the fine to medium grained sandstones of the Katberg Formation (Johnson et al. 2006). However, oval to spherical calcareous concretions (3-10 cm in diameter) are also common in the Katberg Formation (Johnson 1989).

The Burgersdorp Formation is mostly argillaceous, and can be interpreted as a meandering fluvial to lacustrine deposit (Groenewald 1996; Johnson et al. 2006). Although similar in colour to that of the Katberg Formation, sandstones in this formation are fine grained and display horizontal lamination, cross-bedding as well as ripple lamination. Mudstones of both formations are furthermore predominantly red in colour. This dominance of red colours in the mudstones is indicative of more arid conditions that prevailed during deposition.

2.2.3 Soil identification

According to the soil database for southern Africa (SORTERSAF, ver. 2.1) as described by Batjes (2002), the dominant (60%) soil (ZA1812) at the geophagy sites at Tussen-die-Riviere Game Reserve can be classified as Solonetz, which is soil with a noticeable clay accumulation (association of Luvisols, Planosols and Solonetz and in addition, one or more of Plinthosols, Vertisols and Cambisols may be present). According to the SORTERSAF database, the main soil unit composition (60%) of the soil at the study site consists of Haplic Solonetz (SNh) (Fig. 2.11) but also comprises of 18% Eutric Cambisols (CMe), 8% Haplic Solonetz (SNh), and 7% Haplic Luvisols (LVh) and Ferric Luvisols (LVf) each (Batjes 2002).

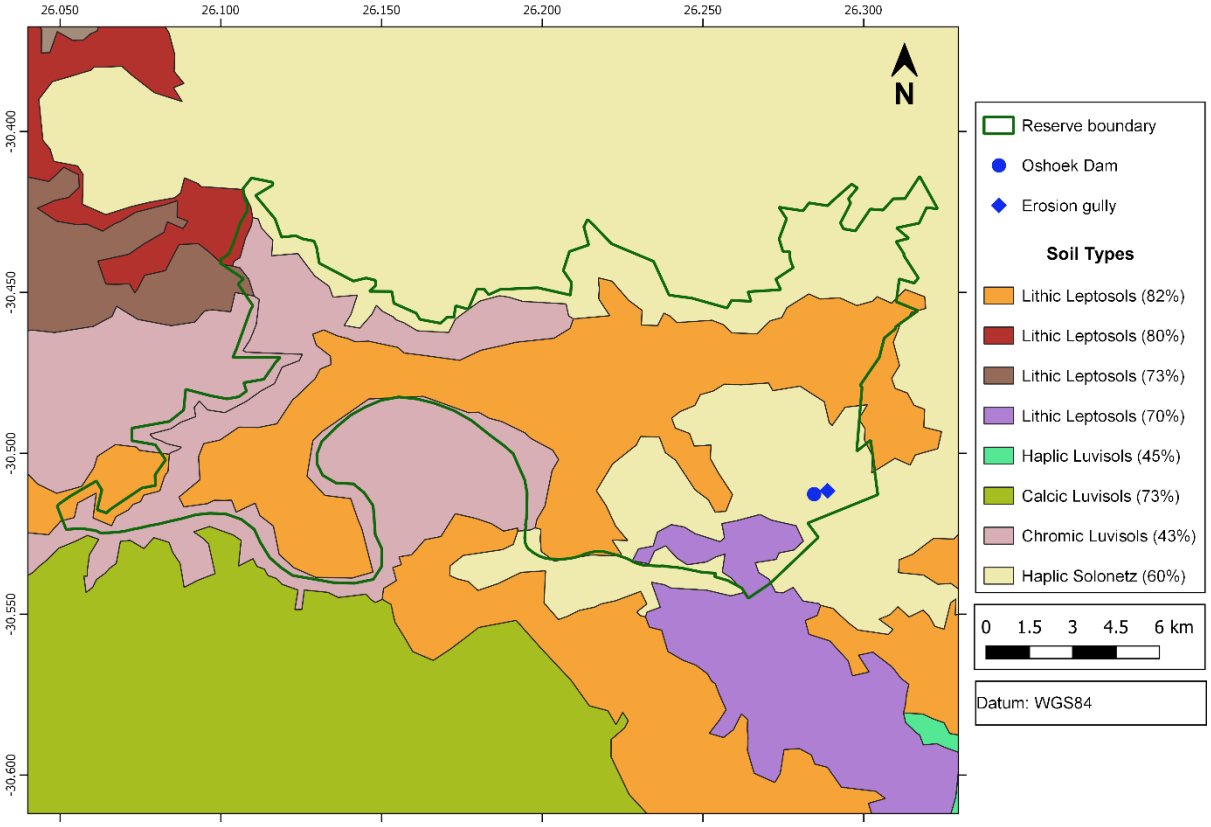

Figure 2.11. *Classification of dominant soil types according to the soil database (SORTERSAF, ver. 2.1) for southern Africa (Batjes 2002) at Tussen-die-Riviere Game Reserve.*

Solonetz is usually linked with flat lands in climates with hot, dry summers or with former coastal deposits that contain a high percentage of salt (Jones et al. 2013). According to Werger (1973), these solonetzic soils consists of a fairly dense, structureless, and slightly acidic A horizon (0.15 – 0.25 m thick) of grey loam that breaks up into clumps and finer material with slight pressure. The column-structured B horizon of dark blackish-brown clay which changes to a lighter brown colour downwards, is alkaline and fairly impermeable to water (Werger 1973). Furthermore, these distinctive columnar-structured soils are characterised by a dense clay-rich subsoil with a high quantity of exchangeable sodium (Jones et al. 2013). Sodium has the ability to disperse clay particles and organic matter in the topsoil which are then washed deeper into the soil, subsequently fill large pores with clay and structural elements (Jones et al 2013).

2.2.4 Description of Geophagy sites

The geophagy sites are situated at the starting as well as the end point of a network of erosion channels which formed in a natural drainage line in the middle of an open grass plain surrounded by a series of small hills or “koppies” (Fig. 2.12). At the confluence of the erosion channels, berms were created to minimise erosion further down which created three shallow artificial dams. The first dam closest to the erosion ditches (Oshoek Dam) has a berm wall of approximately 150 m wide and 2 m high which accumulates water and silt. As a result, a floodplain of approximately 20 x 80 m surrounded by short grass formed at the inflow of the dam. Due to the accumulation of topsoil and silt, the water level in the dam never exceeds 500 mm in depth even in the rainy season and, because of this, plant growth flourishes inside the dam.

Three separate geophagy sites were established around this erosion gully and dam. The geophagy site within the erosion gully (Fig. 2.13 A) is situated about 100 m above the dam wall where red soil, 1.5 m deep, was exposed. Due to the utilisation of soil the wall of the erosion gully formed a vertical concave overhang at the deepest part with an uneven but smooth surface to the opposite side, giving easy access to the geophagy site. Although the

soil in this erosion gully remains moist for up to a week after rain, it is generally a dry hard surface without any plant material present.

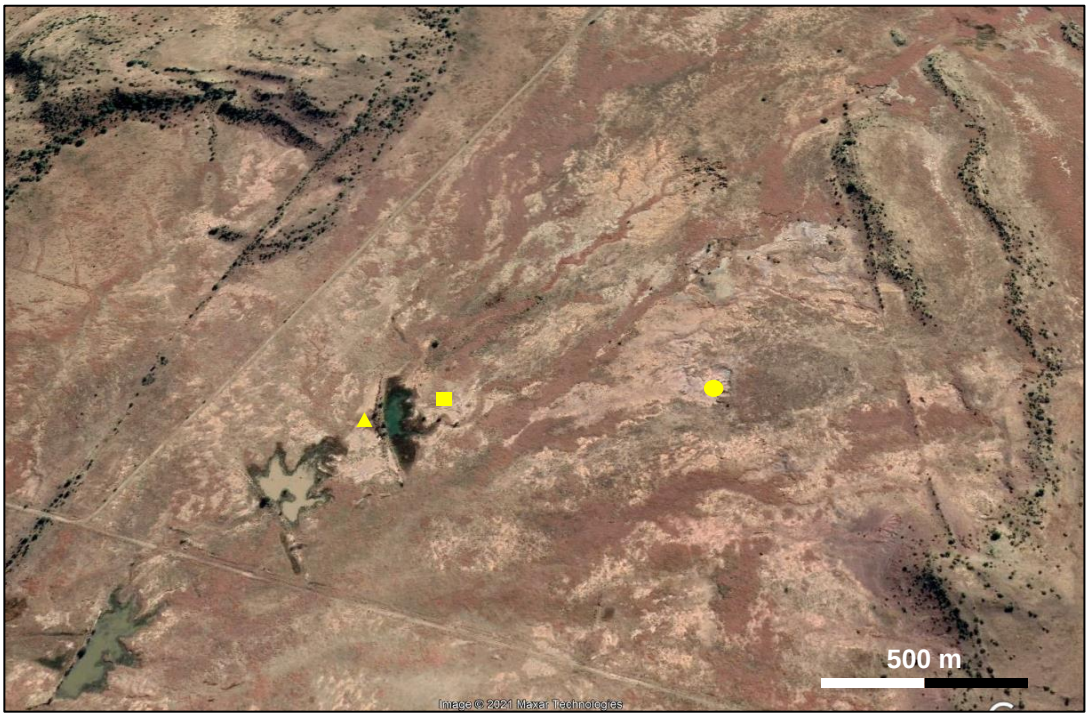

***Figure 2.12**. The location of the geophagy sites at Tussen-die-Riviere Game Reserve (modified from Google Earth™ 2021). Yellow markers indicate the position of geophagy sites at the erosion gully (circle), flood plain (square) and berm wall (triangle) respectively.*

A second site where animals constantly consume soil was established on the flood plain above the water level of Oshoek Dam (Fig. 2.13 B). Although similar in colour to that of the erosion gully, soil in this area is characterised by a soft powdery texture formed by trampling. A third geophagy site occurred at the opposite side at the base of the berm wall (Fig. 2.13 C). Although grass as well as a few scattered trees and shrubs are present on the dam wall, an exposed vertical face of approximately 1 m in height formed at the base. Where this vertical cliff met with the adjacent downward sloping soil, a notable white mineral precipitation is evident, becoming imperceptible for only a few days after rainfall.

Figure 2.13. *Geophagy sites located in the erosion gully (A), the food plain (B) and the base of the dam wall (C) at Tussen-die-Riviere Game Reserve. (Source: HJB Butler©).*

2.3 Willem Pretorius Game Reserve

2.3.1 General overview

The Willem Pretorius Game Reserve is situated approximately 32 km north-east of Winburg (28.26 - 28.34° S; 27.38 - 27.13° E), a small town in the central part of the Free State Province, South Africa (Fig.2.14). Proclaimed in 1971, the reserve surrounds the Allemanskraal Dam which was completed in 1960 (Bourquin 1973). The reserve covers a surface area of 12 082 ha of which 2 771 ha represents the water surface when the dam is full. The dam and the Sand River, which flows through the reserve from east to west and adjoins the Vet River before it flows into the Vaal River, divide the reserve into two management sections. Physiographically, the northern part (maximum 1 525 m above sea level) consists of a series of dolerite intrusions and sandstone ridges that extend from east to west along the river and dam causing a rugged landscape (Müller 1986) while the southern part (maximum 1 375 m above sea level) comprises a more gently sloping landscape of

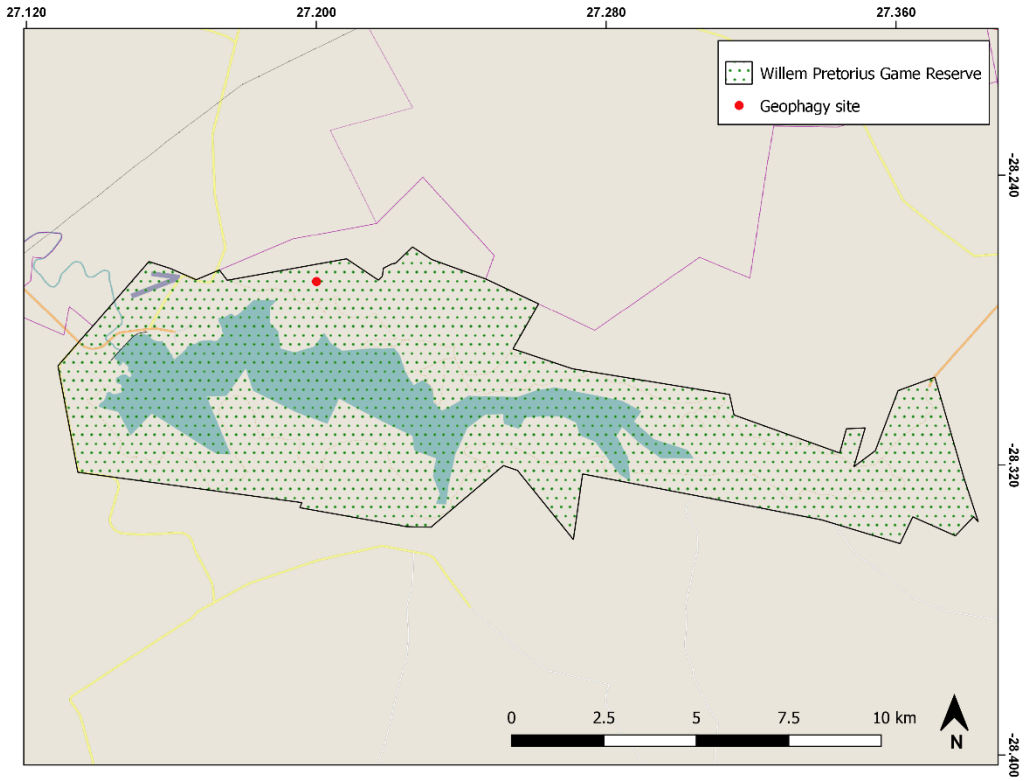

Figure 2.14. *Location of the study site in the Willem Pretorius Game Reserve, Free State Province, South Africa.*

undulating grassy plains (Kok 1975) with intrusions of dolerite koppies and ridges containing sandstone and mudstone of the Beaufort series (Müller 1986).

Meteorological data obtained from the nearest weather station at Welkom, approximately 57 km north-west of the study site, were used as indication of the prevailing climatic conditions at Willem Pretorius Game Reserve. As indicated in Fig. 2.15, annual rainfall is clearly limited to the summer months, a time when daily temperatures above 30 °C commonly occur. During winter, middle May to the end of September, more than 100 days of light to severe frost may be experienced (Bourquin 1973). An absolute minimum temperature of -9.0 °C was registered in July.

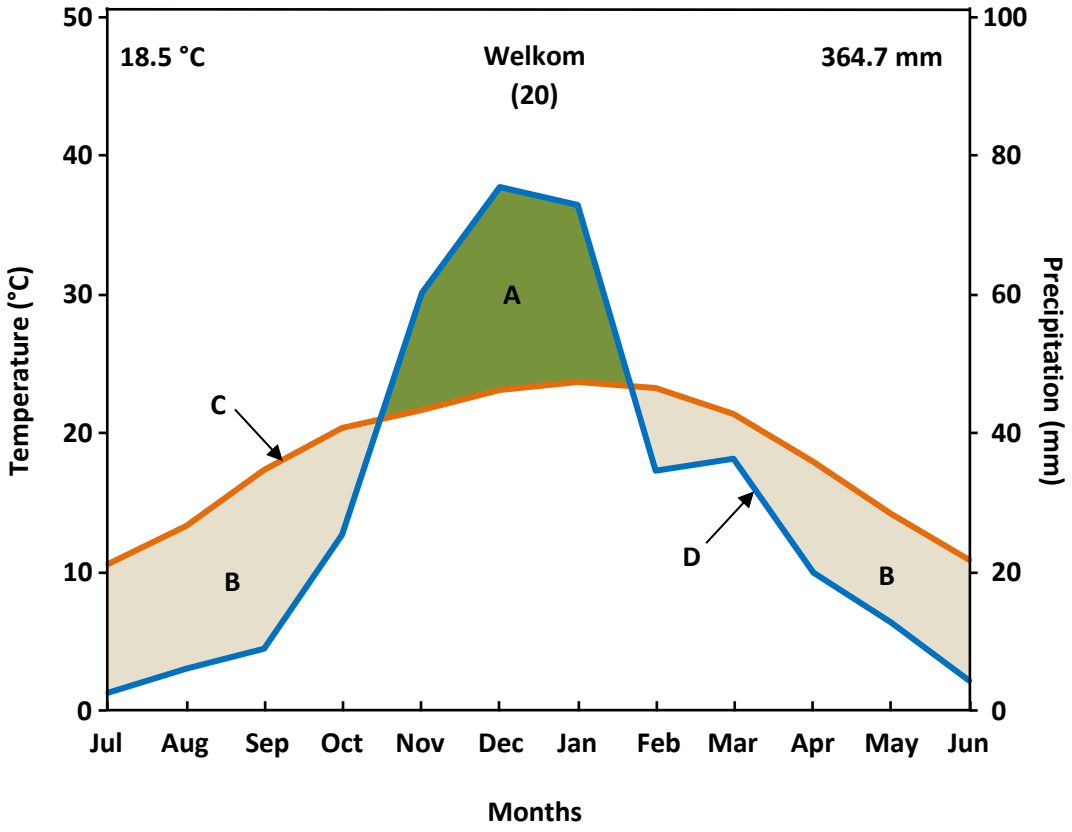

Figure 2.15. *Climatogram of Welkom using the method of Walter and Lieth (1967). Number in brackets indicates total years of observation. Mean annual temperature and precipitation are shown in the top left and right corners, respectively. A, wet season; B, dry season; C, average monthly temperature; D, average monthly precipitation (Data source: South African Weather Service).*

Overall, the vegetation of the Free State, including that of Willem Pretorius Game Reserve, can be categorised as Highveld Grassland (Olson et al. 2001, Mucina and Rutherford 2006). According to Müller (1986), 78% of the terrestrial surface area of the reserve is covered by grass, while Mucina et al. (2014) refer to a small section of the northern side as grassy shrubland. Although no mention is made of trees, buffalo thorn, karee (*Searsia lancea*), white stinkwood (*Celtis africana*) and dense patches of sweet thorn scrub are common in certain areas. Apart from climax species such as *Andropogon appendiculatus*, *Heteropogon contortus* and *Themeda triandra*, the grass component is otherwise dominated by various *Eragrostis* subclimax and to lesser extend *Aristida* pioneer species.

The area around Allemanskraal dam was originally established for the protection of the last remnants of the endemic black wildebeest (*Connochaetes gnou*) in the Free State (Von Richter 1971). Subsequently, with the gradual recovery of the population and the official proclamation of the Willem Pretorius Game Reseve in 1971 (Terblanche 1988), other game species (Table 2.3), predominantly grazers, were introduced. Possible predators are limited to black-backed jackal, caracal and even brown hyena, as identified by means of camera traps during this study.

2.3.2 Geology

According to Johnson et al. (2006), Willem Pretorius Game Reserve is underlain by the Beaufort series of the Karoo Supergroup. The Beaufort Group comprises fluvial deposits in the Permo-Triassic rocks of the Karoo Basin (Catuneanu et al. 2005) and can be divided in the lower Adelaide and the upper Tarkastad Subgroups (Johnson et al. 2006). Within the Adelaide Subgroup, which comprises of alternating red-grey, blue-grey, or green-grey mudrocks to medium grained, grey lithofeldspathic sandstones, Willem Pretorius Game Reseve is situated in the Balfour formation (Johnson et al. 2006). This geological formation comprises of 20 to 25% pale-olive or greenish grey sandstone with thickness that varies between 5 and 40 m and are fine to medium grained and horizontally laminated (Johnson et

Table 2.3. *Population survey of large mammalian herbivores in the Willem Pretorius Game Reserve conducted by DESTEA officials during the annual census of 2015.*

Large herbivore species		2015
African buffalo	*Syncerus caffer*	105
Black wildebeest	*Connochaetes gnou*	346
Blesbok	*Damaliscus pygargus phillipsi*	368
Bushbuck	*Tragelaphus scriptus*	12
Common duiker	*Sylvicapra grimmia*	2
Common reedbuck	*Redunca arundinum*	191
Eland	*Taurotragus oryx*	144
Giraffe	*Giraffa camelopardalis*	26
Impala	*Aepyceros melampus*	186
Klipspringer	*Oreotragus oreotragus*	12
Greater kudu	*Tragelaphus strepsiceros*	118
Plains zebra	*Equus quagga*	150
Mountain reedbuck	*Redunca fulvorufula*	34
Red hartebeest	*Alcelaphus buselaphus*	198
Sable antelope	*Hippotragus niger*	80
Springbok	*Antidorcas marsupialis*	635
Steenbok	*Raphicerus campestris*	6
Warthog	*Phacochoerus africanus*	53
White rhino	*Ceratotherium simum*	17

al. 2006). The Balfour Formation furthermore consists of a high representation (75-80%) of mudstones, comprised of diagenetic carbonate and pedogenic carbonate nodules, which are in general weathered into massive and blocky outcrops (Johnson et al. 2006). In the upper portion of the Balfour Formation mudrocks changes to form the Palingkloof Member, comprised of siltstone rich layers with clay chip breccia lenses, and the first appearance of the reddish brown mudrocks (Catuneanu et al. 2005).

2.3.3 Soil identification

According to the soil database for southern Africa (SORTERSAF, ver. 2.1) as described by Batjes (2002), the dominant soil (ZA1166) at the geophagy site in Willem Pretorius Game Reserve can be classified as Luvisols. The main component of the geophagic soil consists of 26% Calcic Luvisols (LVk) (Fig. 2.16) but different soil types at different levels of Eutric Leptosols (LPe, 13%), Capcic Vertsols (VRk, 6%), Calcic Luvisols (LVk, 18%), Calcic Luvisols (LVk, 18%), Capcic Vertsols (VRk, 5%), Eutric Leptosols (LPe, 12%), Calcic Luvisols (LVk, 8%) and Eutric Fluvisols (FLe, 12%) are also present (Batjes 2004). This slightly acidic soils with a clay-enriched subsoil and high nutrient-holding capacity have a distinct increase in clay content with depth as a result of clay movement from the upper part of the soil to the lower part (Jones et al. 2013). Overall, in Africa, Luvisols which have a well-developed soil

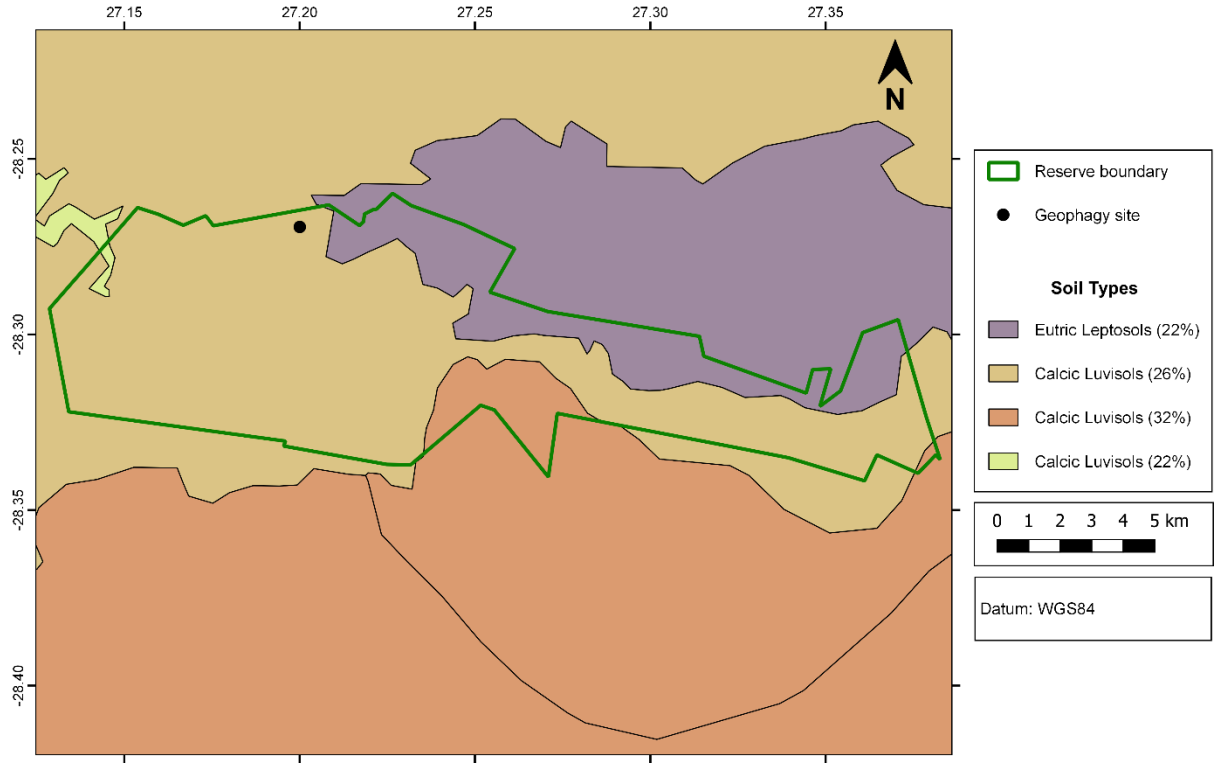

Figure 2.16. *Classification of dominant soil types according to the soil database (SORTERSAF, ver.2.1) for southern Africa (Batjes 2002) at Willem Pretorius Game Reserve.*

structure and therefore contribute to a good water-holding capacity, are mainly found on relatively young surfaces (Jones et al. 2013).

2.3.4 Description of Geophagy site

The geophagy site at Willem Pretorius Game Reseve (Fig. 2.17) is situated in a natural drainage line on a downward sloping grass flat. During the rainy season, water drains from a small range of hillocks (koppies) situated to the east of the geophagy site via a network of shallow ditches towards a dam west of the geophagy site.

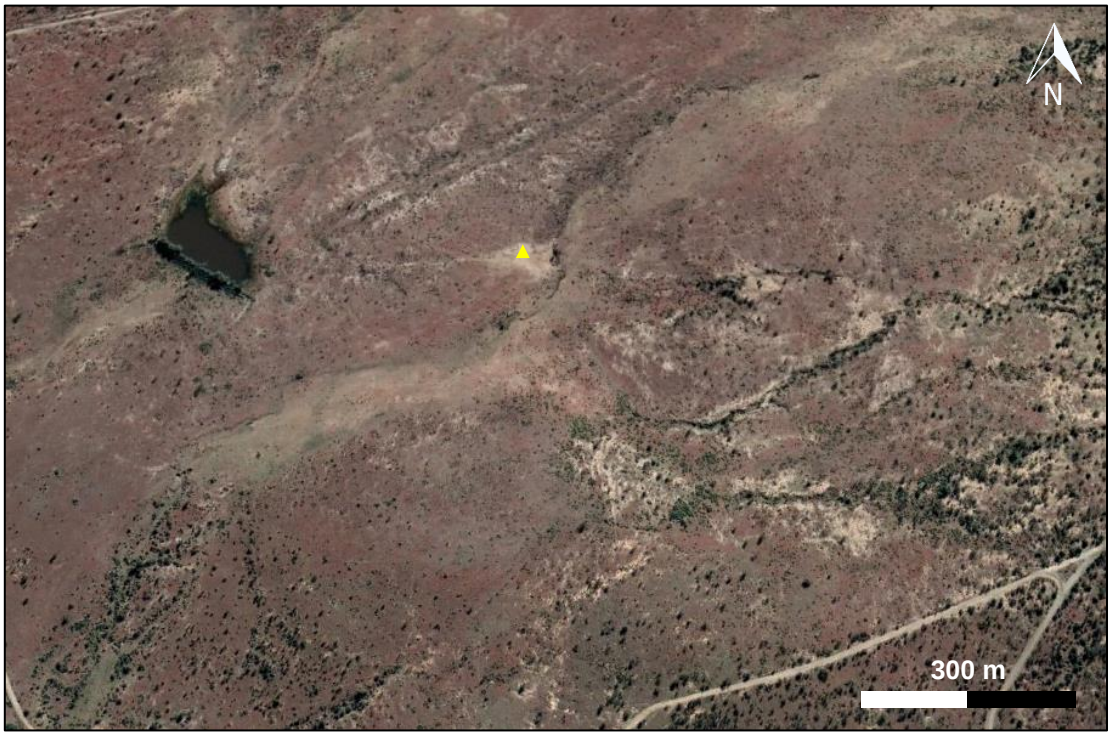

Figure 2.17. *The location of the geophagy site (yellow triangle) at Willem Pretorius Game Reserve (modified from Google Earth™ 2021).*

Several excavation pits where animals consume soil were established in an open exposed area of approximately 25 x 30 m (Fig. 2.18). The largest of these pits was approximately 2 x 3 m in diameter with a depth of 25 to 30 cm. The rest of the pits where animals consume soil were merely indents in the soil and not actively excavated as at the main site. Competition amongst animals to feed at the main excavation site was constantly

Figure 2.18. *Impala consuming soil at the geophagy site in Willem Pretorius Game Reserve with the deeper main lick site in the centre and smaller depressions to the sides. (Source: HJB Butler©).*

captured on camera traps and subordinate animals were forced to utilise the smaller shallower indentations in the soil instead. Rainwater collects in the main excavation pit as well as the smaller soil indentations which keeps these pits moist for up to a week after precipitation (pers. obs). Thereafter the soil in the exposed area becomes dry with a hard crust which is difficult to penetrate.

2.4 Loskop Dam Nature Reserve

2.4.1 General overview

Loskop Dam Nature Reserve, established in 1942 and managed by the Mpumalanga Tourism and Parks Agency (MTPA), is situated approximately 55 km north of Middelburg on the N11 and 32 km south of Groblersdal, Mpumalanga Province. The Loskop irrigation dam, located in the Olifants river valley, is approximately 30 km long and is fed predominantly by the perennial Olifants and the Krantz rivers as well as their respective tributaries. The reserve covers an area of 23 175 ha (Emery et al. 2002) of which 2 350 ha is water surface when the dam is at full capacity (Ferrar and Lotter 2007). Topographically the reserve ranges from hilly highlands with steep slopes and high cliffs on the southern side of the dam to less steep lowlands with undulating plains on the northern side (Van Biljon 1960). Maximum altitudes differ from 1 450 to 990 m above sea level respectively (Filmalter 2010). All monitored geophagy sites were positioned at the northern side of the dam (Fig. 2.19).

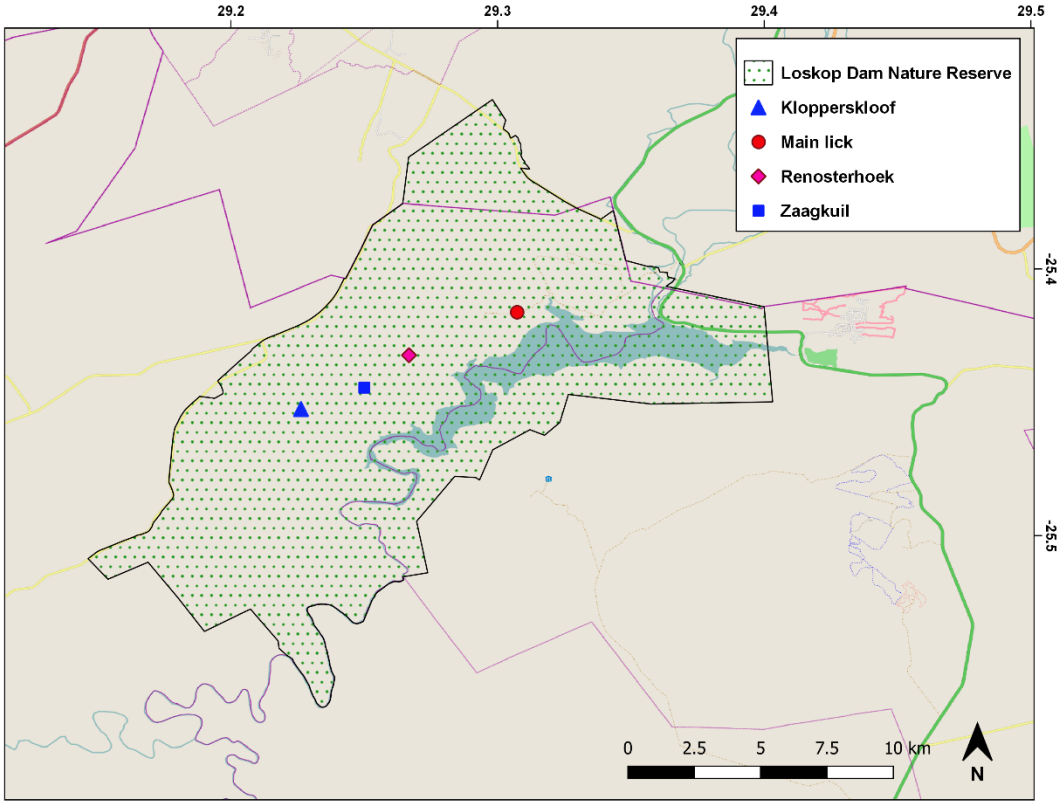

Figure 2.19. *Location of study sites in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa.*

Based on long-term meteorological data obtained from the Oudestad weather station, 26 km north of Loskop Dam Nature Reserve, the reserve experiences a mean annual rainfall of 488 mm, predominantly during midsummer (November – February) (Fig 2.20). Rainfall mainly occurs as showers and high intensity thunderstorms, often accompanied by severe lightning and strong, gusty, southwesterly winds (Nkosi et al. 2016). Warm to very hot summers are followed by moderate winters (Nkosi et al. 2016), even though frost can occur on mountain tops and low-lying areas (Theron 1973, Low and Rebelo 1998).

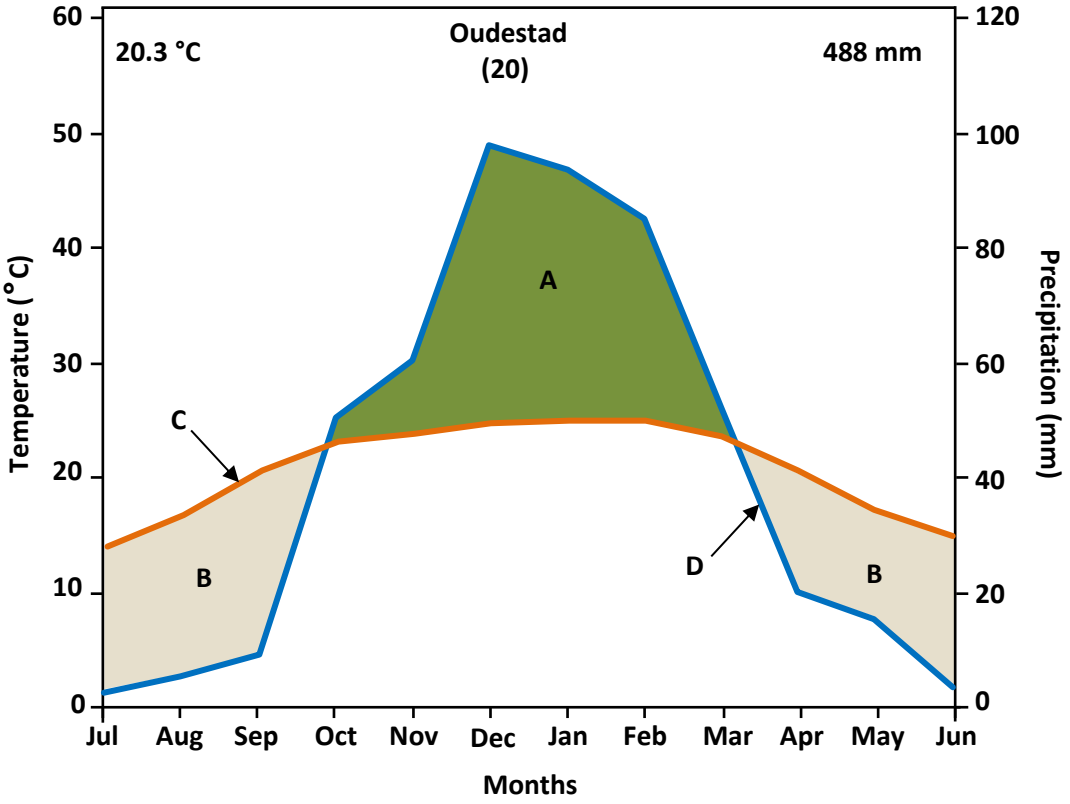

Figure 2.20. *Climatogram of Oudestad using the method of Walter and Lieth (1967). Number in brackets indicates total years of observation. Mean annual temperature and precipitation are shown in the top left and right corners, respectively. A, wet season; B, dry season; C, average monthly temperature; D, average monthly precipitation (Data source: South African Weather Service).*

The Loskop Dam Nature Reserve is located in an ecoregion described as southern African bushveld by Olson et al. (2001). Mucina and Rutherford (2006) and Mucina et al.

(2014) identified three major vegetation types, namely Central Sandy Bushveld, Loskop Mountain Bushveld and Loskop Thornveld. All geophagy sites investigated occurred in the latter two vegetation types where a variety of shrubs and small to medium size trees such as wild syringa (*Burkea Africana*), red bushwillow (*Combretum apiculatum*), velvet bushwillow (*C. molle*), large-fruited bushwillow (*C. zeyheri*), horn-pod tree (*Diplorhynchus condylocarpon*), jacket plum (*Pappea capensis*), mountain karee (*Searsia leptodictya*), blue currant (*S. zeyheri*), black monkey thorn (*S. burkei*), hook-thorn (*Senegalia caffra*), silver terminalia (*Terminalia sericea*), red thorn (*Vachellia gerrardii*) and umbrella thorn are present. The grass component is represented by climax species such as *Digitaria eriantha*, *Enneapogon scoparius*, *Eustachys paspaloides*, *Heteropogon contortus* and *Themeda triandra*.

Several game species have been re-introduced into Loskop Dam Nature Reserve including the threatened sable antelope (*Hippotragus niger*), African buffalo (*Syncerus caffer*) and white rhinoceros (*Ceratotherium simum*) (Anonymous 2015). A list of large mammalian herbivores in the reserve and results from aerial censuses are shown in Table 2.4. Large to medium size predators include leopard, brown hyaena, black-backed jackal and caracal (Eksteen 2003).

2.4.2 Geology

The geology of the greater part of Loskop Dam Nature Reserve consists of the Waterberg System, the Loskop System and Rooiberg felsite. The Waterberg Group comprise of three formations namely the Upper Wilgerivier Formation and the underlying Rust de Winter and Loskop Formations (Johnson et al. 2006). The Main lick, Renosterhoek and Zaagkuil geophagy sites (see section 2.4.3) are all underlain by the Loskop Formation of the Waterberg Group (Transvaal Supergroup). The Loskop Formation underlies the Wilgerivier Formation in the Middelburg Basin and is up to 1000 m thick north of Middelburg. This formation comprises

Table 2.4. *Population surveys (aerial counts) of large mammalian herbivores in the Loskop Dam Nature Reserve conducted by the Mpumalanga Tourism and Parks Agencyduring 2022 and 2013 annual censuses. North, numbers limited to the northern side of the dam only.*

Large mammalian herbivores		**2011**	**2013**	**2013 North**
African buffalo	*Syncerus caffer*	221	282	176
Blue wildebeest	*Connochaetes taurinus*	223	201	135
Bushbuck	*Tragelaphus scriptus*	44	27	25
Bushpig	*Potamochoerus larvatus*	8	4	4
Common duiker	*Sylvicapra grimmia*	47	26	21
Common reedbuck	*Redunca arundinum*	8	14	10
Eland	*Taurotragus oryx*	108	138	138
Giraffe	*Giraffa camelopardalis*	29	32	30
Hippo	*Hippopotamus amphibius*	19	29	26
Impala	*Aepyceros melampus*	1229	770	526
Klipspringer	*Oreotragus oreotragus*	23	14	14
Kudu	*Tragelaphus strepsiceros*	611	342	295
Mountain reedbuck	*Redunca fulvorufula*	386	251	230
Nyala	*Tragelaphus angasii*	67	51	34
Oribi	*Ourebia ourebi*	19	23	23
Plains zebra	*Equus quagga*	447	271	145
Red hartebeest	*Alcelaphus buselaphus*	1	0	0
Sable antelope	*Hippotragus niger*	57	50	49
Steenbok	*Raphicerus campestris*	2	0	0
Tsessebe	*Damaliscus lunatus*	70	66	66
Warthog	*Phacochoerus africanus*	116	80	56
Waterbuck	*Kobus ellipsiprymnus*	155	109	40
White rhino	*Ceratotherium simum*	41	22	18

mainly of argillaceous clastic sedimentary rocks with lesser coarse lithologies. In the basal part the interbedded lavas are mafic to intermediate, changing to acidic in its upper section (South Africa Committee for Stratigraphy, SACS 1980). The basal conglomerates of this formation indicate the reworking of volcanic parent material. According to Martini (1998) the

Loskop Formation is furthermore intruded by the Nebo Granite of the Bushveld Complex. Mudrock, sandstone, volcanic rocks and conglomerates make up the geology of this formation.

The Kloppersklоof site is underlain by sediments of the Selonsrivier Formation of the Rooiberg Group (Transvaal Supergroup). Schweitzer et al. (1995) correlated the Selonsrivier Formation (Doornkloof and Klipnek Members) with the Rooiberg Group (Kwaggasnek and Schrikkloof Formations) thereby rendering the Selonsrivier Formations redundant. It is furthermore suggested that the Rooiberg Group should include the complete volcanic sequence of the Dullstroom, Damwal, Kwaggasnek and Schrikkloof Formations (Schweitzer et al. 1995). The geology of this formation can be described as red porphyritic rhyolite.

2.4.3 Soil identification

Based on the soil database for southern Africa (SORTERSAF, ver. 2.1) as described by Batjes (2002), two soil types, Leptosols (ZA566) and Lixisols (ZA591), dominate the largest part of the Loskop Dam Nature Reserve (Fig. 2.21). The Main Lick as well as Kloppersklоof geophagy sites are underlain by Lithic Leptosols (LPq, 56%), while Haplic Acrisols (Ach, 12%), Lithic Leptosols (LPq, 21%) and Haplic Acrisols (Ach, 11%) form the remainder of the soil (Batjes 2004). Leptosols can be described as shallow soil covering hard rock, gravelly material or highly calcareous deposits (Jones et al. 2013). In Africa, the Leptosols are widespread especially in mountainous and desert regions where hard rock is exposed and the physical weathering of rocks is the main soil-forming processes (Jones et al. 2013).

The dominant soil of the Zaagkuil and Renosterhoek geophagy sites was identified as Haplic Lixisols (LXh, 44%) (Fig.3.5) and according to Batjes (2004), Eutric Regosols (RGe, 18%), Albic Plinthosols (PTa, 6%), Chromic Cambisols (CMx, 15%) and (LPq, 17%) forms the residual properties of the soil in that area. Lixisols are slightly acid with a clay-enriched subsoil, predominantly kaolinite, and low nutrient-holding capacity (Jones et al. 2013). These soils occur mainly in the dry savannah region with low biomass production and consequently low

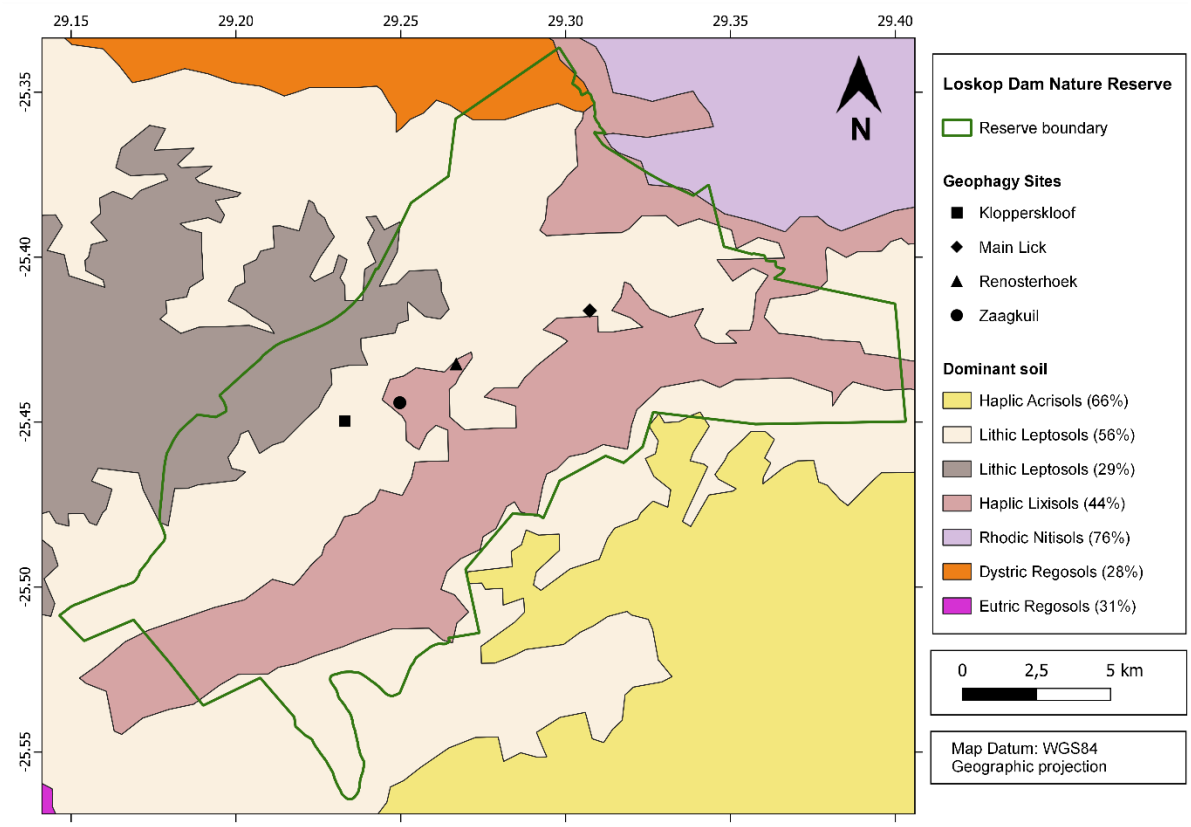

Figure 2.21. *Classification of dominant soil types according to the soil database (SORTERSAF, ver.2.1) for southern Africa (Batjes 2002) at Loskop Dam Nature Reserve.*

organic matter. When high-intensity rainfall does occur, the poorly developed soil structure of Lixisols is prone to erosion (Jones et al. 2013).

2.4.4 Description of Geophagy sites

Although there were numerous places within the Loskop Dam Nature Reserve where animals engage in geophagic behaviour, four geophagy sites were selected based on visitation rates, heterogeneity and accessibility for this study. All four geophagy sites, spaced several kilometres apart, were located on the northern part of the reserve which is characterised by the undulating mountainous terrain (Figure 2.22). All sites are situated in a natural valley formed by mountain ridges and where barren soil is exposed by erosion.

Figure 2.22. *The location of the geophagy sites in the Loskop Dam Nature Reserve. A, Main lick; B, Renosterhoek; C, Zaagkuil; D, Kloppersklоof (Modified from Google Earth™ 2021).*

2.4.4.1 Main lick

The Main lick, the most extensive geophagy site and which was utilised the most by a number of animal species, is situated next to a gravel road between a mountainous foot hill and a network of deep erosion gorges. Animals established several geophagy sites within a radius of 50 m. At the top of the erosion bank, this lick site incorporates an open area surrounded by dense vegetation of trees and shrubs. It is further characterised by loose rocks embedded in the soil with several concave hollows which formed at the base of the feeding place as a result of constant geophagia (Fig. 2.23). Animals often crouch with bent front legs to utilise soil from the concave hollows (Fig. 2.24). A 20 m long bed of loose rocks were deposited to the back of the feeding place (Fig. 2.24) as animals utilised the geophagy site. Several pathways link this rocky geophagy site to the more than 3 m deep erosion gully below. At the bottom of the erosion gully, animals consumed soil from either the wall or the floor. Concave cavities formed in the wall of the gully by a combination of erosion as well as

geophagic actions of animals (Fig. 2.25). Animals often chip off chunks of clay from the wall with their teeth while some animals, especially adult male kudu, use their horns to break off clay pieces which are then eaten from the floor. Markings of this behaviour are clearly noticeable on the wall of the erosion gully up to a height of 1.8 to 2.5 m. (Fig. 2.26).

Figure 2.23. *The Main Lick geophagy site located in the Loskop Dam Nature Reserve with lose rocks suspended in the geophagic soil and concave hollows which formed as a result of geophagia. (Source: CW van Huyssteen©).*

Figure 2.24. *Sable antelope crouch with bended front legs to utilise soil from a concave hollow at the Main lick geophagy site with a bed of loose rocks to the back of the feeding site. (Source: HJB Butler©).*

Figure 2.25. *Kudu females feed on clay from a concave hollow and lose clay chunks on the floor at the erosion gully of the Main lick geophagy site. (Source: HJB Butler©).*

***Figure 2.26**. Markings of clay removal on the wall of the erosion gully at the Main lick site (A) and an enlargement (B) of the section in yellow. (Source: HJB Butler©).*

2.4.4.2 Renosterhoek

The geophagy site at Renosterhoek is a bare flat area of approximately 80 m^2 surrounded by an open savanna bushveld habitat. The site is situated next to a shallow drainage line which is densely vegetated. The geophagy site is a relatively small impression in the soil surface in the middle of an elevated part of the terrain (Fig. 2.27). At the deepest point the impression is 45 cm below the surface. Small to medium sized rocks are scattered over the whole area and are even present inside the geophagy site.

Figure 2.27. *The Renosterhoek geophagy site located in the centre of an elevated part of an open terrain. (Source: HJB Butler©). (Source: HJB Butler©).*

2.4.4.3 Zaagkuil

The Zaagkuil geophagy site is located at the base of a hill approximately 50 m away from a shallow, densely vegetated watercourse. Two separate open areas, divided by a few trees and shrubs, stand about 20 m apart and are surrounded by open bushveld habitat. Both geophagy sites are characterized by a flat sandy soil surface with 40 – 50 cm deep indentations in the surface layer (Fig. 2.28). Rounded irregular shaped banks demarcate the fringes of the geophagy pits which are filled with water for up to a week after rain. Animals did

not utilise the sandy substrate but consumed soil at the bottom of the harder firm fringes of the geophagy pits and thereby create concave hollows towards the bottom part of the pits.

Figure 2.28. *The Zaagkuil geophagy site with lose sandy soil and firm fringes from which animals consume soil. (Source: HJB Butler©).*

2.4.4.4 Kloppersкloof

The Kloppersкloof geophagy site is situated in a deep valley between mountainous ridges on the southern face of a steep mountain side (Fig. 2.29 A). The top half the mountain ridge which consists of open rugged rock formations with sparse vegetation differs from the densely vegetated lower half where the geophagy site is situated. Animals have to endure a steep incline to reach the geophagy site. The geophagy site is a configuration of crevices and protuberances of soft pinkish mudstone (Fig. 2.29 B). Soil from either the deep concave crevices or bulges are equally preferred by animals which engage in geophagia.

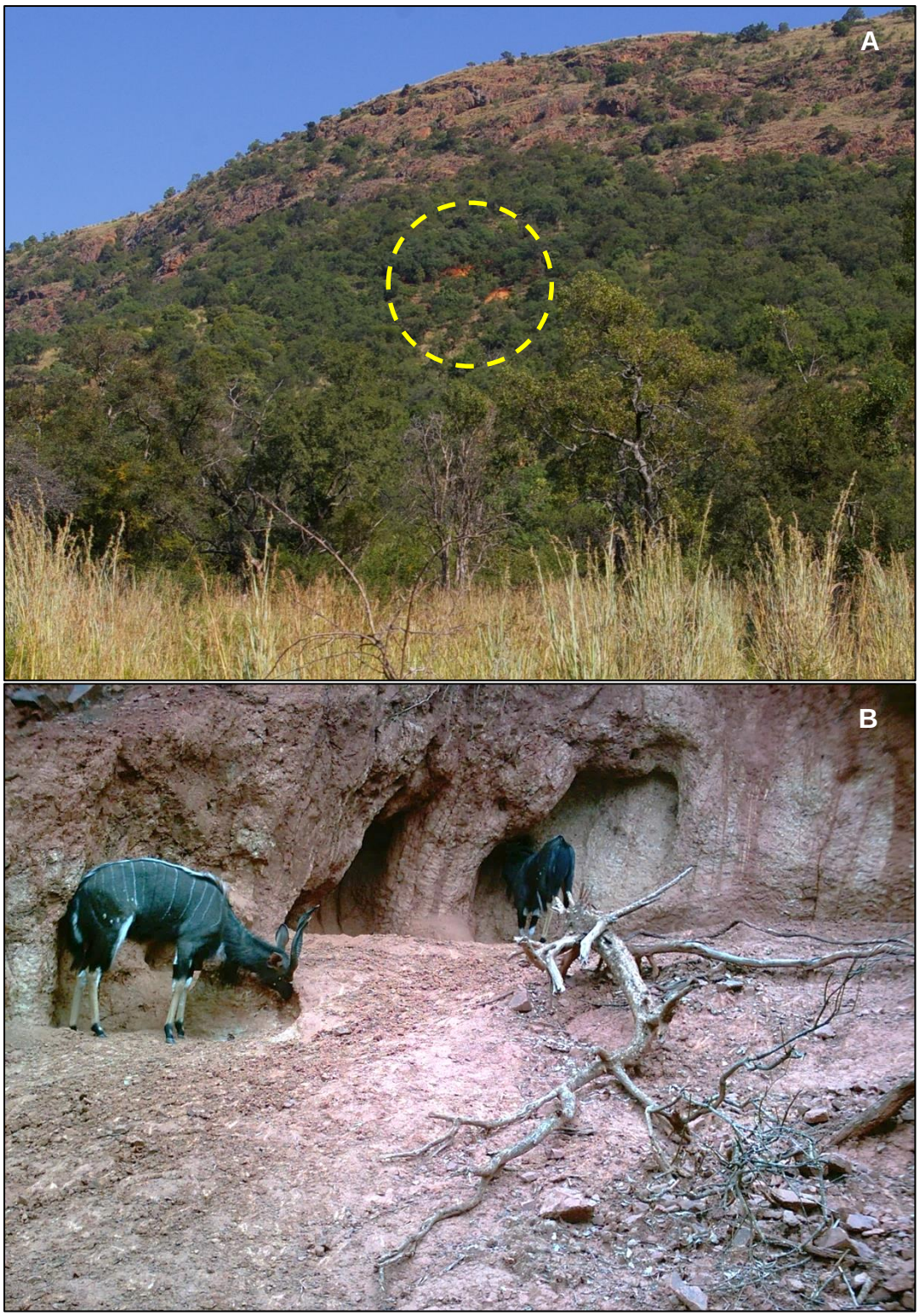

Figure 2.29. *The Kloppersklooof geophagy site in the yellow circle located on a steep mountain slope (A) consist of pinkish mudstone crevices and protuberances (B). (Source: HJB Butler©).*

2.5 Conclusions

In this chapter, the four study areas in this study were described in terms of geology, climate, vegetation, and fauna. Differences in conditions mean that each represents a distinct habitat type, which allows for subsequent study of spatial patterns in geophagy amongst herbivores. The next chapter reports on the geochemistry of these habitats, as well as of the specific geophagy sites within them, demonstrating soil characteristics that form the basis for interpreting geophagy patterns at each location.

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Chapter 3: Geochemistry of geophagic soil

3.1 Introduction

The aim of this chapter was to investigate the geochemistry of geophagic soil with a view to determining its role as nutritional supplementation and/or its function in counteracting possible physiological disorders. Many studies on geophagy refer to “minerals” as a nonspecific description of chemical elements that are essential for physiological functions and metabolic processes in animals. In this chapter, however, the term mineral will refer to naturally occurring inorganic compounds that can break down into simpler structures, whereas elements will refer to a chemical entity in its simplest form.

Large mammalian herbivores require nutrients to sustain all physiological functions on a daily basis. These nutrients can come from a variety of sources and can be obtained from water, energy, protein, vitamins, and elements (McDowell 1985). Herbivores require at least 15 elements which can be grouped into macro and trace elements (McDowell 1985; McDonald et al. 2011; Cherian 2020). Macro elements, including calcium (Ca), chlorine (Cl), magnesium (Mg), phosphorus (P), potassium (K), sodium (Na), and sulphur (S), are required in greater quantities, while trace elements, cobalt (Co), copper (Cu), iron (Fe), iodine (I), manganese (Mn), molybdenum (Mo), chromium (Cr), selenium (Se), and zinc (Zn) are required in smaller quantities (McDowell 1985, McDonald et al. 2011; Cherian 2020). Herbivores attain the bulk of their nutritional needs through the plant material they ingest. However, the species and composition of plants, growth stage and maturity of the plant, the type of soil and climate as well as seasonal conditions are important factors that influence plant mineral compositions, and hence the elemental uptake of these animals (McDonald et al. 2011).

Conversely, plants obtain trace elements from the soil in which they grow. The forming of soil, and ultimately the amount of any element in the soil, is consequently associated with the geochemistry of the underlying rock from which the soil is formed. The underlying geology is therefore the definitive source of trace elements to herbivorous animals. In support of this,

many natural occurring element deficiencies in livestock are associated with specific regions and are directly linked to geology and soil chemistry (McDonald et al. 2011).

Some nutrients that are needed in comparatively large quantities by herbivores are not required, or required only at low levels, by plants (Van Soest 1994). Salt, in the form of NaCl, is probably the best example of such a mineral sought after by herbivores, but not stored by plants (Denton 1984). The physiological need for Na in herbivores is well documented, and according to McDowell (1985), Na is especially required: 1) during lactation when Na is lost through milk; 2) when abundant amounts of Na are lost through sweat and 3) when forages have a high level of K, usually early in the growing season. Terrestrial plants, with the exception of halophytes, do not accumulate Na, and plants rarely provide sufficient Na to meet the nutritional requirements of ruminants (Botkin et al. 1973; Denton 1984; McDowell 1985; Van Soest 1994). According to Arms et al. (1974), the relatively low Na content of land plants is such a common phenomenon that it could well be a defence mechanism for plants against herbivores. As Na is the dominant cation in the bodily fluids of terrestrial animals (Robbins 2013), the low Na content in plants can cause these animals, especially herbivores, to become Na-deficient. Consequently, Na is usually provided to agricultural livestock as a supplement in the form of rock salt. However, wild herbivores often supplement their Na-deficient diet by consuming Na-rich soil or by drinking water from natural mineral sources (Tracy and McNaughton 1995). It is therefore understandable that such areas, where herbivorous animals actively ingest soil, are commonly referred to as salt licks. This description of lick sites implies that the craving for Na is the universal driving force for animals to utilise geophagy sites.

Although herbivores display a strong attraction to Na salts (Fraser and Reardon 1980), and numerous studies have reported elevated levels of Na at geophagy sites (Knight and Mudge 1967; Hebert and Cowan 1971; Calef and Lortie 1975; Weeks and Kirkpatrick 1976; Fraser and Reardon 1980; Selter and Pluth 1980; Tankersley and Gasaway 1983; Watts and Schemnitz 1985; Risenhoover and Peterson 1986; Heard and Williams 1990; Moe 1993; Kennedy et al. 1995; Tracy and McNaughton 1995; Mwangi et al. 2004; Ayotte et al. 2006;

Mills and Milewski 2006; Stephenson et al. 2011; Slabach et al. 2015), Na was not the sole attractant for herbivores to these areas. Results from several studies (Coates et al. 1990; Heard and Williams 1990; Walker 1996) indicated low Na levels at lick sites while other studies suggested that B (Stephenson et al. 2011), Ca (Cowan and Brink 1949; Jones and Hanson 1985; Holl and Bleich 1987; Coates et al. 1990; Heard and Williams 1990; Atwood and Weeks 2003), Cl (Heard and Williams 1990), Co (Mills and Milewski 2006; Stephenson et al. 2011), Cu (Dormaar and Walker 1996; Stephenson et al. 2011), Fe (Dormaar and Walker 1996), I (Mwangi et al. 2004), K (Coates et al. 1990; Heard and Williams 1990), Mg (Holl and Bleich 1987; Coates et al. 1990; Heard and Williams 1990; Dormaar and Walker 1996; Atwood and Weeks 2003; Ayotte et al. 2006), Mn (Dormaar and Walker 1996; Stephenson et al. 2011), Mo (Stephenson et al. 2011), P (Heard and Williams 1990; Slabach et al. 2015), S (Heard and Williams 1990; Atwood and Weeks 2003; Ayotte et al. 2006), Se (Coates et al. 1990; Mills and Milewski 2006; Stephenson et al. 2011) and Zn (Stephenson et al. 2011) were equally important or might even be the main driving force behind the voluntary ingestion of soil by mammals. The reference to geophagy sites as “natural licks” or “licks”, as suggested by Klaus and Schmid (1998), or “mineral licks” is therefore more appropriate.

Deficiencies in macro- and trace elements as a result of inadequate dietary intake may not be the only incentive for herbivores to consume soil. Variation in available minerals at different geophagy sites suggests that such areas serve multiple functions for different species during different seasons (Kreulen 1985). According to Ayotte et al. (2006), digestive ailments, associated with a change in forage, might explain the increased utilisation of mineral licks by many ungulate species during springtime. With the change of seasons from winter to spring and later early summer, herbivores are subjected to an increase in physiological demands associated with lactation, growth and weight gain, which can be aggravated by the loss of electrolytes which are related to the stress of abrupt changes in forage chemistry (Ayotte et al. 2006). After winter months, ruminants must adapt from a high fibrous diet to lush spring forage. This results in an increase in readily fermentable carbohydrates and proteins that alter

the pH of the rumen and consequently impair proper microbial function (Ayotte et al. 2006). According to Kreulen (1985), ruminants which are exposed to sudden drops in dietary fibre, produce less saliva which is high in bicarbonates. A drop in the secretion of saliva reduces the buffering capacity of the rumen (Church 1975; Allen 1997) which can lead to a drop in pH and inhibit the normal function of rumen microbes (Ayotte et al. 2006).

The multiplicity of results of various elements, present in mineral licks all over the world, has discredited the theory of a universal function of geophagy and supports the concept that these licks serve multiple functions across time, location and species. However, all studies on geophagy and specifically studies on geochemistry, focused on one geophagy site or at least geophagy sites in one specific area. Therefore, available evidence does not easily lend itself to determining the type or types of soils, and their elemental compositions, that routinely attract geophagy by herbivores. In this Chapter, I present analyses of the physical, chemical, mineral and chemical element properties of lick soils utilised by herbivores in four habitats of the southern African central interior – the Kalahari savanna, Nama Karoo, Grassveld, and Bushveld. Each of these habitats differ in underlying geology and soil types (see Chapter 2). Comparisons are made between the habitats, but also between lick soils at different sites within habitats (at least within the Bushveld where multiple geophagy sites were sampled), and between soils at different positions (depths) at a specific lick site. These analyses allow a comparative approach to determining whether there are ubiquitous soil properties, such as physical characteristics, Na content, or concentrations of other minerals and elements, that attract geophagy. Concomitantly, absence of any ubiquitous pattern may imply drivers other than nutritional supplementation.

3.2 Methodology

3.2.1 Soil sample collection

Soil samples were collected from all geophagy sites at all four study areas: from Jack's Pan in the Kalahari, in Tussen-die-Riviere Game Reserve (Nama Karoo habitat), in Willem Pretorius Game Reserve (Grassveld habitat), and from four sites within the Loskop Dam Nature Reserve (Bushveld habitat; Main Lick, Zaagkuil, Renosterhoek, and Kloppersklоof). At each site, collections were made at the exact area where visible markings of soil consumption were evident. Three samples were taken along a depth gradient, starting at the top (0 to 5 cm below the surface), middle (midway between the top and feeding depth) and at the feeding depth where geophagy itself occurred. In addition, as a control, samples were taken 10 m beyond the edge of each geophagy site where soil was exposed but with no visual signs of geophagy. Control sites were selected from areas where seepage from the lick site does not influence the geochemistry, but are still part of the same geological formation, as prescribed by Kennedy et al. (1995).

Collection methods followed those described by Mahaney and Krishnamani (2003). A stainless-steel metal tube (40 mm in diameter and 400 mm in length) was used to collect soil at the top, middle and bottom sections of each geophagy site. A plunger, also stainless steel which fit tightly into the tube, was used to eject the soil core into separate paper bags. Each bag was labelled according to the different geophagy sites. To ensure a reliable representation of the soil, a total of three samples were collected and pooled for each site. Collectively, the sampled soil weighed approximately 1.2 kg. Samples were air dried in the paper bags for two weeks, as described by Klaus and Schmid (1998), after which they were lightly ground and passed through a 2 mm sieve.

3.2.2 Physical and chemical analyses

The collected soil was sent to the Department of Soil Sciences at the University of the Free State, Bloemfontein campus for physical and chemical analyses. Soil was categorized according to colour using hue, value and chroma of the revised edition of the Munsell soil

colour charts (Anonymous 1994) and soil texture was described according to the textural system of soil classification (IUSS Working Group WRB 2015). Chemical [pH (water), phosphate (Olsen Method), total nitrogen, organic carbon (Walkley-Black Method), and cation exchange capacity (CEC) (NH_4OHAc extracted at pH 7)] and physical (8-fraction texture) analyses were conducted by the standard soil analytical procedures as described by The Non-Affiliated Soil Analysis Work Committee (1990). The broad characterisation classes of soil pH (H2O) followed the classification as described by Batjes (1995). Each of the soil samples were analysed for each property. Soils were sieved through mesh sizes of 1.0 mm 0.50 mm, 0.25 mm, 0.106 mm, and 0.053 mm. Duplicates for the chemical analyses on each soil sample were conducted and the average between the two samples was calculated.

3.2.3 Mineralogical analyses

Mineralogical analyses, including primary and secondary minerals was performed by means of power X-Ray Diffraction (XRD). Major and trace elements of geophagic soils were analysed by X-Ray Fluorescence (XRF). Analysis took place at the Department of Geology, University of the Free State, Bloemfontein campus. First, samples were milled with an iron mill, to a grain size of approximately 10µm. XRD analyses was completed using a PANalytical Empyrean with a Cu-anode X-ray tube. High-score was used for interpretation. The presence of minerals in soil were classified as either dominant (>50%), major (20-50%), minor (10-19%), accessory (2-9%), or only as trace minerals (< 2%).

For major element analyses, all elements were analysed on a fused bead, except for Na_2O which was analysed on a pressed power briquette. A WD-XRF (Rigaku-Primus IV), with a Rh tube and software ZXS was used for quantitative analyses. In the analytical process of determining the percentage and concentrations of major and trace elements in geophagic soil, samples were heated to over 1000 ^{0}C. Because of the heating process, major elements were expressed in oxide form. As an example, if Ca was present as $CaCO_3$, the heating process releases CO_2, and the element expressed as CaO. Certificates of analyses were issued for

results of all samples. Analysis of concentrations was based on mass, i.e. g/kg and expressed as percentages unless otherwise specified.

3.2.4 Data analyses

To characterize and compare the physicochemical properties of lick sites, and the samples retrieved at each, results of physical and mineralogical analyses are presented descriptively. Variations in elemental composition are, however, more complex because i) they are represented by a large number of variables, and ii) are the essential nutritional supplements for herbivores postulated to drive geophagy. Thus, to characterize and compare elemental compositions, principal component analyses (PCA) were used. PCA reduces the dimensionality of a multivariate system of correlations into a smaller number of dimensions while still accounting for most of the data variance (Murtagh and Heck 1987). The resultant 'new' dimensions (principal components, PC) incorporate information from all variables, with relative importance ranked as indicated by the strength of their correlations with the new variable (factor loadings). Because each PC explains a much larger proportion of total variance observed than does any single variable on its own, this approach facilitates a robust interpretation of multivariate patterns from a small number of dimensions. PCAs were performed in R v 4. 0.2. (R Core Team 2020), first for the essential major elements, and then trace elements, included in the data. All lick sites, as well as the depth profiles and control samples from each, representing all four habitats in the study, were included in the analyses, each being treated as a distinct observation. The overall aim of both the descriptive evaluations, and the PCA results, was to ascertain i) whether samples within lick sites varied, especially along the depth gradient towards the deepest part of a section (the feeding level) and between this feeding level and control samples, ii) whether and how lick soil properties differed between the four habitats, and iii) between lick sites within habitats, the latter based on analyses of only data from the four lick sites in the Bushveld habitat.

3.3 Results

3.3.1 Physical and chemical properties of geophagic soils

The physical and chemical profiles of geophagic soil showed that lick sites were somewhat unique, even considering differences in underlying geology (Table 3.1). In the Kalahari, the geophagic soil was very pale brown to light grey with an intermediate chroma value, and had little variation in bulk density in the entire soil profile with low volume of coarse fragments. A slightly higher fraction of clay with less sand was measured at the feeding depth than the topsoil and was accordingly classified as clay soil. All physical properties of the geophagic soil at the feeding depth was the same as that of the control sample.

Geophagic soil in the Nama Karoo was pink to light reddish brown with an intermediate chroma value. Bulk density decreased from the topsoil layer towards the feeding depth. Although a slight increase in coarse fragments were subsequently calculated for the soil profile, an increase in clay fractions occurred towards the level where geophagy took place with a subsequent decrease in the fractions of sand and silt (Table 3.1). Therefore, the geophagic soil changed from a sandy clay loam to a sandy clay type from the top to the feeding depth.

In the Grassveld, geophagic soil was pink to light brown with an intermediate chroma value. The bulk density of geophagic soil did not change much although a slight decrease in coarse fragments were measured in the soil profile (Table 3.1). However, both the bulk density and coarse fragments were higher in the control soil sample compared with that of geophagic soil. Clay fractions increased with an increase in depth of the soil profile and at the deepest level, where geophagy took place, an increase of 11% in clay fractions was measured compared with the topsoil. Subsequently, a decrease in the amount of sand and silt occurred (Table 3.1) and therefore, the texture of geophagic soil changed from a sandy clay loam to a sandy clay type from the top to the feeding level. A slightly higher sand and silt, and lower clay, content was present in the control sample compared with the geophagic soil.

Table 3.1. *Physical and chemical properties of geophagic soil from all geophagy sites in the four habitats of the study area.*

Habitat	Depth	Munsell	Colour description	Bulk density	Coarse fragments	Sand	Silt	Clay	CEC	pH	Organic Carbon	Nitrogen
	cm	soil colour		g/cm^3	cm^3/dm^3	Fraction (%)			mmol(+)/kg	(H_2O)	g/kg	g/kg
Kalahari												
Geophagic soil	0-5	10YR 8/2	Very pale brown	1.21	5	42.2	14.2	43.5	120	8.4	6.7	0.60
	15-30	10YR 7/2	Light grey	1.21	5	40.1	14.3	45.6	116	8.5	4.9	0.51
	60-80	10YR 7/2	Light grey	1.20	2	40.2	14.2	45.6	118	8.8	4.6	0.44
Control	60-80	10YR 7/2	Light grey	1.20	2	40.2	14.2	45.6	120	8.5	4.0	0.35
Nama Karoo												
Geophagic soil	0-5	5YR 7/3	Pink	1.44	60	56.4	20.2	23.4	211	7.3	13.5	1.40
	5-15	5YR 6/3	Light reddish brown	1.36	62	56.6	20.2	23.2	202	7.4	10.1	1.16
	15-30	5YR 6/3	Light reddish brown	1.28	70	46.6	17.8	35.6	206	7.6	10.2	1.03
Control	15-30	5YR 6/3	Light reddish brown	1.28	82	48.4	18.7	32.9	199	7.6	7.7	1.00
Grassveld												
Geophagic soil	0-5	7.5YR 7/3	Pink	1.30	70	60.4	14.8	24.8	228	7.0	13.9	1.30
	5-15	7.5YR 6/3	Light brown	1.30	62	60.0	14.4	25.6	192	7.0	13.8	1.03
	15-30	7.5YR 6/3	Light brown	1.31	60	50.5	13.7	35.8	193	7.1	10.0	0.91
Control	15-30	3	Light brown	1.36	82	52.4	14.2	33.4	200	7.1	10.5	0.91

(Table 3.1 continue)

Habitat	Depth cm	Munsell soil colour	Colour description	Bulk density g/cm^3	Coarse fragments cm^3/dm^3	Sand	Silt	Clay	CEC mmol(+)/kg	pH (H_2O)	Organic Carbon g/kg	Nitrogen g/kg
						Fraction (%)						
Bushveld												
Main Lick												
Geophagic soil	0-40	5YR 5/6	Yellowish red	1.33	80	43.2	21.4	35.4	192	7.8	20.0	1.55
	40-60	5YR 4/6	Yellowish red	1.38	76	49.6	22.8	27.6	175	7.9	16.1	1.18
	60-80	5YR 4/6	Yellowish red	1.41	92	67.1	16.8	16.1	174	8.2	11.8	1.00
	80-140	5YR 3/4	Dark reddish brown	1.42	89	24.4	30.1	45.5	171	8.0	9.2	0.81
Control	80-140	5YR 3/4		1.45	105	56.6	16.2	27.2	175	6.7	5.9	0.83
Renosterhoek												
Geophagic soil	0-5	7.5YR 7/6	Reddish yellow	1.32	79	52.8	16.9	30.3	195	6.4	22.7	1.61
	15-20	7.5YR 7/8	Reddish yellow	1.36	84	51.5	16.2	32.3	184	6.5	17.9	1.27
	40-50	7.5YR 7/8	Reddish yellow	1.41	115	44.3	15.1	40.6	187	6.5	11.3	0.97
Control	40-50	7.5YR 7/8	Reddish yellow	1.72	120	49.4	15.1	35.5	164	6.5	14.7	0.95
Zaagkuil												
Geophagic soil	0-5	7.5YR 7/3	Pink	1.36	63	60.8	16.3	22.9	199	6.4	10.5	0.96
	15-20	7.5YR 6/3	Light reddish brown	1.39	54	60.8	16.3	22.9	186	6.4	10.4	1.17
	40-50	7.5YR 6/3	Light reddish brown	1.43	80	60.1	15.8	24.1	184	6.5	10.9	1.53
Control	40-50	7.5YR 6/3	Light reddish brown	1.43	74	59.4	15.5	25.1	196	6.3	9.5	0.95
Kloppersklooof												
Geophagic soil	Floor (0-10)	10R 5/4	Weak red	1.33	107	65.2	14.0	20.8	193	5.9	7.3	1.74
	Cave (0-10)	10R 5/4	Weak red	1.48	122	55.4	15.0	29.6	180	6.1	6.6	0.43
Control	0-10	10R 5/4	Weak red	1.45	103	55.2	15.0	29.8	184	6.1	5.1	0.42

The dissimilarity of geophagic soil was further emphasised by the differences which occurred between such licks even within the same habitat. In the Bushveld habitat, soil colour varied from yellowish red to dark reddish brown (Main Lick), reddish yellow (Renosterhoek), weak red (Kloppersкloof) and pink to light reddish brown (Zaagkuil), with chroma values that varied from low to medium (Zaagkuil), medium (Kloppersкloof), intermediate to high (Main Lick) and high (Renosterhoek). The bulk density, as well as the volume of coarse fragments, increased in depth of the soil profile of the Main Lick, Renosterhoek and Zaagkuil geophagy sites, but was lower than that of the control soil at both the Main Lick and Renosterhoek sites (Table 3.1). At the Kloppersкloof site, the bulk density of the geophagic soil at the cliff wall (cave) was higher than that of geophagy places at the bottom (floor), corresponding with the higher quantity of coarse fragments also found in the cave soil. The bulk density of the control soil was not as high as that of the cave, but higher than that of the floor. The quantity of coarse fragments of the control sample was however lower than any of the two geophagic samples. In general, the fraction of clay increased from the top to the feeding depth in geophagic soil at Main Lick, Renosterhoek and Zaagkuil, and the soil texture at the feeding depths of was classified as either clay soil (Main Lick and Renosterhoek) or sandy clay loam type (Zaagkuil and Kloppersкloof). Fractions of clay were higher at feeding depth than in control samples at the Main Lick and Renosterhoek, but lower at Zaagkuil and the floor at Kloppersкloof.

Considering the chemical properties of geophagic soil, a decrease in CEC was noticeable in the soil profile from the top towards the feeding depths of all geophagic soils. (Table 3.1). Compared to the control samples, only soil from Nama Karoo, and two of the Bushveld habitat sites (Renosterhoek and the floor at Kloppersкloof) had higher CEC values. The pH character of geophagic from the Kalahari soil furthermore changed from moderate alkalinity (pH 8.4) at the top, to strongly alkaline (pH 8.5) in the middle and was strongly alkaline (pH 8.8) towards the feeding depth, more so than in the control sample. In the Nama Karoo, the pH changed from neutral (pH 7.3) at the top to more alkaline (pH 7.6) at feeding depth, while in soil from the Grassveld, the pH of the two top layers of geophagic soil were

constant at a neutral pH (7.0) with only a slight increase at the feeding depth (pH 7.1). The pH of the geophagy sites in the Bushveld habitat ranged from moderately alkaline (Main Lick) to slightly acidic (Renosterhoek, Zaagkuil and Kloppersкloof).

Furthermore, in all the habitats the concentration of organic carbon, and consequently that of nitrogen, decreased from the top to the feeding depths in the geophagic soil, except at Zaagkuil, where an increase for both was noted. In general, the concentration of organic carbon as well as nitrogen was also higher at the feeding depths than in control samples, except for the concentration of nitrogen at Main Lick and organic carbon at Renosterhoek where the control soil had higher concentrations of these elements respectively (Table 3.1).

3.3.2 Mineralogical properties of geophagic soils

As with physical and chemical properties of geophagic soil, mineralogical properties also had dissimilarities in the lick sites of the different habitats as listed in Appendix A, Table S.1. The variables of minerals in each site are observably different. Quartz was the only mineral that occurred in geophagic soil of all the lick sites, albeit in dissimilar quantities. Since some minerals did not occur throughout the soil profiles, results on important minerals will focus on those that occurred at the feeding depth of each geophagy site.

Apart from quartz, Kalahari geophagic soil had ankerite (21%) and calcite (35%), as major minerals, and sepiolite (14%) as minor mineral at the feeding depth. However, the sodium containing minerals glauberite (9%) and halite (9%) also occurred, only as accessory minerals, at the feeding depth. In soil from the Nama Karoo, muscovite (15%), as minor mineral and kaolinite (9%), anatase (8%) and calcite (3%) all as accessory minerals, were present at the feeding depth. Grassveld habitat was dominated by clinopyroxene (20%) as a major mineral, and plagioclase (19%) as a minor mineral while orthoclase (6%) and calcite (2%) occurred only as accessory minerals.

Although similar in some mineral compositions, the geophagy sites in the Bushveld habitat did show some differences. Almost equal concentrations of kaolinite (19%), smectite

(18%) and muscovite (17%), all as minor minerals, were present at the Main Lick although orthoclase (13%) and plagioclase (12%), also as minor minerals but in lower concentrations, were also present. Goethite (6%), as accessory mineral only occurred at the feeding depth. Kaolinite (12 and 10 %), muscovite (16 and 19%), orthoclase (12 and 10%) and plagioclase (10 and 7%) dominated both the Renosterhoek and Zaagkuil geophagy sites, all as minor minerals except for plagioclase that only occurred as an accessory mineral at Zaagkuil. The iron containing minerals hematite and ilmenite were also present, both as accessory minerals, at these two sites. Geophagic soil from the floor and the cave at Kloppersklоof both had kaolinite and muscovite present as major minerals while similar concentrations of hematite and ilmenite occurred as accessory minerals at both feeding sites. Differences between the two geophagy sites at Kloppersklоof was that soil from the floor contained clinopyroxene which did not occur in the cave, while the latter had the mineral orthoclase which was absent from the floor soil.

According to Mahaney and Krishnamani (2003) a detailed study of the profile of the geophagic soil under investigation should also be considered for understanding of geophageous behaviour in animals. The definitive criteria of importance are, firstly, whether these minerals increase in the soil profile towards the feeding depth, and second to that, if the concentration of a mineral is higher at the feeding depth of the geophagy site than the same depth of the control sample. With these criteria in mind, the important minerals at each geophagy site in all study areas were identified and are listed in Table 3.2.

Based on the above criteria, minerals of importance for geophagy in the Kalahari are ankerite, calcite, glauberite and halite, and to a lesser extend sepiolite (Table 3.2). In the Nama Karoo, calcite was identified to be an important mineral with the addition of anatase, kaolinite and muscovite. The only minerals in the Grassveld habitat that met the criteria were clinopyroxene and plagioclase. In the Bushveld, Goethite, as well as orthoclase and smectite, were identified to be important minerals at the Main Lick site. But this site seems to be different from other sites in this habitat. Renosterhoek, Zaagkuil, and Kloppersklоof all had hematite as

well as kaolinite identified as important minerals, with the addition of ilmenite and orthoclase at both Renosterhoek and Zaagkuil. The only difference in important minerals between Renosterhoek and Zaagkuil was the presence of plagioclase at Renosterhoek, and of muscovite at Zaagkuil (Table 3.2).

Table 3.2. *Identification of important minerals in geophagic soil of four habitats in the study area based on increase/decrease in concentration in the soil profile as well as increase/decrease in concentration at feeding depth compared with the control sample. ML, Main Lick; RH, Renosterhoek; ZK, Zaagkuil; KK, Kloppersklоof.*

	Habitats							
Minerals	**Kalahari**	**Nama Karoo**	**Grass-veld**	**Bushveld**				
				ML	**RH**	**ZK**	**KK**	
							Floor	**Cave**
Anatase		X		O				
Andalusite				/				
Ankerite	XX							
Bassanite	/							
Calcite	XX	XX	O		/	O		
Clinopyroxene			XX				O	/
Glauberite	XX							
Goethite				XX				
Gypsum			/					
Halite	XX							
Hematite		/		/	XX	XX	XX	XX
Ilmenite					XX	XX	O	O
Kaolinite		X		O	XX	XX	XX	XX
Muscovite		X		O	O	X	O	O
Orthoclase			O	X	X	X	/	O
Plagioclase	/		X	O	X	O		
Sepiolite	X							
Serpentine					/			
Smectite				X				

XX Mineral concentration **increased** in profile depth; **higher** concentration at feeding depth than control

X Mineral concentration **same** in profile depth; **higher** concentration at feeding depth than at control

O Mineral concentration stays the **same/decrease** in profile depth; concentration **same/lower** at feeding depth than control

/ Mineral **absent** at feeding depth; concentration **lower/same** as control

Anatase TiO_2

Andalusite $Al_2(SiO_4)O$

Ankerite $Ca(Fe^{2+},Mg)(CO_3)_2$

Bassanite $Ca(SO_4) \cdot 0.5H_2O$

Calcite $CaCO_3$

Clinopyroxene $(Ca,Na,Mg,Fe,Al,Ti)_2Si_2O_6$

Glauberite $Na_2Ca(SO_4)_2$

Goethite $FeO(OH)$

Gypsum $CaSO_4 \cdot 2H_2O$

Halite $NaCl$

Hematite Fe_2O_3

Ilmenite $Fe^{2+}TiO_3$

Kaolinite $Al_2(Si_2O_5)(OH)_4$

Muscovite $KAl_2(Si_3AlO_{10})(OH)_2$

Orthoclase $K(AlSi_3O_8)$

Plagioclase $NaAlSi_3O_8$/ $CaAl_2Si_2O_8$

Quartz SiO_2

Sepiolite $Mg_4(Si_6O_{15})(OH)_2 \cdot 6H_2O$

Serpentine $Al_2Si_2O_5(OH)_4$

Smectite $(Na,Ca)_{0.33}(Al,Mg)_2(Si_4O_{10})(OH)_2 \cdot nH_2O$

3.3.3 Elemental compositions of geophagic soils

Results of XRF analyses showed there was substantial variation in in major and trace element compositions between geophagy sites, as well as along the depth profiles sampled at each (Appendix A, Tables S2 to S8). However, not all elements are essential for herbivore nutrition and focus will therefore be only on elements that are essential for herbivore nutrition as mentioned by McDowell (1985), McDonald et al. (2011) and Cherian (2020). To identify the important elements in the soil that drive geophagy, the same definitive criteria as for minerals was applied. Elements that increase in the soil profile towards the feeding depth, and where the concentration of that element was higher at the feeding depth compared with the control sample, were considered to be of importance. By applying these criteria, different elements of importance in the four habitats were identified (Table 3.3).

According to this, in the Kalahari, major elements including Mg, Mn, Ca, Na and trace elements of Co and Mo were identified to be important for soil consumption. In the Nama Karoo, major elements of importance were identified to be Fe, Na and K, with the addition of Co and Zn as important trace elements. In the Grassveld habitat, Mg, Mn, and Ca were the major elements and Cr, Co and Zn the trace elements that probably stimulate geophagy. It further seems that herbivores gain different nutritional supplementation from the dissimilar geophagy sites in the Bushveld habitat (Table 3.3). At the Main Lick site, major elements including Mg, Mn and P with the inclusion of Zn as trace element, were identified to be important drivers of geophagy. Geophagic soil from Renosterhoek contained Fe, Mg, Mn and Na as major elements, and Co and Zn as trace elements while Zaagkuil, only had trace elements of Cr and Mo identified as a main attraction for ingesting soil. At the Kloppersкloof geophagy site, both the floor and cave soil were identified to be important for the supplementation of the major element Ca while trace elements of Co and that of Cr, Co and Zn, occurred as trace elements in the cave and floor soil respectively. Although Se was not identified to be of importance, this element was also present at the Main Lick and Zaagkuil geophagy sites in the Bushveld habitat.

Table 3.3*. Identification of important essential elements for herbivore animals in geophagic soil in four habitats based on increase/decrease in concentration in the soil profile as well as increase/decrease in concentration at feeding depth compared with the control sample. ML, Main Lick; RH, Renosterhoek; ZK, Zaagkuil; KK, Kloppersklоof.*

		Habitat							
	Essential elements	Kalahari	Nama Karoo	Grassveld	Bushveld				
					ML	RH	ZK	KK	
								Floor	Cave
Major elements	Fe	O/	XX	OX	OO	XX	OO	O	O
	Mg	XX	/X	XX	XX	XX	OO	O	/
	Mn	XX	OO	XX	XX	XX	X/	O	O
	Ca	XX	OX	XX	XO	OO	OO	X	X
	Na	XX	XX	/O	X/	XX	OO	O	O
	K	XO	XX	/O	OO	OX	OX	O	O
	P	OX	/O	OX	XX	OO	OX	O	O
Trace elements	Cr	//	OO	XX	XO	XO	XX	O	X
	Co	XX	XX	XX	OO	XX	O/	X	X
	Cu	/X	OO	/X	OO	OX	OX	O	O
	Zn	OX	XX	XX	XX	XX	OO	O	X
	Se				//		//		
	Mo	XX	//	//	//	//	XX	/	/

Element concentration in soil profile		***Element concentration at feeding depth compared with control sample***	
X	Increase	X	Higher
O	Decrease	O	Lower
/	Same	/	Same

These habitat-based differences in compositions of key elements were supported, and visualized, by results of the PCAs on both major and trace elements. For the major elements, three principal components (PC) had eigenvalues > 1 (Appendix A, Fig. S1), and although these three cumulatively explained 85.0% of total variance in the data, PC1 and PC2 on their

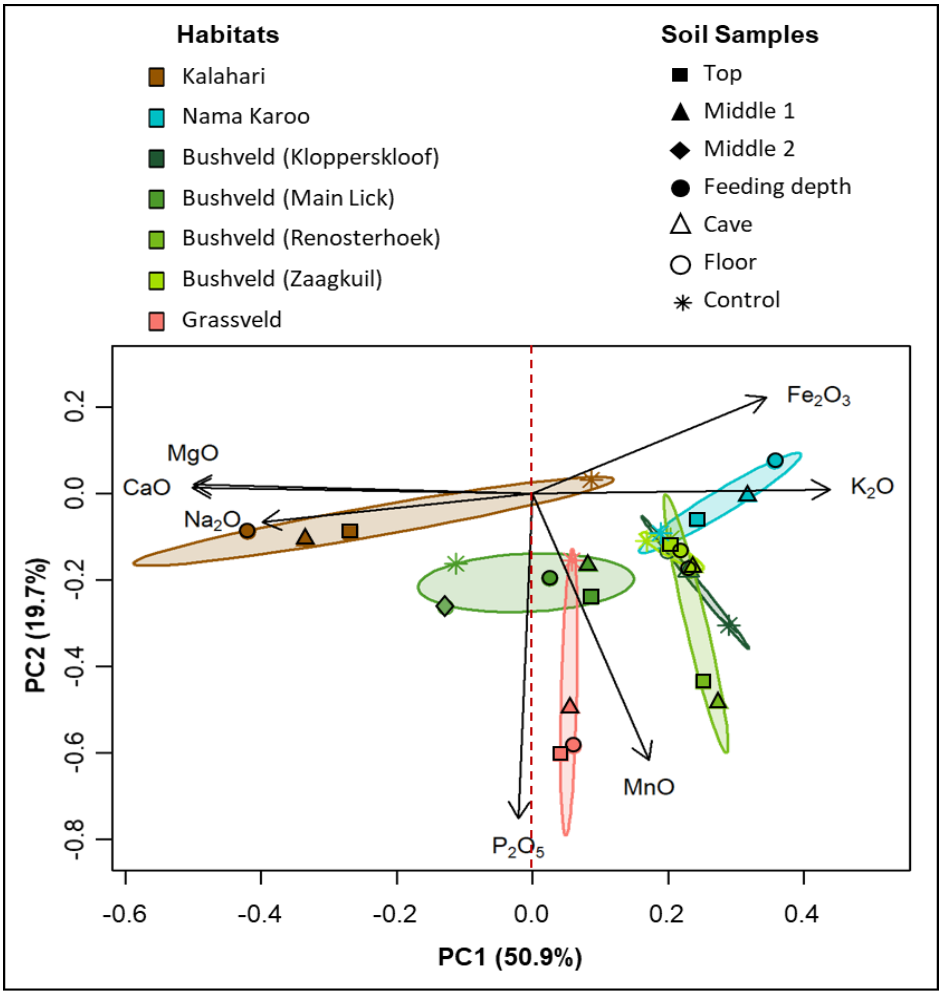

Figure 3.1. *Principal component analyses of essential major elements (oxide form) in soil samples from different habitats in the study area.*

own accounted for >70% and were therefore the focus of this discussion. PC1, which accounted for 50.9%, distinguished the Kalahari habitat, especially the soil from the geophagy site, from the other habitats, as well as from the control soil at the pan (Fig. 3.1). On the other hand, PC1 did not consistently distinguished between the Grassveld and Main Lick of the Bushveld habitat, but it did separate these two sites from other Bushveld sites as well as the Nama Karoo. Intra-site differences also emerged along PC1, especially at feeding depths where it became clear that soil from the Nama Karoo was somewhat different from the rest (Fig. 3.1). Moderate positive linear coefficients of K (0.4382) and Fe (0.3443) but also a weak positive loading of Mn (0.1717) was calculated on PC1 (Appendix A, Table S9). Moderate negative loadings of Ca (-0.5013), Mg (- 0.4998) and Na (-0.3981) as well as weak negative

loadings of P (-0.0211) were also calculated on PC1. The second factor (PC2) explained 19.7% of the variance in major elements between the four geophagy sites in the study area. Although weak, Fe (0.2219) indicated a positive linear coefficient and in addition very weak positive linear coefficients of Mg (0.0209), Ca (0.0130) and K (0.0090) were also calculated. Moderate to strong negative linear coefficients of both P (-0.7520) and Mn (-0.6165) as well as a very weak loading of Na (-0.0667) were also calculated. On this PC axis, the arid habitats of the Kalahari and Nama Karoo were distinct from the Grassveld, with Bushveld sites mostly central.

Based on the PCA of essential trace elements at all the geophagy sites in the study area, the first three principal components, all with eigenvalues > 1, explained a cumulative 83.5% of the variance, with nearly 70% explained by PC1 and PC2 alone (Appendix B, Fig. S2). Trace elements occurring in all geophagy sites in the study area, also isolated the Kalahari habitat separately (Fig.3.2) as in the case of major elements. The PCA furthermore grouped the Nama Karoo and Grassveld habitats and additionally portrayed a similarity between the Main Lick and Zaagkuil geophagy sites as well as a similarity between Renosterhoek and Kloppersкloof, all in the Bushveld habitat. The first factor explained 40.7% of the total variance in trace elements between all the study sites with moderate to weak positive loadings of Mo (0.4951), Se (0.3827) and Zn (0.0217). In addition, moderate to weak negative linear coefficients were also calculated for Co (-0.5334), Cr (-0.4888) and Cu (-0.2908). The second factor (PC2) explained 26.1% of the variance with moderate positive linear coefficients for Cu (0.6362), Zn (0.4130), Co (0.3790) and Se (0.3725), a weak positive loading for Mo (0.1244) but also a moderate negative loading for Cr (-0.3561).

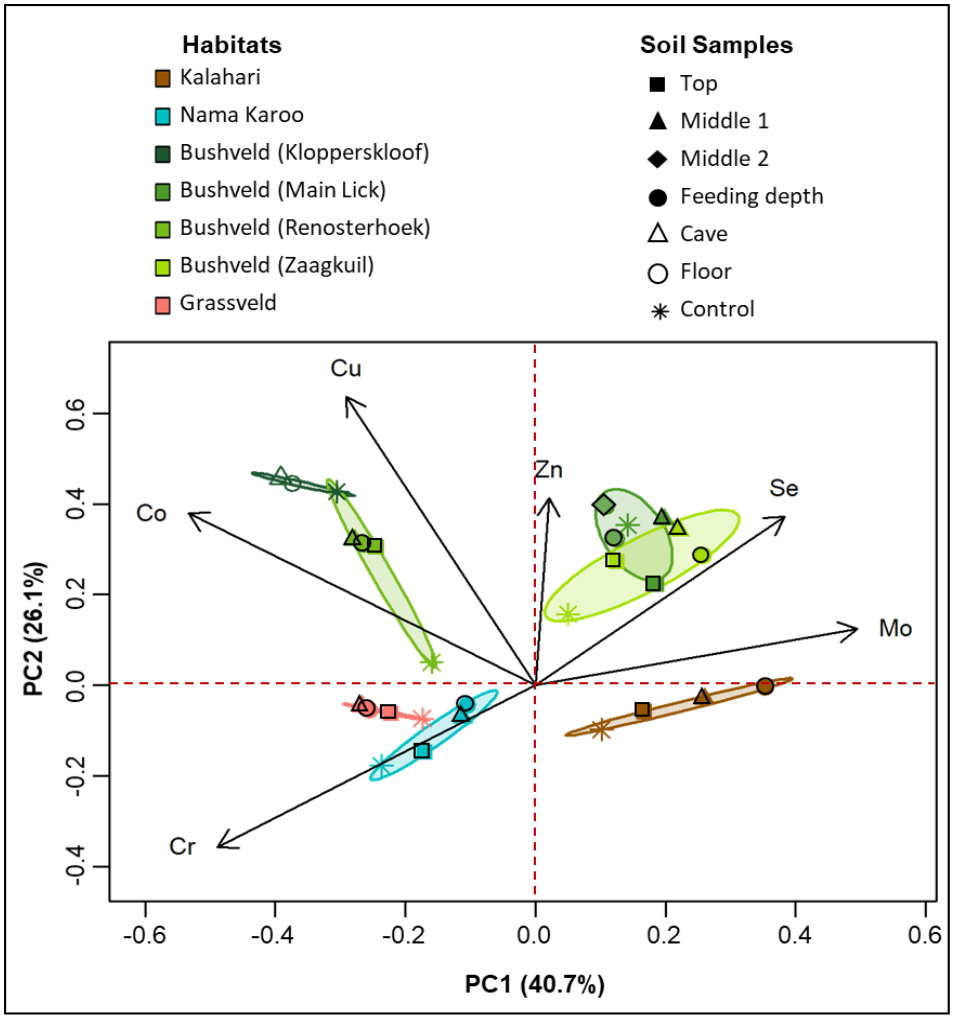

Figure 3.2. *Principal component analyses of essential trace elements in soil samples from different habitats in the study area.*

3.3.4 Within-site variations (Bushveld habitat)

The PCA of essential major elements in oxide form, including all the soil samples from different depths, showed an overall similarity between the Kloppersklоof, Renosterhoek and Zaagkuil lick sites, whereas the Main Lick was separated from these three sites on the first PC (PC1; Fig. 3.3). The first three principal components all had eigen values >1, and collectively explained ~90% of the total variance in the data (Appendix A, Fig. S3); the first two principal components on their own explained almost 72% of the variance. The first factor (PC1) accounts for 47.1% of the total variance and has moderate positive linear

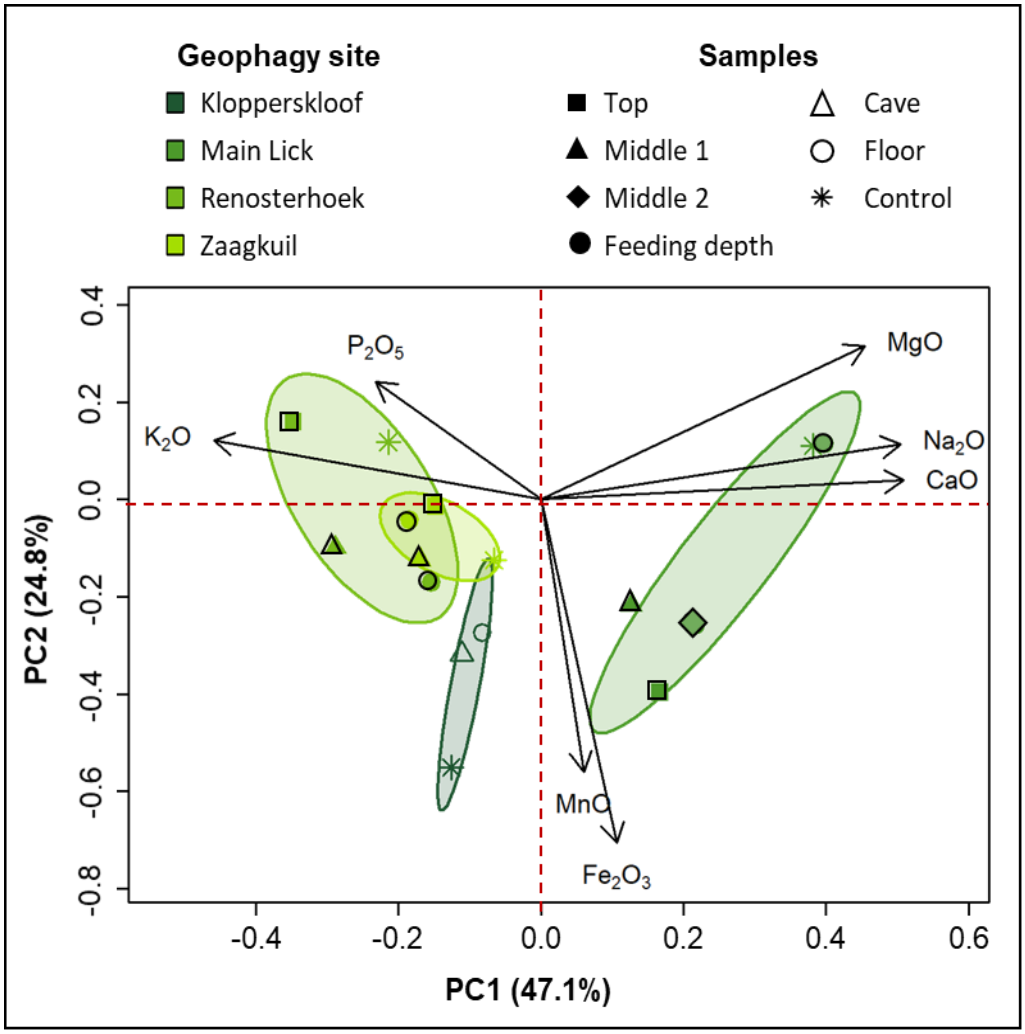

Figure 3.3. *Principal component analyses of essential major elements (oxides) in soil samples from four geophagy sites at Loskop Dam Nature Reserve.*

coefficients (loadings) of Ca (0.5092), Na (0.5047) and Mg (0.4545) in descending order, which were all higher at the Main Lick than the other sites, as well as weak positive linear coefficients of Fe (0.1061) and Mn (0.0599). The Main Lick site was also separated from the other geophagy sites by moderate and weak negative loadings of K (-0.4591) and P (-0.2321) respectively. The second factor (PC2), which accounts for 24.8% of the total variance, was distinct between the Renosterhoek and Zaagkuil licks on the one hand, and the Kloppersklоof lick on the other. PC2 had moderate to weak positive loadings for Mg (0.3150), P (0.2418), K (0.1214), Na (0.1139) and Ca (0.0389) in descending order but also high to moderate negative

loadings for Fe (-0.7067) and Mn (-0.5601), respectively. In considering the major elements of the soil at the feeding depth, the Main lick was separated from the other geophagy sites mainly because of higher concentrations of Mg, Na and Ca. The Main Lick was different from the other three geophagy sites based on lower amounts of K and P and also Mn and Fe although only slightly so (Fig. 3.3).

Principal component analyses of essential trace elements (Fig.3.4) showed an overall similarity between Main Lick and the Zaagkuil lick, as well as between the Kloppersкloof and Renosterhoek lick sites, with the two pairs separated by PC1. The first two principal components explained 81.6 % of the variance (Appendix A, Fig. S4). The first factor (PC1) accounted for 60.5 % of the total variance and had weak to moderate positive linear coefficients (loadings) of Se (0.4493) and Mo (0.3585) respectively as well as a very weak positive linear coefficient of Zn (0.0877). The geophagy sites at Kloppersкloof and Renosterhoek were, however, also separated from those at the Main Lick and Zaagkuil by moderate negative linear coefficients of Cu (-0.4185), Cr (-0.4842) and Co (-0.5023) in descending order. The second factor (PC2) accounted for 21.1% of the total variance in essential trace elements between the four geophagy sites (Fig. 3.4). Moderate positive linear coefficients were calculated for Mo (0.4309) and Cu (0.3408) while weak positive coefficients exist for both Se (0.1796) and Co (0.1234). Based on the trace elements at the feeding depth, however, the Main Lick site differed from that of Zaagkuil mainly because of the amounts of Mo and Se which were higher at the Zaagkuil geophagy site, but also because of the lower amounts of Zn at the Main Lick site. A weak negative loading of Cr was also calculated on PC2.

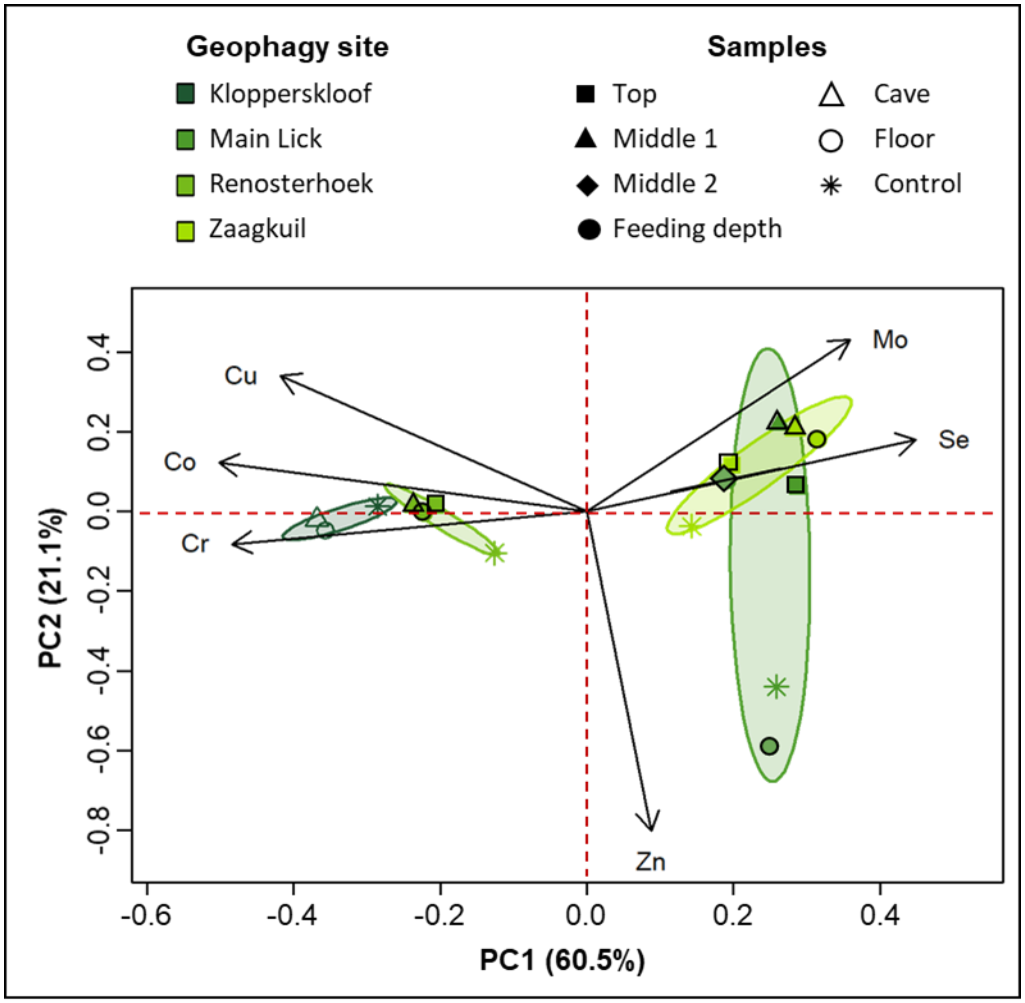

Figure 3.4. *Principal component analyses of essential trace elements in soil samples from four geophagy sites at Loskop Dam Nature Reserve.*

3.4 Discussion

3.4.1 Physical and chemical properties of geophagic soil

Based on the physical descriptions of all the geophagic soils utilised by herbivores in the study area (see Chapter 5), animals consumed soil of divergent colour, structure and composition. Soil colour varied from light grey in the Kalahari to light reddish brown and light brown in the Nama Karoo and Grassveld habitats respectively. Even within the same locality of the Bushveld habitat, geophagy sites with an assortment of soil colours, which varied from light brown, reddish brown, reddish, dark reddish brown and even reddish yellow, were utilised. According to Mahaney and Krishnamani (2003), the distinctive reddish colour of

geophagic soil is due to oxidation of Fe^{+2}. Although most geophagic materials mentioned in the literature had a reddish hue, many did not, and in agreement with Wilson (2003), it is unlikely that soil colour was the principal stimulus for geophagic behaviour.

In general, the bulk density of geophagic soil at the feeding depth were the same or lower than that of the control soil. The only exception to this was found in the soil of the cave at Kloppersкloof (Bushveld habitat) where the bulk density of the geophagic soil was slightly higher than that of the control soil sample. The bulk density of all the geophagic soils were however all of a medium texture and varied only between 1.20 and 1.31 g/cm3. This is characteristic of soil with about 50% pore space (Arshad et al. 1996) and can be classified as clay, sandy clay or sandy clay loam types (Linsley et al. 1982). It seems therefore that animals that engaged in geophagy, prefered to do so at specific areas where soil was not compacted. Furthermore, it seems that the presence of coarse fragments did not play an essential role in whether soil is consumed or not. As illustration, geophagic soil at the feeding depth at the Main Lick site in the Bushveld habitat had a high coarse fragment content, while soil consumed in the Kalahari had a low number of rock fragments. The texture of geophagic soils did, however, seem to follow a similar pattern in all four habitats. Geophagic soil at the feeding depth of all the feeding sites in general had lower fractions of sand with a higher percentage of clay. The only exceptions were geophagic soil form the Kalahari habitat as well as soil from the Kloppersкloof site in the Bushveld habitat. In the Kalahari, the fraction of sand remained the same as that from the as well as the control sample but a slight increase in the amount of clay, present in the geophagic soil at the feeding depth, was noticed. At Kloppersкloof however, soil from the cave had higher fractions of sand and lower clay contents compared with the control sample, while soil from the floor had almost the same fractions of both sand and clay as that from the control soil. Although Mahaney and Krishnamani (2003) stated that geophagic soil is either clay (>40% clay), silty-clay to clay-loam (27 to 40% clay), Diamond et al. (1999) reported on geophagy by birds in New Guinea utilizing soil with a clay content of only 13%.

The preference for clay soils of fine particles for geophagy may be a strategy by animals to prolong the retention time of digesta in the colon, which increases fermentation time (Mahaney et al. 2016). Because of the small particle size and therefore large surface area, as well as specific surface charge characteristics, clay minerals have the ability for taking up water, nutrients, organic molecules, and polymers (Theng and Yuan 2007). According to Caton et al. (1999) the selection of soils which is high in finely divided clay particles for ingestion, may be a strategy of orangutans (*Pongo pygmaeus*) to extend the retention time of digesta in the colon, which increases fermentation time. Ruminants might also gain similar benefits from the deliberate consumption of soil during geophagy, as well as accidental ingestion of soil during grazing (Abrahams 2012).

On the other hand, such soils may act as detoxification agents. This is because clay content is associated with CEC, a measure of the soil's ability to hold positively charged ions (Boul et al. 1997), and an important property influencing soil structure stability, nutrient availability and pH (Hazelton and Murphy 2007). Clay minerals are composed of sheets of Al-Si crystals, often with high CEC's (Cairns-Smith and Hartman 1986), whereas very few cation exchange sites occur in sand in silt fractions (Weil and Brady 2017). Experimental trials revealed that geophagic materials have the capability to bind high quantities of possibly toxic or unpalatable compounds (Wilson 2003), and it has been shown that soils with high clay content and CEC serve to reduce the bioavailability of alkaloids and tannins in a diet of fruit and seeds (Mahaney et al. 1996; Diamond et al. 1999; Gilardi et al. 1999; Brightsmith 2004; Brightsmith et al. 2008). Indeed, Diamond et al. (1999) went so far as to consider CEC a surrogate measurement for toxin binding capacity.

Soil reaction (pH) can be defined as the negative logarithm of the hydrogen ion concentration in solution, and is largely influenced by soil composition, processes of cation exchange, and hydrolysis reactions of the different organic and inorganic components in the soil (Thomas and Hargrove 1984). Local variations in soil pH are further influenced by seasonal climate, land management practice, and environmental pollution, factors which can

change soil pH values even over relatively short time scales (Batjes 1995). Nonetheless, pH of the lick sites included here showed consistent patterns across the four habitats, varying from alkaline (~8.5, but increasing towards the feeding depth) in the Kalahari, slightly alkaline (~7.9) at Main Lick of the Bushveld habitat and the Nama Karoo (~7.5), neutral in the Grassveld, and slightly acidic (5.9 to 6.5) at other Bushveld sites. For geophageous herbivores, alkaline soils, such as in the Kalahari and Nama Karoo, may function as a remedy for acidosis. The antacid function of geophagic soil, especially clays of alkaline nature, can buffer the gastrointestinal acidic pH (Gomes 2018). This is due to the ability of clay to adsorb fatty acids, one of the main products of fermentation, by effectively eliminating excessive acid production (Davies and Baillie 1988). Slightly acidic soils elsewhere may prevent proliferation of harmful bacterial species in the alimentary canal, and might also contribute to the detoxification of food particles (Johns, 1991). Acidic soils could also be effective in alleviating excess acidity, if they contain aluminous minerals as demonstrated by the use of reactive aluminium hydroxide in many pharmaceutical antacid preparations (Wilson 2003).

Soil organic carbon content has important influences on the ability of water to infiltrate soil, moisture holding capacity, and nutrient availability (Yost and Hartemink 2019). Further, organic carbon may also increase CEC and, ultimately, the inclusive adsorption capacity of soil and may also contribute as a source of N, P or S to soil (Young et al. 2008). Samples analysed here revealed higher organic carbon, and nitrogen content in geophagic compared with control samples at all sites. However, the small absolute amounts of organic C and N implies this property is not a major driver of geophagy, as concluded for geophagic soils elsewhere (Voros 2000; Young et al. 2008). Indeed, in many instances soil organic C decreased along the depth profiles towards the feeding level. Despite that soil organic content did not always increase from surface to feeding depth, herbivores showed some degree of selectivity for soil richer in organic carbon. Actually, both Voros (2000) and Young et al. (2008) suggested that animals usually avoid soils with high organic matter content. According to Mahaney et al. (2016), such avoidance prevents health or digestive illnesses linked with

organic matter, including soil bacteria involved in decomposition processes. This is worsened if high organic content is coupled with a pH around 6.5, optimal for survival and functioning of bacteria, blue-green algae, fungi and Protozoa – including harmful forms (Smith and Doran 1996). Such optimal microbial conditions were observed in this study at Zaagkuil in the Bushveld habitat.

3.4.2 Important mineralogical and elemental compositions of geophagic soils

Available information on the element requirements of ungulates in southern Africa is restricted to domesticated agriculture animals (Roosendaal 2014; Table 3.4). The only mineral that occurred in all the geophagy sites is quartz (SiO_2), which is not surprising as this is one of the most common minerals found in the crust of the earth (Emsley 2003). This mineral was identified as a major mineral (between 20 and 50 % occurrence) in soil from all the geophagy sites except at the Main Lick (Bushveld) where it only presents as a minor mineral (*vide* Appendix A, Table S1). The only geophagy sites where the amount of quartz was higher compared with the control sample were the Grassveld, and both the floor and cave at Kloppersкloof in the Bushveld habitat. According to Emsley (2003), Si is an element that is necessary for bone growth and is furthermore used in veterinary medicine to alleviate bloating in cows. However, quartz cannot be considered as a driver of geophagy. According to McNaughton et al. (1984), silica acts not only as a growth promotor in African grasses, but also evolved as a plant defense strategy against herbivory, since the coarse, hard angular particles have the potential to damage dental enamel during ingestion (Ngole and Ekosse 2012). Thus, the lower quartz content of geophagic than control soils, with the exception of the Grassveld and Bushveld (Kloppersкloof) habitat, and the general decrease downwards through soil profiles at least in the Kalahari and Bushveld habitats, likely contributed to geophagy occurring at the depths observed in this study. However, quartz is an inactive mineral that contributes negligible value to accessible soil nutrients (Hardy and Cornu 2006) and Si is not listed by Roosendaal (2014) as an element that is required on a daily basis by ungulates.

Table 3.4. *Daily element requirements of South African ungulates as prescribed by Roosendaal (2014).*

Element	g/kg body mass	mg/kg body mass
P	6	
Ca	12	
S	2.5	
Fl	0.04	
Na	1.2	
Co		0.15
Mn		60
Zn		60
I		0.75
Cu		5
Se		0.15
Fe		50

In the identification of important minerals and major elements in geophagic soils, a variety of minerals were identified to be of importance across all habitats (*vide* Tables 3.2 and 3.3). The Ca-containing minerals dominated in the drier habitats of the Kalahari (ankerite, calcite and glauberite), Nama Karoo (calcite) and Grassveld (clinopyroxene) while it was less important in the Bushveld habitat (smectite, only at the Main Lick site). Ca, as major element was furthermore also prominent in the Kalahari, Grassveld as well as the Kloppersklоof geophagy site in the Bushveld (*vide* Table 3.3). Although no mineral contained P, this element was identified to be important in soil from the Main Lick in the Bushveld habitat. The identification of Ca and P as important minerals concurs with observations made by Grasman and Hellgren (1993), who noted that animals in dry environments are susceptible to a lack of P and Ca in their diet. Calcium is essential to almost all organisms and performs a variety of functions (Emsley 2003), while both Ca and P have important functions as structural components in the animal body (Cherian 2020). According to Roosendaal (2014), Ca (12 g/kg body mass) and P (6 g/kg body mass) are the elements that are required in the largest quantities on a daily basis by ungulates (Table 3.4). The majority of Ca (99%) and P (80%) in

the animal body occurs in bones and teeth as hydroxyapatite (Cherian 2020). The remaining Ca is distributed in cellular fluids from where it becomes involved in a variety of metabolic and physiological functions including blood coagulation, nerve impulses and muscle contractions, activation of enzymes or activators of ion channels (Cherian 2020). The remaining P remains in the soft tissues of the animal body, and is responsible for energy metabolism as part of phosphorylation reactions. Within the diet of herbivores, the relationship between Ca and P is very important as high P in the diet can inhibit Ca absorption (Cherian 2020). According to recommendations for livestock, the optimum ratio of Ca:P is 1:1 for small animals (Cherian 2020) and 2:1 for large animals (Roosendaal 2014; Cherian 2020). According to He et al. (2014), leaves of annual and perennial desert plants contain higher concentrations of P compared with shrubs. Further, because P contents of fresh growth in plant species increase during the early rain in the Kalahari (Stapelberg et al. 2008), animals might well ingest soil Ca to maintain this crucial ratio.

The importance of Ca in geophagic behaviour amongst large mammalian herbivores in the Kalahari is further supported by observations made at a calcrete pan, about 20 km north-east of the study site, where gemsbok consume calcrete rock on a regular basis (Fig 3.5. A). Deep concave cavities with visible teeth marks in the soft calcrete (Fig. 3.5. B) occured all over the pan. Similar observations where gemsbok consume calcrete rock were made in the Kgalagadi Transfrontier Park. At a public picnic site (Melkvlei) these antelope utilise calcrete to such an extent that cave-like cavities were formed on the vertical rockface (Fig. 3.6. A). In the same area, where park officials used calcrete for road maintenance, gemsbok were observed to consume soil from recently maintained roads (Fig. 3.6.B).

An observation was also made that many antelope of different species have deformed horns (Fig. 3.5. A; Fig.3.6. B) which might indicate a shortage of minerals. Bredin et al. (2008) found that osteophagy, the eating of bones, as observed in P deficient cattle, is associated

Figure 3.5. *A gemsbok cow with deformed horn (yellow arrow) consumes calcrete sedimentary rock at a pan in the Kgalagadi Wildlife Management area in Botswana (A). Visible teeth marks in the soft calcrete sedimentary rock (B). (Source: HJB Butler©).*

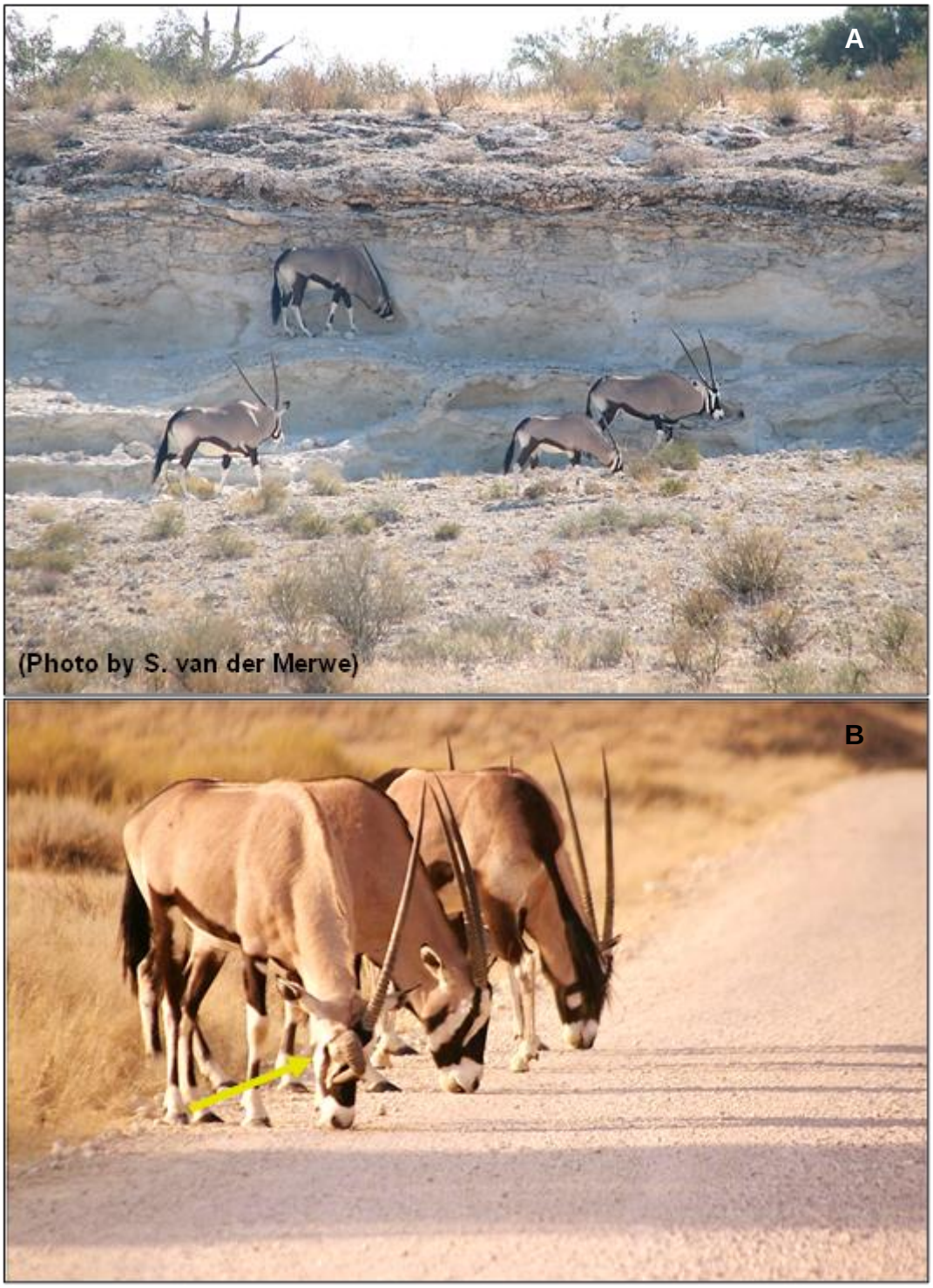

Figure 3.6. *Gemsbok consume calcrete rock from a calcrete rock face (A) as well as recently maintained roads (B) in the Kgalagadi Transfrontier Park. Yellow arrow (B), deformed horn of a gemsbok cow. (Source: HJB Butler©).*

with a decline in the inorganic phosphate fraction of blood plasma and a withdrawal of Ca and P from the reserves in bones. Cáceres et al. (2011) stated that the metabolism of P and Ca are closely connected, and linked osteophagia among Cervidae to the maintenance of the balance between these two minerals, and furthermore concluded that this behaviour was the result of a lack of P and Ca in the diet of the animals. The importance of calcium is furthermore elevated during certain physiological states of female animals. According to Suttle (2010), around one-fifth of Ca in the skeleton of sheep and dairy cows is mobilized during parturition and the onset of lactation. Pletscher (1987) found that the production of milk required 15% of the total Ca budget in white-tailed deer (*Odocoileus virginianus*) does. Other studies on geophagia, including Cowan and Brink (1949), Jones and Hanson (1985), Holl and Bleich (1987), Coates et al. (1990) and Heard and Williams (1990), also mentioned the importance of Ca in the mineralogy of the ingested soil. According to Roosendaal (2014), South African ungulates require a maximum of 12 g/kg body mass of Ca on a daily basis (Table 3.4). This implies that a gemsbok male with a body mass of $\bar{x}$ 176 kg (Estes 1991) requires a maximum amount of 2.112 kg, and a gemsbok female with body mass of $\bar{x}$ 162 kg (Estes 1991) requires a maximum of 1.944 kg, of Ca on a daily basis. It is therefore possible that herbivore mammals also consume Ca-rich soil to replenish the shortfall of this element in their diet.

Electrolytes, including Na and K, play a vital role in maintaining the acid-base balance, signal transductions across cell membranes, as well as osmotic pressure in intra- and extracellular fluids (Cherian 2020). However, these electrolytes cannot be stored in body tissues, and thus need to be supplemented in the diet (Cherian 2020). According to Roosendaal (2014), animals need 1.2 g/kg body mass of Na on a daily basis (Table 3.4). According to Kreulen and Jager (1984), animals ingest soil at Kalahari pans mainly for salt (NaCl). In this study, minerals that contain Na as element were identified as important in the Kalahari (glauberite and halite), Grassveld (clinopyroxene) as well as in the Bushveld (smectite, only at the Main Lick site) habitats. As a major element in the soil, however, Na was also identified to be an important driver for geophagy in the Nama Karoo, as well as

Renosterhoek in the Bushveld. Results from a previous study at the same location in the Bushveld by Eksteen and Bornman (1990), mentioned elevated levels of Na at the Main Lick site. In this study, results concur with that of Eksteen and Bornman (1990) as Na was found at higher levels in the geophagic soil compared with the control sample, although Na was not identified to be the main attraction for geophagy at the Main Lick site.

Potassium was identified as an important stimulant for geophagy in the Nama Karoo (muscovite) as well as the Main Lick, Renosterhoek and Zaagkuil geophagy sites in the Bushveld (muscovite and orthoclase), while it was also important as an element in the Nama Karoo. According to Singh and Schulze (2015), minerals including K-feldspars (orthoclase) and micas (muscovite), which are widely distributed in most soil types, act as important reservoirs for K as most of the available K in soil (90%) are found in the structures of these minerals.

Depending on the mineral composition, elements of Fe or Mg might also be considered to be drivers of geophagy. Soil might be a source of Fe from ankerite (Kalahari), clinopyroxene (Grassveld) or goethite (Main Lick in the Bushveld), hematite (all geophagy sites in the Bushveld) or ilmenite (Renosterhoek and Zaagkuil in the Bushveld). Although Fe is present in all animal body cells, the largest proportion (>65%) is found as a component of haemoglobin (Cherian 2020). Iron is furthermore a constituent of several metalloenzymes and during an increase in metabolic need, such as periods of active growth and gestation, the absorption of Fe in the body increases (Cherian 2020). The daily requirement of Fe by South African ungulates is 50 mg/kg body mass (Roosendaal 2014). Most animals are, however, efficient in conserving Fe and loss is therefore minimal unless it is due to blood loss during parasitic infections, injuries or parturition, in which case anaemia and reduced growth occurs (Cherian 2020).

Magnesium, an essential element for nearly all living organisms (Emsley 2003), is the third most abundant element in the body of animals. It is present as phosphates and carbonates, is found in bone, the liver and skeletal muscle cells, where it provides a role in the forming of structures and activation of enzymes that split and transfer phosphates (Cherian 2020). Magnesium is also important, along with Ca, Na and K, in the contraction and transmission of nerve impulses (Cherian 2020). According to Cherian (2020), herbivores that feed on native pastures in the spring season, are at risk of a condition referred to as grass tetany, a highly fatal disease associated with low levels of Mg in the blood. High levels of N and K, usually present in lush plant growth during spring, inhibit Mg absorption and causes hypomagnesemia in animals (Cherian 2020). Magnesium could be supplemented by means of geophagia as a component of ankerite and sepiolite (Kalahari) or clinopyroxene (Grassveld). Apart from conformation as important element in soil at both habitats, it was also identified to be in soil from the Main Lick and Renosterhoek geophagy sites in the Bushveld habitat.

The occurrence of kaolinite as important stimulus for geophagy in the Nama Karoo and Bushveld habitats indicated that soil at these sites were consumed for reasons other than mineral or elemental supplementation. The consumption of clay with high amounts of kaolinite has been reported for birds (e.g., Symes et al. 2006) and mammals including primates (e.g., Davies and Baillie 1988; Krishnamani and Mahaney 2000; Voros et al. 2001), forest elephants (*Loxodonta Africana cyclotis*) (e.g., Klaus et al. 1998), and ungulates (e.g., Panichev et al. 2014). A 1:1 clay mineral (Si:Al = 1:1), like kaolinite, is very effective against gastric disorders (Davies and Baillie 1988, Voros et al. 2001) and according to Davies and Baillie (1988), red leave monkeys (*Presbytis rubicunda*) also ingest kaolin for the elimination of excessive acid production in the forestomach. According to Mahaney et al. (2016), great apes, such as orangutans (*Pongo pygmaeus*), which are prone to diarrhoea because of a leaf-eating diet, may control or partially alleviate this nearly constant ailment by ingesting soil rich in 1:1 (Si:Al) clay minerals such as kaolinite. Furthermore, kaolinite also has the ability to absorb bacteria

and their toxins (Said et al. 1980) and can therefore decrease the load on the detoxification system of animals that consume neutralising alkaloids with clay minerals (Davies and Baillie 1988).

Chemical trace elements that were identified to be possible stimulants for geophagy include Mn, Cr, Co, Zn and Mo (*vide* Table 3.3). Manganese was identified as important in the Kalahari, Grassveld as well as the Bushveld (Main Lick and Renosterhoek). As trace element, Mn is a dietary essential for all animal species (Emsley 2003; Cherian 2020) and although it is widespread in the animal body, it is concentrated in bone tissue and the liver (Cherian 2020). Apart from being essential for bone formation, large quantities of Mn are located within the mitochondria, where it activates metal-enzyme complexes, and assists in lipid metabolism in cholesterol and fatty acid synthesis (Cherian 2020). Chromium, a possible stimulant for geophagy in the Grassveld and Bushveld (Zaagkuil lick site), is an essential nutrient in animals, and is needed to assist the body to utilise glucose (Emsley 2003; Cherian 2020). Animals with a Cr deficiency in their diet have a reduced ability to utilise glucose as an energy source; diabetes with reduced cholesterol levels are common symptoms of this deficiency (Cherian 2020).

Cobalt was identified as an important nutrient supplement form geophagic soil in almost all the geophagy sites with the exception of the Main Lick and Zaagkuil sites in the Bushveld habitat. According to Emsley (2003) and Cherian (2020), ruminant animals have high cobalt requirements due to the requirement for rumen microbes to synthesise vitamin B12 (Emsley 2003; Watanabe and Bito 2018; Cherian 2020), the only vitamin that is synthesised only by microorganisms (Watanabe and Bito 2018; Cherian 2020). Vitamin B12 is needed in the formation of red blood cells and DNA (Emsley 2003) and Co-deprived ruminants suffer from anaemia (Emsley 2003), have reduced appetite, and ultimately experience emaciation (Cherian 2020). Vitamin B12 also assists in the maintenance of nerve tissue and is functional in the release of energy from carbohydrates and fats (Emsley 2003).

Zinc was identified to be a possible attractant for geophagia in the Nama Karoo, Grassveld and three of the Bushveld geophagy sites namely Main Lick, Renosterhoek, and the cave site at Klopperskloof (*vide* Table 3.3). Widely distributed in the animal body, Zn forms part of more than 200 enzymes which regulate growth, development, longevity and fertility (Emsley 2003). It is also a component of insulin and therefore plays a part in carbohydrate metabolism (Cherian 2020). As nutritional supplement, Mo was found to important only in the Kalahari and at Zaagkuil in the Bushveld. An essential element to all animal species, Mo is mostly found in bones, skin, liver and kidneys (Emsley 2003). Molybdenum is also a cofactor of xanthine oxidase which produces uric acid, a way in which the body excretes nitrogen waste.

Although Se was not identified to be the main driver for geophagy at any geophagy site in the study area, this element is worth mentioning. This element has the lowest concentration of all nutrient elements in igneous bedrock and is unevenly distributed in landscapes, frequently at deficient levels for herbivores, especially to wild populations that are confined to remnant portions of their historical distribution (Flueck et al. 2012). Identified as an essential micronutrient in all animals, adequate levels of Se are vital for reproductive performance, bone metabolism, immune function and iodine metabolism (Flueck et al. 2012). Amongst other functions, Se is a component of selenoproteins in the blood and muscle of animals, and is also required for the forming of sperm; deficiency of this element causes nutritional muscular dystrophy in all species (Cherian 2020). Selenium occurs in geophagic soil of the Main Lick and Zaagkuil sites of the Bushveld habitat, but at very low concentrations (< 1 mg/kg soil). Concentrations of Se did not increase through the soil profile, nor was it higher in geophagic than control soils. In a previous study at the same location by Stephenson et al. (2011), Se was, however, identified to be one of the main drivers of geophagy with concentrations of 0.3 mg/kg in the consumed soil. One reason for the difference from the present study is they used inductive coupled plasma spectrometry (ICP-MS), a much more sensitive method that can detect element concentrations < 1 mg/kg. According to Cherian

(2020), Se is required by ungulates in very small quantities (0.02 mg/kg), whereas concentrations of 5mg/kg and more are considered to be toxic.

3.5 Conclusions

Although geophagic soil across the four diverse habitats share some common physicochemical properties, several differences do occur. Based on the results of this study, it is unlikely that soil colour is the principal stimulus for geophagic behaviour as claimed by some studies. In general, animals consume soil with lower quantities of quartz, and this might be one explanation for the preference to consume soil at a specific depth. Although geophagic soils have in general lower fractions of sand and higher clay contents, animals prefer to establish geophagy sites in soil with low bulk density where soil is not compacted. The volume of coarse fragments in the geophagic soil however do not play a major role, as animals consume soil with very low coarse fragments, as seen in the Kalahari habitat, but even in soil with relatively high amounts of coarse fragments as evident from the geophagy sites in the Bushveld habitat. It is furthermore concluded that high CEC values are not necessarily a prerequisite for geophagic soil. In this study, even soils with moderate CEC, representing a wide range of pH levels, were consistently consumed by herbivores.

According to this study, animals ingest soil deliberately for different reasons in the four study areas. In the more arid habitats like the Kalahari, Nama Karoo and to a lesser extent Grassveld, the main reason for geophagy was identified to be the supplementation of Ca present in geophagic soil. However, secondary benefits in the form of salt (Halite) or other essential minerals mainly Fe, Mg, K, Mn, P, Cr, Co, Zn and Mo might strengthen this behaviour. In addition to Ca, animals supplement their nutritional needs, specifically Na, Mg, Mn, Co and Mo by eating soil. In the Nama Karoo animals ingest soil rich in Na, Fe, K, Co and Zn. The presence of kaolinite, although at low quantities, might relieve animals of gastric disorders. The craving for salt seems not to be the driving force behind geophagia in the

Grassveld habitat. Rather, geophagic soil from this habitat supply animals, apart from Ca, mainly with essential minerals including Mg, Mn Cr, Co and Zn.

The occurrence of kaolinite in all the geophagic soils in the Bushveld habitat indicated that animals might consume this soil for relief of gastric disorders, since this habitat mainly includes browser species that are subjected to high secondary plant compounds. The benefits of nutritional supplements of essential elements cannot, however, be discarded. Geophagic soil from the Main Lick site can supplement Mg, Mn, Ca, Na, P, Cr, Zn and probably Se. At Renosterhoek, animals can obtain Fe, Mg, Mn, Na, Cr, Co, and Zn while ingesting soil from Zaagkuil, animals can supplement their diet with Mn, Cr, and Mo. Although Ca seems to be of least importance at the Kloppersklоof geophagy site, Co and Zn were also identified to be a possible reason why animals ingest soil from that specific site. The occurrence of the iron-containing clays, hematite and ilmenite, in all the geophagy sites in the Bushveld habitat, might be an important indication to the role of Fe in the stimulus of geophagia in the Bushveld habitat. However, only at Renosterhoek, Fe seems to be the driving factor that attracts animals to this geophagy site. In conclusion, it seems therefore that large mammalian herbivores, that are free to roam over large areas, do not ingest soil for the main purpose of mineral or element supplementation. In small confined areas however, such animals obtain scarce nutrients from geophagy sites or may even find relief of gastric ailments.

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Chapter 4: Evaluation of nutritional and defensive roles of geophagy

4.1 Introduction

The preceding chapter provided information about the possible mineral and nutritional gains of geophagy in the study area. Several other studies, all with variations of chemical elements in geophagic soil that explained the reason behind geophagy, were also mentioned. Whether animals actually obtain nutritional supplementation from geophagic soils is a question that remains to be answered. According to Wilson (2003), total chemical analyses of geophagic soil provide little information unless such results are supported by physiologically based extraction tests, which is essential in studies about the nutrient supplementation role of geophagy. Most studies, however, on bioavailability of nutrients from geophagic soil focused on the physiology of humans (e.g., Hooda et al. 2002; Dominy et al. 2004; Yanai et al. 2009; Eigbike et al. 2022). Different simulations, such as the physiological based extraction test (PBET) developed by Smith et al. (2000), as well as the TNO Gastro-Intestinal Model (TIM) as described by Minekus (2015) of the human intestines, have been used to study the bioavailability of essential and toxic elements in soil consumed by humans. These simulations of the human intestines, however, involved a cocktail of pepsin and various organic acids which was adjusted to pH levels which was similar to that of conditions in the human gut. While this might be possible for humans or *in vitro* models, it proves to be difficult for animals, especially for free roaming animals in the wild since only a few studies have evaluated the bioavailability of elements to animals from geophagic soil. The reason for this is that techniques would require a simulation of the biochemistry of the alimentary canal of the species – or even the individuals - under investigation, with consideration of the reproductive state and physiological needs of such animals.

In an attempt to elucidate on the bioavailability of chemical elements in geophagic soil to chimpanzees (*Pan troglodytes*), some studies (Aufreiter et al. 2001; Reynolds et al. 2015)

also used *in vitro* methods, but these experiments did not simulate the digestive tract of the species under investigation. In simulating the intestinal conditions of chimpanzees in a Caco-2 cell culture model, Pebsworth et al. (2019) concluded that iron was bioavailable from geophagic soil under physiological conditions. In the same experiments by using a physiologically based extraction test (PBET), Pebsworth et al. (2019) concluded that Ca and Mg were released from geophagic soil. Wilson (2003) and Pebsworth et al. (2019), however, emphasised the importance of *in vivo* studies to test the bioavailability of nutrients in geophagic soil to the consumer.

The advantage of *in vivo* models for assessing the bioavailability of nutrients from geophagic soil to consumers was illustrated by Seim et al. (2016) who fed broiler chickens (*Gallus gallus*) with varying dosages of geophagic material to test the bioavailability of iron. The use of experimental animals, such as chickens, do not simulate the diverse complexity of elementary canals found in herbivores. As stated by Owens and Basalan (2016), the complexity of particularly the ruminant digestive system, necessitates a greater assortment of methods to study nutritional physiology than that of any other animal. According to Castillo and Hernández (2021), it is impossible to replicate the complex system of the reticulo-rumen in a laboratory. To date, surgical fistulation and cannulation of the rumen is the best method to conduct studies on the physiology and biochemistry of the ruminant digestive system (Castillo and Hernández 2021). While fistulas are widely used in ruminant digestive research of domesticated animals, this method requires tamed or semi-tamed animals which must be housed for regular observations. The difficulty of this procedure for game species, is evident in the few studies involving wildlife species, as have been trialled for white-tailed deer (*Odocoileus virginianus*) (Veteto et al. 1972), reindeer (*Rangifer tarandus*) (Dieterich 1972), topi (*Damaliscus lunatus jimela*) and wildebeest (*Connochaetes taurinus*) (Usenik et al. 1977), impala (*Aepyceros melampus*) (Visser et al. 1990) and water buffalo (*Bubalus bubalis*) (Rafee et al. 2015). Unless mechanisms, such as ruminal fistulation and cannulation are used to

investigate the nutritional effect of geophagy on wild herbivores, other methods must be implemented.

A method whereby excreted soil from geophagic behaviour, found in faeces of animals are analysed, might be a method to overcome the difficulty in determining assimilation of chemical nutrients by means of *in vitro* and *in vivo* studies. The amount of soil ingested as well as retention time of such soil in the digestive tract of animals, will determine the amount of soil that is excreted, per unit mass. However, if enough geophagic soil is excreted by a single individual, chemical analyses on such soil might provide information on chemical elements that were assimilated from geophagic soil. By implication, this might elucidate on the nutritional function of geophagy, by acting as a proxy for *in vitro* or *in vivo* situations. Panichev et al. (2014) as well as Stephenson et al. (2010) also reported on clay-containing dung pellets from the Caucasian State Biosphere Reserve (Russia) and Loskop Dam Nature Reserve (South Africa) respectively. The presence of argillaceous dung, with no visible macro-organic matter present (Fig 4.1), found in close vicinity of geophagy sites in this study, therefore provided an opportunity to test the nutritional function of geophagy.

Furthermore, the deliberate ingestion of soil by humans has long been suspected to be a source of soil-transmitted helminth infections (Halsted 1968; Hunter 1973; Wong et al. 1991; Glickman et al. 1999; Young et al. 2007; Ivoke et al. 2017). Although Young et al. (2007) concluded that geophagy poses no threat of parasitic infestation to pregnant women in Pemba (Tanzania), Pebsworth et al. (2012) found that geophagic soil in the Wildcliff Nature Reserve (Western Cape, South Africa) was a potential source of soil-transmitted helminth infections to chacma baboons (*Papio ursinus*). On the contrary, Bicca-Marques and Calegaro-Marques (1994) as well as Knezevich (1998), concluded that geophagy provided protection against parasite infection to black howling monkeys (*Alouatta caraya*) as well as rhesus macaques (*Macaca mulatta*) respectively. According to Young (2010), there are two mechanisms by which geophagic earth may be protective: by reducing the permeability of the gut wall to toxins and pathogens and by binding directly to toxins and pathogens. Geophagic earth, especially

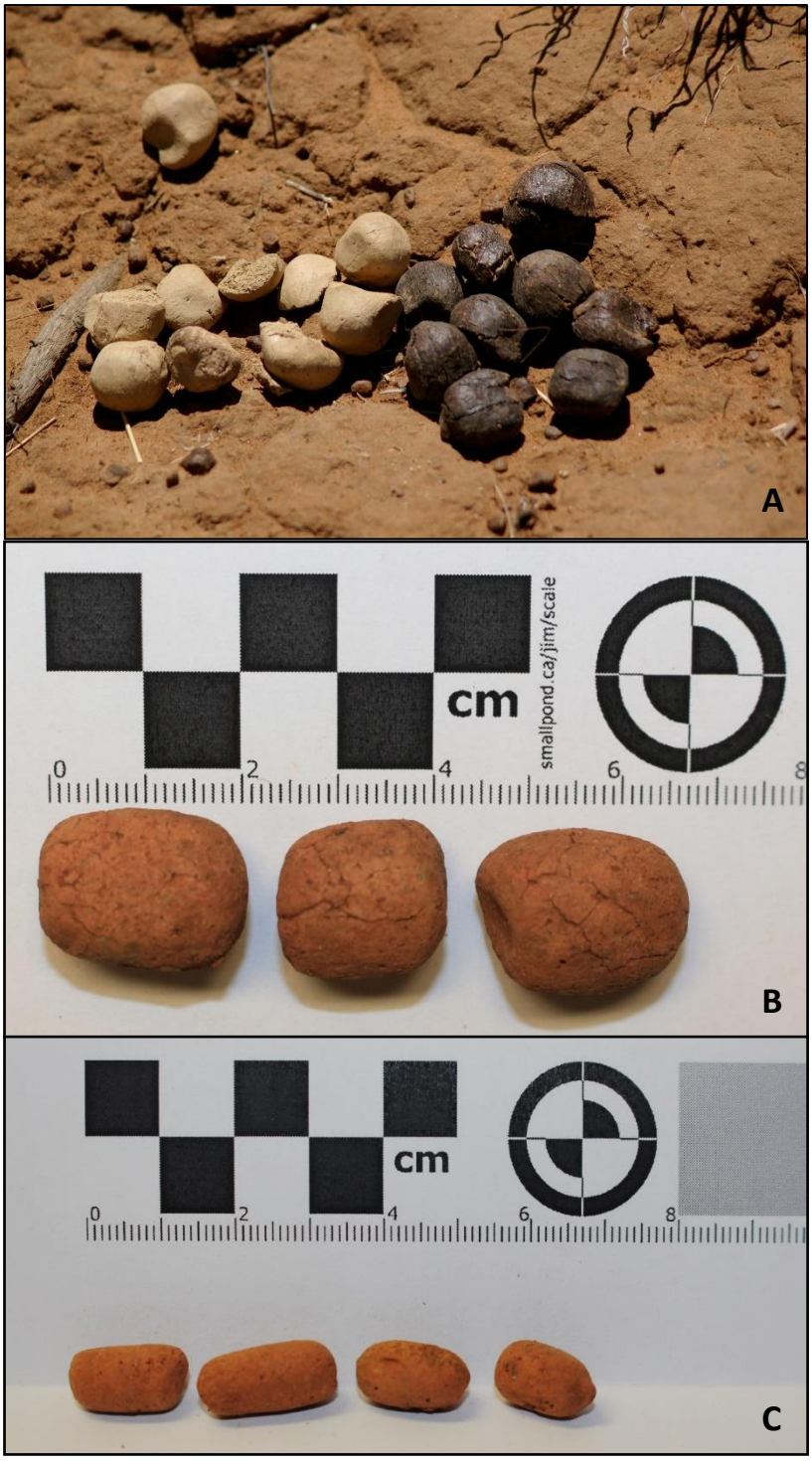

Figure 4.1. *Clay containing dung pellets of kudu to the left of normal dung pellets at Willem Pretorius Game Reserve (A) and clay containing dung pellets of kudu (B) and impala (C) found in the vicinity of the Main Lick site at Loskop Dam Nature Reserve. (Source: HJB Butler©)*

soil rich in clay, have the potential to bind with and thereby reinforce the protective mucosal layer and/or enhance mucosal secretion, thus reducing the permeability of the intestinal walls

(González et al. 2004). Geophagic soil can also be protective by binding directly to toxins, parasites, and other pathogens whereby render them unabsorbable by the gut or by inhibit their respiration (Young et al. 2011). Various clays found in geophagic earths have the ability in binding pathogens, including viruses (Lipson and Stotzky 1983; Rey 1989; Dornai et al. 1993), fungi (Smith and Carson 1984; Lavie and Stotzky 1986a,b; Phillips et al. 2008), and bacteria (Maigetter and Pfister 1975; Said et al. 1980; Ditter et al. 1983; Gardiner et al. 1993), as well as toxins, including poisonous herbicides (Okonek et al. 1982; Lotan et al. 1983), and plant secondary compounds (Johns 1986; Johns and Duquette 1991; Gilardi et al. 1999; Houston et al. 2001; Dominy et al. 2004). It was also postulated by Krishnamani and Mahaney (2000) that geophagic earth might prevent larger pathogens such as geohelminths from colonizing hosts although the mode by which this occurs has not been explained.

According to Altizer et al. (2003), the organised nature of herd-forming animals such as herbivores, provides ample opportunities for the transmission of parasites. The herding of animals increases contact between susceptible and infected individuals and as found by Côté and Poulinb (1995), Ezenwa (2004), and Burger et al. (2012), an increase in group size of parasite hosts, can directly be linked to increases in both prevalence and intensity of transmittable parasites. Although Ezenwa (2002) found that wild bovids avoided areas with concentrations of dung while feeding, possibly to lower the risk of exposure to nematode infections, areas with high concentrations of faeces cannot always be avoided. An increase in the density of wild herbivores around waterholes, which is amplified in drier areas and during drier seasons, increases the risk of potential faecal-oral parasite transmissions (Cross et al. 2004; Titcomb et al. 2021). The aggregation of animals, and therefore the prevalence of constant fresh faeces, at places such as waterholes and geophagy sites where contact with other individuals is unavoidable, could therefore increase the rate of parasite infections. Analysis of the relationship between prevalence of parasite eggs in argillaceous dung pellets with their relative soil content, will help clarify on the potential benefits that geophagic soil might have on the eradication of parasite eggs and furthermore, elucidate on the risks of

faecal-oral parasite transmission to herbivores that consume soil at established geophagy sites.

The first objective of this chapter was to evaluate the assimilation of chemical elements from geophagic soil by some large herbivore mammals. If there does exist a nutritional basis for geophagy, it follows that herbivores should be able to assimilate at least some of the mineral elements found in such soils. This was approached by analysing the relationship between the elemental composition of lick soils and clay-containing dung pellets. A second objective was to assess the potential eradication of faecal parasite eggs by the ingestion of geophagic soil. This was done by analysing the relationship between faecal egg load and faecal soil concentration by means of a standard egg flotation method.

4.2 Methodology

Fresh dung from various herbivore species were collected at geophagy sites and included eland (*Taurotragus oryx*), from Jack's Pan in the Kgalagadi district No.12, Tussen-die-Riviere Game Reserve, and Willem Pretorius Game Reserve, blesbok (*Damaliscus pygargus phillipsi*) from Tussen-die-Riviere Game Reserve, gemsbok (*Oryx gazella*) from Jack's Pan in the Kgalagadi district No.12 and Tussen-die-Riviere Game Reserve, impala (*Aepyceros melampus*) from Loskop Dam Nature Reserve, kudu (*Tragelaphus strepsiceros*) (Tussen-die-Riviere Game Reserve, Willem Pretorius Game Reserve, Loskop Dam Nature Reserve), nyala (*Tragelaphus angasii*) from Loskop Dam Nature Reserve, red hartebeest (*Alcelaphus buselaphus*) from Jack's Pan in the Kgalagadi district No.12 and Tussen-die-Riviere Game Reserve, and springbok (*Antidorcas marsupialis*) from Jack's Pan in the Kgalagadi district No.12 and Tussen-die-Riviere Game Reserve. All samples were taken during the winter months (June, July, and August) as, according to Horak (1980), this is the time when prevalence of internal parasites of bovids are high. Faecal droppings were collected in the early morning within 10 min. after an animal was observed to defecate. Sampling of droppings was done from centre of the faecal mass, and only those pellets that were not in

contact with soil or substrate were collected. At least 20 dung pellets from each individual animal were divided equally and placed in two separate paper bags, one for mineralogy and chemical analyses, and one for faecal egg counts. Pairs of paper bags were sealed and labelled with the geophagy site name, date of collection, and species as well as a unique identification number. Samples destined for faecal egg counts were placed in a cooler box with ice packs until, within 5 h of sampling, they were analysed using a standard egg flotation method (see section 4.2.2).

Without direct observation of defecation, dung pellets that were still warm and moist, and consisted of high levels of clay, expelled by various antelope species, were collected in close vicinity (radius of 20 m) of different geophagy sites at Loskop Dam Nature Reserve (Bushveld habitat) as well as Willem Pretorius Game Reserve (Grassveld habitat). Pellets were identified according to descriptions in Walker (1996) and Stuart and Stuart (1994). Argillaceous dung pellets, identified as kudu dung, were collected from the Main Lick, Renosterhoek and Zaagkuil sites at Loskop Dam Nature Reserve as well as the geophagy site at Willem Pretorius Game Reserve, while those identified as impala dung were found only at the Main Lick (Loskop Dam Nature Reserve). Similar clay containing dung pellets, identified as nyala dung, were collected at Kloppersкloof geophagy site (Loskop Dam Nature Reserve). After colour matching with soil from the nearby geophagy site, it was ascertained that the clay, present in the collected dung pellets, was consumed at the specific geophagy site where it was collected from. These samples were treated the same way as previously described.

4.2.1 Assimilation of minerals and chemical elements

At least 10 dung pellets from each animal that was collected for the purpose of mineral and chemical analyses, were put in labelled glass petri dishes, crushed and soaked with double distilled water for two days. In order to remove any plant material, crushed dung was rinsed through a series of soil sieves with mesh sizes that ranged from 2.0 mm, 1.0 mm, 0.50 mm, 0.25 mm, 0.106 mm, and 0.053 mm. Any soil in the dung was collected at the bottom of the sieves after which the soil containing fluid was filtrated with a numbered Whatman

qualitative filter paper with particle retention of 11µm. The filter paper and residue were then air dried and the dry soil was scraped from the paper and collected in a similarly marked polytope glass tube.

Since a minimum of 15 mg of soil is needed for XRD and XRF analyses, not all soil collected from the dung pellets could be analysed for chemical compositions. Only dung pellets that consisted almost entirely of clay, found at lick sites in Willem Pretorius and Loskop Dam Nature Reserves, identified as belonging to kudu, impala, or nyala, could be analysed. Mineralogical analyses, including primary and secondary minerals as well as major and trace elements of clay containing dung pellets were analysed the same way (XRD and XRF respectively) as that of geophagic soil as described in Chapter 3, section 3.2.3.

4.2.2 Transmission of parasite eggs

To determine the prevalence of parasitic eggs in faecal matter, the modified McMaster test as described by Zajac and Conboy (2012) were used. Within five hours of collection, 10 dung pellets were crushed with a stainless-steel teaspoon in a glass petri dish and the dry faecal matter was well mixed. From this, 4 g of faecal material was mixed with 56 ml of flotation solution (sodium nitrate with a specific gravity of 1.22). The mixture was stirred for five minutes and strained through a metal tea strainer to remove any large pieces of plant material. Each chamber of a double chamber McMaster slide was filled using a pipette. The slide was allowed to sit for five minutes before examining took place under a microscope with 100x magnification (10x objective and 10x eye piece magnification). To determine the number of parasite eggs (eggs per gram, epg) of faeces, the total counts for both chambers were multiplied by 50. Therefore, each egg observed represents 50 epg in the final count. Although parasite species were not identified, visual identification of eggs were done according to the reference pictures of Hendrix and Robinson (2012). The remaining mixture was filtered through soil sieves with mesh sizes that ranged from 2.0 mm, 1.0 mm, 0.50 mm, 0.25 mm, 0.106 mm, and 0.053 mm to remove as much plant material as possible. The filtrate collected in four 15 ml plastic test tubes and centrifuge for 2 min. The top layers in the test tubes were decanted which left the

soil at the bottom of the tube. This was washed out with a chemical squeeze bottle filled with tap water and collected in a petri dish. The contents of the petri dish were oven dried at 70 ^{0}C in an oven until all fluid had evaporated. The remaining soil was weighed and the amount of soil was calculated as a percentage of the original faecal mass. This procedure was done for all collected dung samples individually.

4.3 Data analyses

4.3.1 Assimilation of mineral and chemical elements

In order to evaluate whether chemical elements were extracted from geophagic soil, the relationship between major and trace element compositions of dung pellets and soils were analysed. This could only be achieved for major and trace elements because of the variation in mineral compositions between different soil types in the study area. This was done using simple linear regression models, with concentrations in dung pellets as the response variable. Regressions were performed independently for each soil depth, as well as the control sample, as independent variable, and the models were compared using the small-sample corrected Akaike's Information Criterion (AIC_c). This approach scores the best model, in this case the soil sample most strongly related to dung pellets, as the model with the lowest AIC_c. To compare models, the ΔAIC_c for each model was calculated as the difference between its AIC_c score and that of the best model according to the method of Burnham and Anderson (2001; 2002). Following guidelines suggested by these authors, models with > 10 are poorly-supported by the data. This approach is based on the prediction that, if nutrients are extracted from ingested soils during digestion, then the relationship of elemental composition between dung pellets and geophagic soil should be weaker than those between dung pellets and soil sampled at other depths, and indeed the control soils. From the worst-fit model, the assimilation of specific nutrients (elements) was then interpreted as follows: elements falling below the 95% confidence interval of the regression were presumed to be under-represented in dung pellets, and therefore indicative of significant assimilation into body tissues, whereas

elements above the 95% confidence interval occur in significantly higher proportions in dung than in ingested soil, and thus indicate precipitation of that element.

4.3.2 Transmission of parasite eggs

To evaluate the relationship between the amount of soil in faecal matter and parasitic egg load in faeces, a regression analyses was used with egg load as the dependent variable (based on the hypothesis that geophagy leads to a reduced parasite infestation). To account for differences between species, which were unevenly distributed throughout the dataset and, more importantly, which differ in digestive physiology and so may have different ways of mediating any soil-egg correspondence, and for differences across localities (because local conditions may lead to inherent changes in prevalence and infestation rates), Species and Reserve (Locality) were included as random factors in the analyses using a mixed effects linear model (MELM). Species had to be nested within Locality because of differences in species representation at each site. Visually the relationship appeared logarithmic, and residuals were non-normally distributed (Shapiro-Wilk's test $p < 0.05$), therefore % soil was ln-transformed for the analyses. This increased the marginal R^2 by ~ 0.12, supporting the non-linear shape of the relationship. However, residuals were non-normally distributed even after transformation. A non-parametric version of the test using ranked data were therefore performed, but since this yielded qualitatively similar results, only the parametric results are reported here. Analyses were carried out using R v 4.0.2 (R Core Team 2020) with the lmerTest package (Kuznetsova et al. 2017).

4.4 Results

4.4.1 Assimilation of minerals and chemical elements

Evidence for nutrient extraction is drawn from analyses of the relationship between argillaceous dung pellet elemental composition with those of soils at lick sites (see Appendix A, Tables S1 - S8 for results of chemical analyses). In all cases, i.e., at all habitats, and for all

species, these relationships were positive and statistically significant at $p < 0.05$, with high R^2 values (generally > 0.9; Table 4.1) indicating that sampled dung pellets represented geophagy at the particular lick site where they were sampled. With the exception of Renosterhoek, feeding depth soils had weaker relationships (higher ΔAICc scores) than most other soil depths, as well as control soils. Thus, soils that differed the most from herbivore faeces in terms of both major and trace element compositions were the soils actually ingested, which supports the prediction that elements are extracted during digestion. In addition, in about two-thirds of cases, slopes of these regressions were significantly < 1.0, i.e., 95% confidence intervals excluded 1.0, providing further evidence for digestive extraction of chemical elements (Table 4.1).

In general, the mineral composition of dung pellets corresponded to that of geophagic soil. The exception, however, was for that of anatase, calcite, and ilmenite which was not present in geophagic soil from both the Main Lick or Renosterhoek sites (Table 4.2) but was present in argillaceous dung pellets of both impala and kudu dung pellets. Orthoclase, plagioclase and smectite on the other hand, although present in geophagic soil at relative high amounts (13, 12 and 18 % respectively), was absent in both impala and kudu dung from the Main Lick site. The same anomaly was observed for calcite (Grassveld) and clinopyroxene (Kloppersкloof, Bushveld) which was present in geophagic soil but absent in kudu and nyala dung respectively. The difference between mineral contents of geophagic soil and that of dung pellets (Table 4.2), clearly indicated that some minerals (e.g., ilmenite, muscovite and kaolinite) were only affected slightly or not affected at all while others, including orthoclase, plagioclase and smectite, were clearly transformed in the digestive tract of animals.

A number of chemical elements fell below the 95% confidence band and it can be argued that such elements were extracted from geophagic soil by animals. Essential major elements to herbivores, as identified by McDowell (1985), McDonald et al. (2011) and Cherian (2020), that fell notably below the 95% confidence band i.e., those that were most noticeably assimilated, could therefore be identified. This included Ca and Mg in Willem Pretorius Game

Table 4.1. *Linear regression models of chemical element compositions of dung pellets of mammalian herbivores and geophagic soil where argillaceous pellets were collected. Models are compared based on the regression parameter (slope); estimates are presented with 95% confidence intervals in parentheses.*

Site / Species	Major Elements				Trace Elements			
	Soil	R^2	ΔAIC_c	Slope	Soil	R^2	ΔAIC_c	Slope
Willem Pretorius NR								
Kudu	Control	0.993	0.00	0.9054 (0.855 to 0.9557)	Control	0.760	0.00	0.8876 (0.6766 to 1.0986)
	Top	0.991	2.95	1.0366 (0.9697 to 1.1035)	Top	0.697	4.49	0.7943 (0.5724 to 1.0163)
	Middle	0.989	5.02	1.0653 (0.989 to 1.1416)	Middle	0.639	7.79	0.757 (0.516 to 0.9979)
	Bottom	0.984	8.51	1.0877 (0.9947 to 1.1807)	Bottom	0.638	7.84	0.7834 (0.5336 to 1.0333)
Loskop Dam NR: Main Lick								
Kudu	Middle2	0.949	0.00	0.9859 (0.8326 to 1.1391)	Middle1	0.963	0.00	1.1364 (1.0423 to 1.2305)
	Middle1	0.932	2.80	1.0077 (0.8259 to 1.1895)	Middle2	0.946	7.36	1.1111 (0.9984 to 1.2238)
	Control	0.932	2.84	0.97 (0.7947 to 1.1454)	Top	0.872	23.73	0.9748 (0.8164 to 1.1333)
	Bottom	0.926	3.66	0.9726 (0.7889 to 1.1563)	Control	0.594	45.59	0.571 (0.3712 to 0.7708)
	Top	0.814	12.91	1.0085 (0.6859 to 1.3311)	Bottom	0.457	51.13	0.456 (0.2453 to 0.6667)
Impala	Middle2	0.940	0.00	0.7644 (0.6351 to 0.8937)	Middle1	0.867	0.00	0.8396 (0.7006 to 0.9787)
	Middle1	0.923	2.52	0.781 (0.6298 to 0.9322)	Middle2	0.825	5.31	0.8077 (0.65 to 0.9655)
	Control	0.877	7.20	0.7329 (0.549 to 0.9169)	Top	0.508	24.91	0.5793 (0.3377 to 0.8208)
	Bottom	0.865	8.14	0.732 (0.5381 to 0.9259)	Control	0.368	29.67	0.3498 (0.1556 to 0.544)
	Top	0.805	11.81	0.781 (0.5233 to 1.0387)	Bottom	0.286	31.99	0.2809 (0.0928 to 0.4689)
Loskop Dam NR: Renosterhoek								
Kudu	Bottom	0.981	0.00	0.8133 (0.7374 to 0.8892)	Bottom	0.948	0.00	0.8284 (0.7434 to 0.9134)
	Middle	0.962	6.93	0.7907 (0.6853 to 0.8961)	Middle	0.934	4.26	0.8268 (0.7306 to 0.923)
	Top	0.937	11.96	0.6954 (0.5746 to 0.8161)	Top	0.900	11.78	0.7916 (0.6759 to 0.9072)
	Control	0.915	14.93	0.6334 (0.5043 to 0.7625)	Control	0.805	23.77	0.6903 (0.5416 to 0.8391)
Loskop Dam NR: Zaagkuil								
Kudu	Top	0.956	0.00	0.8946 (0.7654 to 1.0238)	Middle	0.966	0.00	1.4295 (1.3191 to 1.54)
	Middle	0.951	0.90	0.8695 (0.7379 to 1.0011)	Top	0.927	15.02	1.4677 (1.2992 to 1.6362)
	Control	0.939	3.15	0.7393 (0.6133 to 0.8654)	Control	0.758	39.10	1.0767 (0.8271 to 1.3262)
	Bottom	0.870	10.74	0.6271 (0.4647 to 0.7894)	Bottom	0.691	43.99	0.9456 (0.6862 to 1.205)
Loskop Dam NR: Klopperskloof								
Nyala	Cave	0.997	0.00	0.9581 (0.9214 to 0.9948)	Cave	0.871	0.00	0.7411 (0.6161 to 0.8662)
	Floor	0.990	11.01	0.9345 (0.8722 to 0.9967)	Control	0.841	3.76	0.5978 (0.4838 to 0.7117)
	Control	0.987	14.10	0.9676 (0.8922 to 1.043)	Floor	0.794	8.38	0.7784 (0.6049 to 0.9519)

Reserve (Fig. 4.2 a), Mg and Na for both kudu and impala at the Main Lick (Fig. 4.2 b and c), Na at Renosterhoek (Fig. 4.2 d) and K at Zaagkuil (Fig.4.2 e). At Klopperskloof, the assimilation of Ca was also possible as it fell on the 95% confidence band (Fig. 4.2 f). On the other hand, major elements essential to herbivores, that fell notably above the 95% confidence

Table 4.2. *Comparison between primary and secondary mineral concentrations (%) of X-Ray diffraction (XRD) analyses of geophagic soil at the feeding depths and argillaceous dung pellets in the Grassveld and Bushveld habitats.*

Habitat and Geophagy site	**Minerals**												
	Anatase	**Calcite**	**Clinopyroxene**	**Goethite**	**Hematite**	**Ilmenite**	**Kaolinite**	**Muscovite**	**Orthoclase**	**Plagioclase**	**Quartz**	**Smectite**	**Total**
Grassveld													
Feeding depth		2	20						6	19	53		100
Kudu dung		0	26						12	10	52		100
Difference		-2	6						6	-9	-1		
Bushveld													
Main Lick													
Feeding depth	0	0		6		0	19	17	13	12	15	18	100
Impala dung	16	5		9		7	19	18	0	0	26	0	100
Difference	16	5		3		7	0	1	-13	-12	11	-18	
Kudu dung		6		9		6	19	19	0	0	41	0	100
Difference		6		3		6	0	2	-13	-12	26	-18	
Renosterhoek													
Feeding depth		0			5	5	12	16	12	10	40		100
Kudu dung		3			6	5	17	19	10	11	29		100
Difference		3			1	0	5	3	-2	1	-11		
Zaagkuil													
Feeding depth		6			5	5	10	19	10	7	38		100
Kudu dung		6			4	5	9	19	10	7	40		100
Difference		0			-1	0	-1	0	0	0	2		
Kloppersklоof													
Floor			4		8	7	25	22			34		100
Nyala dung			0		8	7	27	22			36		100
Difference			-4		0	0	2	0			2		
Cave					8	8	24	21	7		32		100
Difference					0	-1	3	1	-7		4		

Anatase TiO_2	Hematite Fe_2O_3	Orthoclase $K(AlSi_3O_8)$
Calcite $CaCO_3$	Ilmenite $Fe^{2+}TiO_3$	Plagioclase $NaAlSi_3O_8$/ $CaAl_2Si_2O_8$
Clinopyroxene $(Ca,Na,Mg,Fe,Al,Ti)_2Si_2O_6$	Kaolinite $Al_2(Si_2O_5)(OH)_4$	Quartz SiO_2
Goethite $FeO(OH)$	Muscovite $KAl_2(Si_3AlO_{10})(OH)_2$	Smectite $(Na,Ca)_{0.33}(Al,Mg)_2(Si_4O_{10})(OH)_2 \cdot nH_2O$

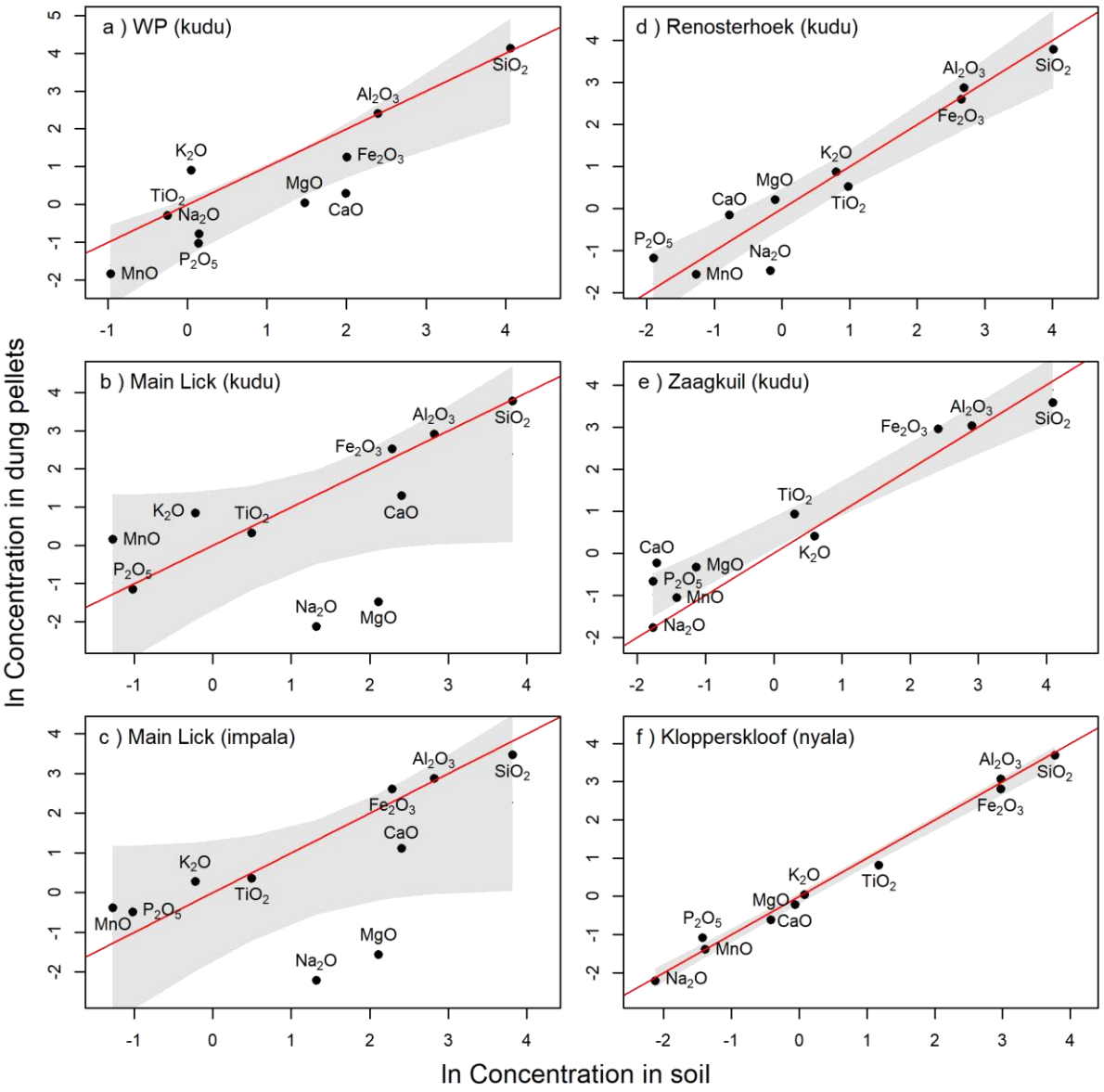

Figure 4.2. *Relationships between concentrations of major elements (in oxide form) in dung pellets and geophagic soil at the feeding depth in (a) Willem Pretorius Game Reserve (Grassveld) and (b-f) Loskop Dam Nature Reserve (Bushveld). Red lines are 1:1, shaded area represents the 95% confidence interval of the regression.*

band, were those elements that were adsorbed by the geophagic soil from the intestinal contents of the animals. Elements that were identified to be adsorbed by geophagic soil, and therefore deprived the animal from nutritional supplementation, included K at Willem Pretorius Game Reserve, (Fig. 4.2 a), Ca at both Renosterhoek and Zaagkuil (Fig. 4.2 d and e) and P at Kloppersklоof (Fig. 4.2 f). The only geophagy site where Fe might be assimilated from

geophagic soil was at Willem Pretorius Game Reserve. However, although below the 1:1 line, Fe fell inside the 95% confidence band in kudu dung (Fig. 4.2 a). On the contrary, by ingesting geophagic soil at the Main Lick and Zaagkuil, Fe might be absorbed from the digestive tract of animals.

Using the same criteria as for major elements, different essential trace elements were also assimilated from geophagic soil by animals at the different geophagy sites. At Willem Pretorius Game Reserve, kudu might gain nutritional supplementation in the form of Mo, Cu and Co (Fig. 4.3 a). At the Main Lick site, Mo and possibly Se was assimilated by kudu (Fig. 4.3 b) while at the same lick site, impala assimilated Mo, Cr and possibly Se (Fig. 4.3 c). If kudu indeed assimilated Cu at Renosterhoek is unclear as this element, although below the 1: 1 line, fell on the border of the 95% confidence band (Fig. 4.3 d). It further seems that, Mo was the only essential element that might have been assimilated by animals at Zaagkuil as well as Kloppersкloof although it fell on the edge of the 95% confidence band for both geophagy sites (Fig. 4.3 e and f). Essential trace elements that were adsorbed by the geophagic soil in the intestines of animals, i.e., those that fell outside and above the 95% confidence band, were Co at all four geophagy sites at Loskop Dam Nature Reserve as well as Cu at the Main Lick (both kudu and impala), as well as Zaagkuil.

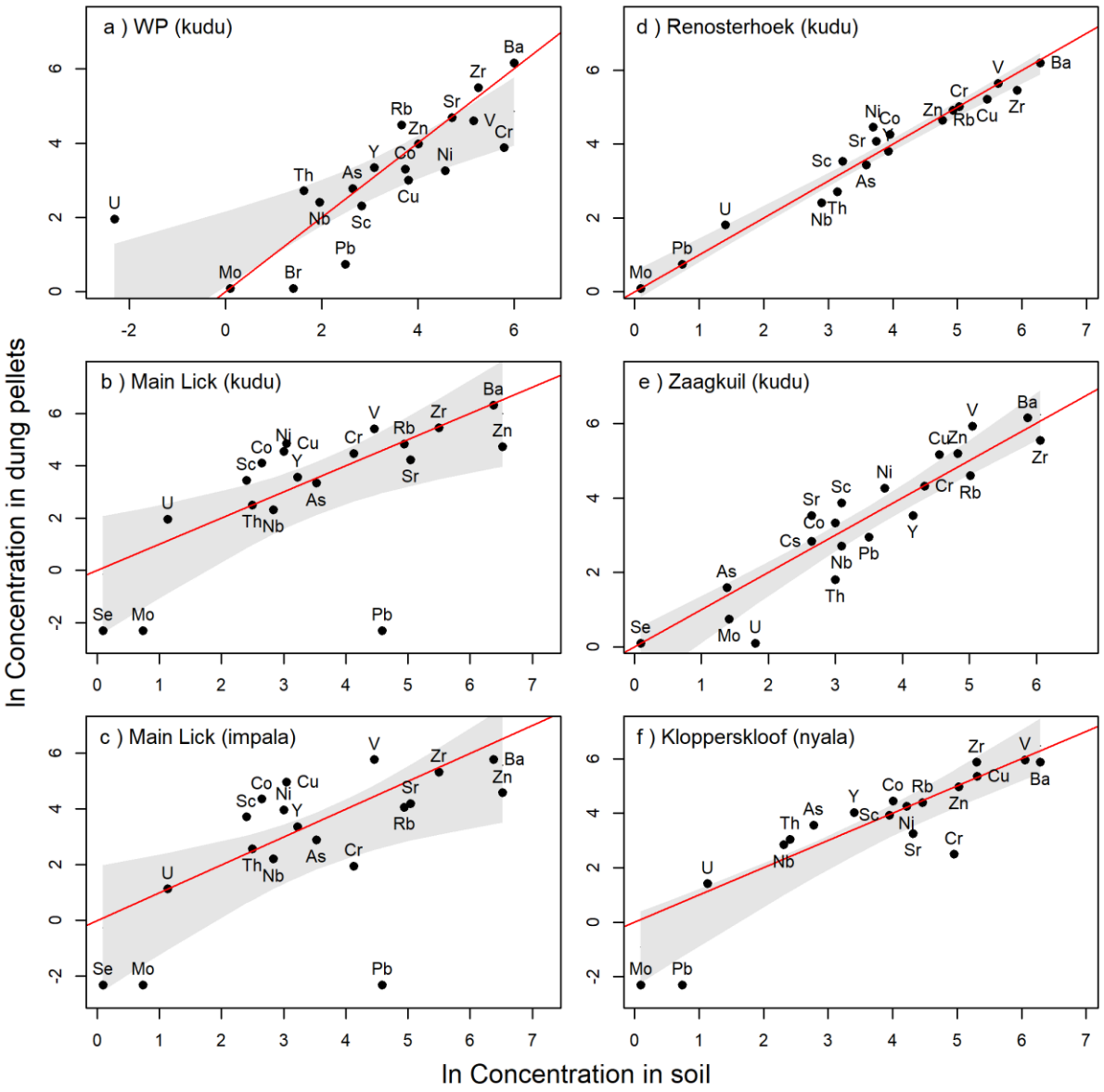

Figure 4.3. *Relationships between concentrations of trace elements in dung pellets and geophagic soil at the feeding depth in (a) Willem Pretorius Game Reserve (Grassveld) and (b-f) Loskop Dam Nature Reserve (Bushveld). Red lines are 1:1, shaded area represents the 95% confidence interval of the regression.*

Although not identified as essential elements for herbivores, the occurrence of the heavy metals As, Pb and U is also worth mentioning. Notably, Pb was assimilated by all the animals with the exception of kudu at Renosterhoek while As and U were extracted from the geophagic soil by kudu at Renosterhoek and Zaagkuil respectively (Fig. 4.3). Conversely, U was adsorbed from the intestines of the animals by the geophagic soil at Willem Pretorius Game Reserve as well as Kloppersklоof, while higher levels of As was also found in the nyala dung at Kloppersklоof than in the geophagic soil.

4.4.2 Transmission of parasite eggs

The MELM (Table 4.3) showed the effect of ingested soil content was significant (X^2 = 51.3179, p < 0.0001), with a strongly negative slope (mean = -7.721; 95% CI -9.514 to -5.928), even after accounting for the random effects Locality (non-significant with p = 0.355) and Species (p < 0.0001). The relationship was moderately strong with a marginal R^2 of 0.618, and excluding the random effects, i.e., the conditional R^2, was 0.869. Thus, it appears that at any given locality, and regardless of species ID, stomach soil content accounts for the majority of variance in faecal egg counts. There was a strong negative relationship between faecal egg count and % soil in the stomach (Fig. 4.4). It seems that the amount of soil ingested during geophagy eradicated at least parasite eggs in the elementary canal of large mammalian herbivores.

Table 4.3*. Results of a linear mixed model for the relationship between faecal egg load (as a percentage) with faecal soil content (expressed as a percentage, ln-transformed), accounting for the random effects Locality and Species as a nested term.*

$r^2_{marginal}$	Effect	Effect Type	X^2	p	Slope estimate (95% CI)
0.6181	ln % Soil	Fixed	51.3179	<0.0001	-7.721 (-9.5144 to -5.9277)
	Locality	Random	0.8567	0.3547	
	Locality/Species	Random	38.9082	<0.0001	

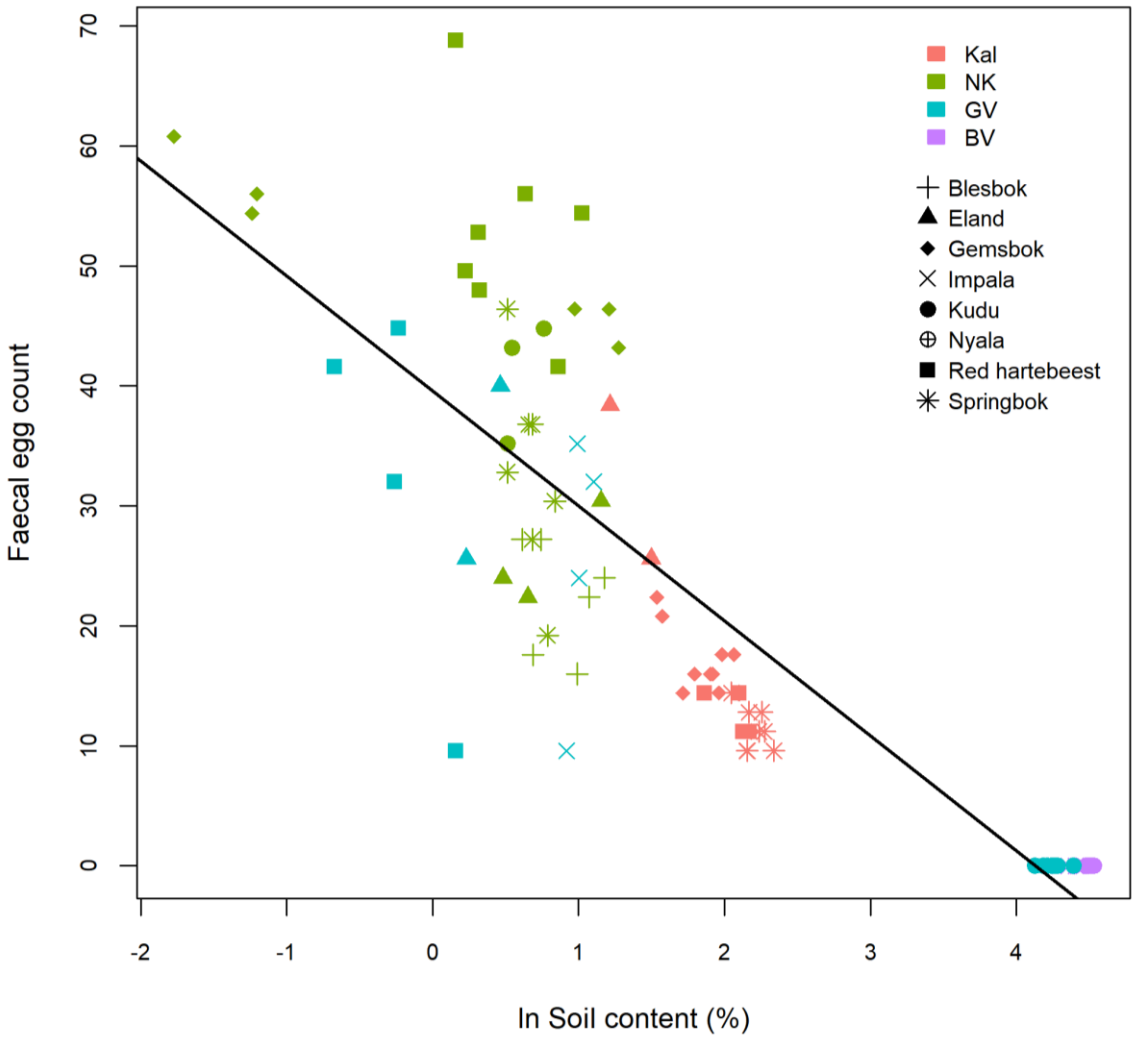

Figure 4.4. *Relationships between parasite egg counts and soil content in dung pellets of large mammalian herbivores different habitats in the study area.*

4.5 Discussion

4.5.1 Assimilation of minerals and chemical elements

The presence of primary and secondary minerals in geophagic soil have been emphasised by numerous studies (including Kreulen 1985, Klaus and Schmid 1998, Ayotte et al. 2006). Not much research has however, focused on chemical weathering that results from chemical changes to minerals that become unstable when exposed to surface conditions or during oxidation. Chemical changes that occur are highly specific to the mineral involved, as well to the environmental conditions in which it occurs; some, like quartz, are virtually unaffected by

chemical weathering (Earl 2019). Chemical weathering can also alter an original mineral to become a totally different mineral (Churchman and Lowe 2012; Earl 2019). According to Churchman and Lowe (2012), all minerals have the ability to be dissolved in water to some extent and, by the process of hydrolysis, the more soluble components are removed selectively from the mineral. This removal may leave a solid residue which differs in composition from the original mineral and neogenesis of new clays and other secondary material may form from the break-down products of the original mineral. The breakdown and argillisation (the process by which rock minerals transform into clay) of minerals often takes place in an acid milieu and, as commonly found in soils, involves various organic compounds which can enhance breakdown and affect the end products which are formed (Churchman and Lowe 2012). Furthermore, several studies reported on the influence that clay minerals have on the formation of carbonates. For instance, low levels of montmorillonite (from the smectite group) can cause the precipitation calcite (Kralj and Vdović 2000) while Molnár et al. (2021) illustrated that the presence of smectite triggers the formation of calcite-type structures. As an example, one of the calcium-bearing feldspar minerals, plagioclase, can react with carbonic acid (formed from rain and carbon dioxide) to form kaolinite with dissolved calcium and carbonate ions (see chemical reaction below). Calcium and carbonate ions can furthermore combine to form the mineral calcite.

$$CaAl_2Si_2O_8 + H_2CO_3 + ½O_2 \leftrightarrow Al_2Si_2O_5(OH)_4 + Ca^{2+} + CO_3^{2-}$$

Plagioclase + carbonic acid ↔ kaolinite + dissolved calcium ions + dissolved carbonate ions

Chemical weathering of minerals inside the digestive tract of animals might undergo similar changes, and this needs to be investigated further. Since *in vivo* and even *in vitro* methods to investigate element assimilation can be perplexing, the strong relationships between soil and dung pellet geochemistry found here support that this method can be a good proxy for assimilation. While other techniques may be needed to validate the approach, and perhaps coupled with knowledge of absolute amounts of intake models can be refined, it is not unreasonable – given the strong relationships – to presume that deviations from the

regression line can be used (as done here) to differentiate between assimilated and undigested (precipitated) minerals. Although this method of comparing chemical elements from geophagic soil with that found in dung pellets might be indicative of the bioavailability of elements, it may be relevant only for individual animals and cannot be projected to all animals or all species. In comparison between similar clay-containing dung from the Main Lick at Loskop Dam Nature Reserve and geophagic soil, Stephenson et al. (2010) found that Co, Zn, Se, Mo and Mn were the essential elements that were assimilated by kudu. It seems therefore that assimilation of elements by animals is specific to individuals and depend on the physiological state of each animal.

Based on concentration as well as the increase of chemical elements in the soil profile of geophagic soil towards the feeding depth, various elements were identified to be of importance (see Chapter 3). It was concluded that these chemical elements might act as possible stimulation for geophagy. However, analyses of argillaceous dung pellets indicated that only certain elements were actually assimilated. While Ca, Mg, Mn, Cr, Co and Zn were identified to be of importance in Willem Pretorius Game Reserve, only Ca and Mg were actually assimilated by kudu in this habitat. In Loskop Dam Nature Reserve, Mg, Mn, Ca, Na, P, Cr, Zn and probably Se was identified to be the main driver at the Main Lick site while only Na and Mg were assimilated by both impala and kudu. At Renosterhoek, only Na was absorbed from geophagic clay by kudu while Fe, Mg, Mn, Na, Cr, Co, and Zn were all elements that were identified as important. None of the elements that were identified as important at Zaagkuil, which were Mn, Cr, and Mo were actually absorbed. However, K was the only essential element that was assimilated by kudu at this geophagy site. While Ca, Co and Zn were elements that were identified to possibly stimulate geophagy at Kloppersklоof, only Mo was at lower levels in the dung pellets of nyala compared with that of geophagic soil. This suggested that geophagy is not practiced at this site for supplementation of chemical elements and might serve a protective function against secondary plant metabolites.

The elements Co and Cu that were found at higher levels in the clay-containing dung pellets than in geophagic soil might be an indication that geophagy can deprive animals of such elements but on the other hand might be a way in which animals avoid high toxic levels of elements from their diet. The absorption of U and As by geophagic soil is an example of the detoxification function that geophagy might provide. In similar analyses of clay-containing dung from the Caucasian State Biosphere Reserve (Russia) Panichev et al. (2014) found that animals did not ingest soil for the purpose of Na, as was initially predicted, but rather for the removal of heavy rare elements from the body. The assimilation of As, Pb, and U by animals in certain habitats is therefore a matter of concern and should be investigated further.

4.5.2 Transmission of parasite eggs

The behaviour of geophagia clearly influenced the prevalence and therefore transmission of internal parasite eggs. Several authors (Kreulen 1985, Klaus et al. 1998, Knezevich 1998, Krishnamani and Mahaney 2000, Papaioannou et al. 2005) also speculated on the protective role that geophagy plays against internal parasites. According to Knezevich (1998), the mechanical and pharmaceutical properties of kaolinitic clays counteract the effects of parasitosis in animals. Robinson et al. (2008) mentioned that several bird species with diets of soft food items ingested small stones as a way to remove parasites from the stomach wall mechanically. Whether the abrasive action of soil contents or the constrain of respiration of parasites, as suggested by Young et al. (2011), was the mode of eradication is unclear and should be investigated further by means of post-mortem studies on animals that ingested soil. Another possibility might be that soil that is high in element concentrations, influence the osmotic pressure and might desiccate the parasite eggs in the digestive tracks of animals. Nevertheless, the ingesting of soil seems to eradicate the prevalence of internal parasites of the animal that practiced geophagy. This will result in a lower burden of internal parasites to the animal that practice geophagy and ultimately lower the risk of dispersal of parasite eggs not only at geophagy sites, but elsewhere as well.

4.6 Conclusions

This preliminary investigation using faecal analyses to uncover patterns and drivers of geophagy showed promise for the approach, revealing strong associations between soil and faecal geochemistry. Emergent patterns help elucidate ideas about the supplementation and protection role of geophagy. The supplementation role of geophagy, at least for some chemical elements, was clearly illustrated. However, the deliberate ingestion of soil might deprive animals from certain elements. Furthermore, geophagy also has a protective function with respect to detoxification of heavy metals as well as protection against the dispersal of internal parasites.

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Chapter 5: Spatial and temporal utilisation of geophagy sites

5.1 Introduction

Most of the studies done on geophagy only analysed the geochemistry of geophagic soil. Comparatively few studies investigated effects of behavioural aspects such as seasonality, or differences between sexes or age groups of animals. In general, research on geophagy suggested two alternative explanations to why animals ingest soil.

The protection hypotheses predicts that geophagy, especially ingestion of soil with high clay contents, acts as detoxification strategy of mammals and birds, whereby bacteria and toxins (Oates 1978, Vermeer and Ferrell 1985) as well as plant secondary metabolites (PSMs) such as tannins and alkaloids (Hladik 1977, Kreulen 1985, Knight et al. 1988, Klaus et al. 1998) that otherwise act as antifeedants, are absorbed. The protection function of geophagy had been the explanation in a diversity of cases including humans (Johns and Duquette 1991), non-human primates, (Krishnamani and Mahaney 2000; Ta et al. 2018; Pebsworth et al. 2019), bats (Voigt et al. 2008), elephants (Chandrajith et al. 2009) and parrots (Gilardi et al. 1999). The main protection function of PSMs to plants is to serve as a defence mechanism against insect herbivores, and to protect cell walls of plants against penetration of microbial and fungal organisms (Cooper and Owen-Smith 1985). Thus, PSMs might reduce the effectiveness of fermentation and degradation of plant tissues in the rumen of large mammals which depend on microbial symbionts (Cooper and Owen-Smith 1985). Although protein-precipitating properties of tannins do not determine the selection of plants as food source by browsing ruminants, plant species in the South African savanna that have high concentrations of condensed tannins in their leaves, benefit from reduced levels of herbivory by ungulates (Cooper and Owen-Smith 1985; Arnason and Bernards 2010). Thorn trees of the genera *Senegalia* and *Vachellia* in Botswana, all have high concentrations of phenolic substances in young leaves and immature fruits while low levels are present in mature leaves and pods (Ernst et al. 1991). On the other hand, plants appear to have high levels of variations of PSMs between different species (Owen-Smith 1993) and change across seasons (Du Toit

2003). Furthermore, condensed tannins in woody plants in a South African savanna have a strong deterrent effect on browsing ruminants during the late summer (Cooper and Owen-Smith 1985). For herbivores, the protection function of geophagy should therefore be important during times of the ingestion of high levels of PSMs which coincide with the growing phase of plants which is during spring and summer. Animals that ingest soil to benefit from the protection function thereof, should consequently do so during spring (September to November) and summer (December to February). On the other hand, as the dry season progresses and the availability of high-quality food (i.e., high nutritional values and low chemical defences) declines, herbivores is forced to expand their diet breadth to incorporate plants that they would usually avoid during spring and summer (Owen-Smith and Cooper 1989, O'Reagain and Grau 1995, Owen-Smith 2002). Therefore, browsing herbivore species would potentially increase their geophagy as the increased intake of minerals would help neutralise this seasonal increase in plant secondary compounds.

Alternatively, the supplemental nutrition hypothesis (Brightsmith and Aramburu Munoz-Najar 2004; Powell et al. 2009; Lee et al. 2010) supports the idea that differences in plant nutrition (Jones and Hanson 1985; Kreulen 1985; Knight et al. 1988; Eksteen and Bornman 1990; Ayotte et al. 2008) during consecutive seasons might be the key driving force for geophagy. This hypothesis suggests that animals should engage in geophagy when availability of plant nutrition is at its lowest level. In a southern African context, this coincides during the colder dry seasons of autumn (March to May) and winter (June to August) and if animals ingest soil for supplementation reasons, this should happen during these seasons.

Apart from the seasonal differences in plant nutrients which might explain seasonality of geophagy among herbivores, seasonality of geophagy might also reflect changing physiological needs of animals (Ceacero et al. 2009). Firstly, more minerals that cannot be replenished by forage are required during spring and the warmer summer months because of the loss of Na from sweat or urine (Langman 1978; Jones and Hanson 1985, Kreulen 1985, Heymann and Hartmann 1991). Atwood and Weeks (2003) found that female white-tailed deer

(*Odocoileus virginianus*) preferred mineral licks with high concentrations of Mg, Ca and P in spring, and salt licks with high amounts of Na in the summer. The warm to very hot summertime in southern Africa occurs between December, January, and February. In areas where Na was identified to be one of the main driving forces for geophagy, higher occurrences of this behaviour should thus occur during this time of elevated physiological heat stress.

Seasonal demands of animals during gestation (Atwood and Weeks 2003, Bravo et al. 2008), parturition (Tankersley and Gasaway 1983; Atwood and Weeks 2003) as well as the following period of lactation (Fraser and Reardon 1980; Tankersley and Gasaway 1983; Moe 1993; Holdø 2002; Atwood and Weeks 2003) and even during the growing phase, such as forming of antlers (Fraser and Reardon 1980; Atwood and Weeks 2003), horns, tusks and skeletal bones (Henshaw and Ayeni 1971), might also be a reason why animals revert to geophagy as a source of mineral supplementation. In support of this hypotheses, calves of Iberian red deer (*Cervus elaphus hispanicus*) consumed much more cobalt-supplement than hinds in a free-choice experiment, probably because of the high mineral requirements for young growing ruminants (Ceacero et al. 2009). The same study found that no geophagy occurred during the mating season of the animals, and that consumption is limited during the winter months (Ceacero et al. 2009). Ping et al. (2011) found significant differences in monthly salt lick use, as well as time spent at the licks, between male and female sika deer (*Cervus nippon*) in Taohongling Nature Reserve, China. Accordingly, female sika deer used licks frequently during the time of lactation, males utilised the same licks during the rut, and both sexes frequently used salt licks during the period of pelage change (Ping et al. 2011). The breeding season of most mammal species in southern Africa is initiated at the time of year when environmental conditions are optimal for the survival of the young (Skinner et al. 1974), and the general lambing or calving period in the spring or early summer, follows the general pattern of summer rainfall (Skinner et al.1974). Thus, geophagy during spring might be indicative of physiological demands of lactation on female animals.

All these mentioned examples are indications that the behaviour of geophagy is seasonal and different sexes and age groups utilise geophagy sites at different times of the year for various reasons. Despite the large occurrence of geophagy among large mammalian herbivores in Africa (*vide* Fig.1.1), information related to seasonality of this behaviour is relatively very limited. Apart from studies on seasonal activities of African elephants (*Loxodonta africana*) by Abrahams (1999) and Holdø et al. (2002), and forest elephants (*Loxodonta africana cyclotis*) by Klaus et al. (1998), no data exist on seasonal, sexual or age differences regarding geophagy. The investigation of spatial and temporal frequencies of geophagy across different habitats will therefore fill the present knowledge gap that exist of why animals take part geophagia.

The first objective of this study was to determine whether frequency of visiting geophagy sites differed between habitats, and across seasons. Second to that was to determine whether there were differences in geophagy site use between feeding niches, namely between browser (BR), grazer (GR), and intermediate-feeder (IM) species, using diet classifications in Codron et al. (2019). The third objective was to evaluate variations in time of day at which various herbivore species were active at geophagy sites. The final objective was to assess if differences in visitation frequencies to geophagy sites exist between sexes of these large mammalian herbivores.

5.2 Methodology

5.2.1 Camera traps

To identify large mammal species that consume soil on a deliberate basis, digital motion-activated infrared LED flash camera traps (Bushnell HD, WildView and Cuddeback) were placed in a manner as to capture any activity at geophagy sites. After initial reconnaissance, geophagy sites were selected based on accessibility, size, and visual signs of frequent activity at these sites (pers. obs.). Different numbers of digital camera traps were placed at active geophagy sites at the four study areas based on the number of active geophagy sites as well as the number of available camera traps. Standard procedures for the

use of camera traps in wildlife ecology, as describe by O'Connell et al. (2011), were applied. Where possible, camera traps were affixed to natural vegetation to conceal the visibility thereof. At the Kalahari Wildlife Management Area study site, where natural vegetation on Jack's Pan is absent, metal stands were used as trap supports. Camera traps were placed at a hight of ± 1.8 m above ground and were positioned within 15 m from the most utilised part (pers. obs.) of the geophagy site.

Camera traps were deployed for a minimum of 14 consecutive days during each season. At Jack's Pan (Kalahari habitat), camera traps were deployed in 2010 during March, July, September and December, while Tussen-die-Riviere Game Reserve (Nama Karoo habitat) was sampled during February, March, June September and October of 2012. In Loskop Dam Nature Reserve (Bushveld habitat), camera traps were deployed during March, June and September and December of 2013 as well as during January of 2014. In Willem Pretorius Game Reserve (Grassveld habitat), camera traps were deployed during February, April, July, August, October, November and December of 2015.

Traps were set to take three consecutive pictures with 15 min intervals. That resulted in 1 505.65 camera trap days (CTD) including all the geophagy sites over all four seasons. Digital images, stored on a four-megabyte SD card, were downloaded and data including date, time, temperature, moon phase, species, sex, and age category (juvenile, subadult or adult), and specific behaviour of individual animals was logged in a spreadsheet. Information of each animal in any of the three images were captured only once in a data set. Because of tampering by animals or defective camera traps, trap failures did occur and therefore the number of consecutive trappings were not the same for each study site or for each season. Therefore, the number of camera trap days (CTD) were calculated and the number of animals per study site and season were calculated as visitation frequency (see below).

5.2.2 Statistical analyses

5.2.2.1 Visitation frequency

Habitats were defined based on the reserve in which data were collected: Jack's Pan in the Kalahari Wildlife Management Area = 'Kalahari', Tussen-die-Riviere Game Reserve = 'Nama Karoo', Willem Pretorius Game Reserve = 'Grassveld', and Loskop Dam Nature Reserve = 'Bushveld'. Seasons were defined as Spring (September to November), Summer (December to February), Autumn (March to May), and Winter (June to August). To simplify the structure of the dataset, data for habitats and seasons represented by multiple field excursions were combined, i.e. "Year" was not included as a factor in any of the analyses that follow. For each species *i*, the visitation rate ρ was calculated as the number of individuals (*C*) captured photographically I for the j^{th} habitat in the k^{th} season, as a proportion relative to the total number of camera trap days (CTD) in each case, i.e.,

$$\rho_{ijk} = \frac{C_{ijk}}{\mathrm{CTD}_{jk}} \qquad \text{(equation 5.1)}$$

This provided an index of visitation frequency independent of the variation in CTD across habitats and seasons. Hourly intervals (per day) were used as the unit of replication to minimize pseudoreplication effects, i.e., recording the same individual in consecutive images.

Visitation rates were then compared using a general linear model (LM) with a nested hierarchical design Habitat / Season / Diet niche. Where necessary, pairwise comparisons were made using Tukey's HSD post hoc test. Of the 24 species in the complete data, nine had fewer than 35 records, a number too low to allow further stratification by season and/or habitat. The remaining 15 species had between 105 and 9 089 records, making seasonal and habitat sub-division possible. Therefore, for statistical models, data were filtered by removing all species for which the total number of photographic records was < 100. This resulted in a total 25 598 records distributed across 15 species. To account for species' abundances in the different habitats (see Chapter 2), as which almost certainly influence estimates of ρ, each

species' relative abundance (n_{ij}) was included as a covariate in the model. Relative abundances were calculated as the proportion of each species relative to total animal numbers (N) on each reserve, i.e.:

$$n_{ij} = \frac{N_{ij}}{\sum N_j} \quad \text{(equation 5.2)}$$

In order to satisfy assumptions of normality and homoscedasticity of residuals, estimates of *p* were ln-transformed prior to analyses (see Appendix B, Fig. S1). This was achieved after records with a *C* of zero (i.e., time units (hrs) during which species *i* was not encountered during the sampling season) were excluded, as the high frequency of zeroes would bias the results, and the focus was on comparisons between groups (populations, per season) rather than within them. In a second model, patterns within a particular reserve or habitat were compared, focusing on Loskop Dam Nature Reserve where data were collected from two distinct types of sites – 'Erosion licks' which included Main Lick and Renosterhoek, and 'Mountain slope sites' which included Zaagkuil and Kloppersklоof. This second LM thus used only data from Loskop Dam, and replaced the Habitat with a Site term. Statistical significance was set at α = 0.05. All analyses were carried out using R v 4.0.2 (R Core Team 2020).

Since a low number of replicates in many cases precluded species as an effect in the LM described above, the issue of species-level differences in geophagic activity was further explored by plotting relative visitation rates (ρ^*) as a function of relative abundance at each habitat (n_{ij}, see equation 2). Relative ρ^* was estimated as

$$\rho^*_{ij} = \frac{\rho_{ij}}{\sum \rho_j} \quad \text{(equation 5.3)}$$

to be on a scale commensurate with n_{ij}. Accordingly, 1:1 lines drawn through the plots indicate whether species visited geophagy proportionately or disproportionately to their abundances:

points above the line indicate more-than-expected visitation, and vice versa for points below the line.

5.2.2.2 Activity times

Kernel densities were used to evaluate distributions of hourly counts per habitat, season, and species – summed over the duration of a field season, treating the integer variable 'Hour of Day' as continuous (see Appendix B, Figs S2 to S5). For these analyses, only groups for which the number of observations exceeded 30 – a widely-held estimate, based on central limit theorem, of the minimum number of samples needed for the means to converge on normality – were included, with the initial assumption that densities were normal, i.e., $_{ii}d\ N\ (\mu,\ \sigma^2)$ (but see below for treatment of bimodal distributions). This allowed for the estimation of the peak activity times for each group (populations, per season), as well as the degree of temporal overlap between paired groups, i.e., the area of intersection between each pair of densities. Overlap between species pairs *i* and *j* (O_{ij}), both within and between habitats and seasons, was computed by numeric integration (trapezoids) in a Bayesian framework (package bayestestR; Makowski et al. 2019). Overlap is expressed on a scale from 0 to 1 relative to the area of *i* so that the outcomes were non-symmetric, i.e., $O_{ij} \neq O_{ji}$. Peak activity times were represented by estimated means ($\hat{\mu}$).

Several species showed bimodal activity patterns throughout the day. Thus, two densities per group (i.e., each species per habitat per season) were evaluated using mixture models, assuming both densities were normal (package mixtools; Benaglia et al. 2009) and, consequently, means of two peak activity times per group were estimated; however, only those derived from densities that accounted for at least 30% of variation in activity times were included as representing a "true" second mode in the data.

To compare patterns of peak activity time, and of temporal niche overlap, across habitats and seasons, two-factor crossed-design LMs were used. As above, pairwise comparisons were made with Tukey's HSD, with α-level set to 0.05. Residuals were normal

and homoscedastic (Shapiro-Wilk's and Breusch-Pagan tests, respectively) without requiring transformation.

5.2.2.3 Sex ratios

Visitation frequency of females with males were compared using a generalized linear mixed model (GLMM) with a binomial distribution and logit link function, with sex (male or female) as the dependent variable and habitat and season (as well as their interaction) as predictors. Species was included as a random effect. Within-site comparisons of male:female ratios were based on 95% confidence intervals (CI): differences in sex ratios were inferred between groups (populations, per season) for which CI's did not overlap. Individuals that could not be sexed from camera trap photographs were omitted from these analyses. Unfortunately, information about sex ratios of the various populations sampled were not available, and therefore these analyses do not necessarily inform about differences in visitation rate; nevertheless, it may be reasonable to expect a 50:50 sex ratio in many herbivore populations, and thus the models that were used can provide some insights about sex-based differences in geophagy, albeit cautiously.

5.3 Results

A total of 27 261 images of large mammalian herbivores, representing 24 species - 10 of which are new records of species practicing geophagy -, were recorded from a cumulative 1 222.22 trap days (27 970 trap hours) across all study areas and field seasons.

5.3.1 Visitation frequency

Geophagy sites were utilised at different frequencies in the four habitat types. The summed visitation rate (ρ) for each habitat was 194.48/CTD in the Kalahari, 191.18/CTD in the Grassveld, 86.74/CTD in the Bushveld and 41.74/CTD in the Nama Karoo (Table 5.1). The linear model (LM) fit to these data revealed a significant effect of habitat ($F_{3,977} = 108.264$, $p < 0.0001$; Table 5.2), and *post hoc* pairwise tests confirmed that ρ for the Kalahari and Grassveld habitats was significantly higher than the Bushveld, and that Nama Karoo

experienced lower ρ than all three habitats ($p < 0.0001$ in all cases). However, there was also a significant effect of the nested terms season ($F_{12,977} = 14.223$, $p < 0.0001$) and diet niche ($F_{32,977} = 2.347$, $p < 0.0001$), indicating not only a seasonal component to geophagy, but also one that varies across ecological or environmental contexts (Fig. 5.1). A detailed description of these variations follows.

Table 5.1. *Seasonal visitation frequencies of large mammalian herbivores of different feeding niches (browser/intermediate-feeder/grazer) that practice geophagy in four different habitats in southern Africa based on number of animals (n) per camera trap days (CTD).*

		Spring		Summer		Autumn		Winter		Total	
		n	n/CTD	n	n/CTD	n	n/CTD	n	n/CTD	n	n/CTD
Kalahari	**CTD**	**58.52**		**68.95**		**58.51**		**59.77**			**245.75**
Browser											
Taurotragus oryx *	Eland	7	0.12	897	13.01	68	1.16	6	0.10	**978**	**14.39**
Tragelaphus strepsiceros	Greater kudu	18	0.31							**18**	**0.31**
Raphicerus campestris *	Steenbok			2	0.03			1	0.02	**3**	**0.05**
	Browser total	25	0.43	899	13.04	68	1.16	7	0.12	**999**	**14.74**
Intermediate-feeder											
Antidorcas marsupialis *	Springbok	213	3.64	688	9.98	9	0.15	480	8.03	**1 390**	**21.80**
Grazer											
Alcelaphus buselaphus *	Red hartebeest	207	3.54	175	2.54	7	0.12	24	0.40	**413**	**6.60**
Oryx gazella	Gemsbok	1 991	34.02	2 924	42.41	1 154	19.72	3 298	55.18	**9 367**	**151.33**
	Grazer total	2 198	37.56	3 099	44.95	1 161	19.84	3 322	55.58	**9 780**	**157.93**
	Habitat total	**2 436**	**41.63**	**4 686**	**67.96**	**1 238**	**21.16**	**3 809**	**63.73**	**12 169**	**194.48**
Nama Karoo	**CTD**	**136.11**		**99.49**		**76.61**		**222.61**			**534.82**
Browser											
Diceros bicornis	Black rhinoceros	6	0.04					4	0.02	**10**	**0.06**
Taurotragus oryx	Eland	14	0.10	12	0.12			121	0.54	**147**	**0.76**
Tragelaphus strepsiceros	Greater kudu	25	0.18	91	0.91	8	0.10	110	0.49	**234**	**1.68**
Sylvicapra grimmia	Grey duiker	1	0.01							**1**	**0.01**
Raphicerus campestris	Steenbok							1	0.004	**1**	**0.004**
	Browser total	46	0.34	103	1.04	8	0.10	236	1.06	**393**	**2.54**

(Table 5.1 continue)

		Spring		Summer		Autumn		Winter		Total	
		n	n/CTD	n	n/CTD	n	n/CTD	n	n/CTD	n	n/CTD
Intermediate-feeder											
Antidorcas marsupialis	Springbok	29	0.21	84	0.84	157	2.05	178	0.80	**448**	**3.90**
Grazer											
*Connochaetes gnou **	Black wildebeest	68	0.50	85	0.85	617	8.05	257	1.15	**1 027**	**10.55**
*Damaliscus pygargus phillipsi **	Blesbok	3	0.02	15	0.15	92	1.20			**110**	**1.37**
Oryx gazella	Gemsbok	62	0.46	832	8.36	17	0.22	83	0.37	**994**	**9.41**
*Redunca arundinum **	Common reedbuck	1	0.01					7	0.03	**8**	**0.04**
Alcelaphus buselaphus	Red hartebeest	43	0.32	70	0.70	169	2.21	8	0.04	**290**	**3.27**
*Phacochoerus africanus **	Warthog	41	0.30	38	0.38	11	0.14	159	0.71	**249**	**1.53**
Equus quagga	Plains zebra	42	0.31	71	0.71	611	7.98	35	0.16	**759**	**9.16**
	Grazer total	260	1.91	1 111	11.17	1517	19.80	549	2.47	**3 437**	**35.34**
	Habitat total	**335**	**2.46**	**1 298**	**13.02**	**1 682**	**21.95**	**963**	**4.31**	**4 278**	**41.74**
Grassveld	**CTD**	**19.4**		**15.82**		**11.14**		**29.55**			**75.91**
Browser											
Sylvicapra grimmia	Grey duiker	9	0.46	6	0.38	3	0.27	8	0.27	**26**	**1.38**
Taurotragus oryx	Eland			1	0.06					**1**	**0.06**
Giraffa camelopardalis	Giraffe			5	0.32	3	0.27	20	0.68	**28**	**1.26**
Tragelaphus strepsiceros	Greater kudu	135	6.96	226	14.29	53	4.76	145	4.91	**559**	**30.91**
Raphicerus campestris	Steenbok	6	0.31	1	0.06					**7**	**0.37**
	Browser total	150	7.73	239	15.11	59	5.30	173	5.85	**621**	**33.99**

(Table 5.1 continue)

		Spring		Summer		Autumn		Winter		Total	
		n	n/CTD	N	n/CTD	n	n/CTD	n	n/CTD	n	n/CTD
Intermediate-feeder											
Aepyceros melampus	Impala	342	17.63	143	9.04	17	1.53	205	6.94	**707**	**35.13**
Grazer											
Redunca arundinum	Common reedbuck					3	0.27			**3**	**0.27**
Redunca fulvorufula	Mountain reedbuck	11	0.57	4	0.25			11	0.37	**26**	**1.19**
Alcelaphus buselaphus	Red hartebeest	28	1.44	26	1.64	3	0.27	6	0.20	**63**	**3.56**
Hippotragus niger	Southern sable antelope	106	5.46	198	12.52	119	10.68	269	9.10	**692**	**37.77**
Phacochoerus africanus	Warthog	14	0.72	9	0.57	2	0.18	20	0.68	**45**	**2.15**
Ceratotherium simum	Southern white rhinoceros	1	0.05	7	0.44	16	1.44	22	0.74	**46**	**2.67**
Equus quagga	Plains zebra	54	2.78	121	7.65	297	26.66	1 104	37.36	**1 576**	**74.45**
	Grazer total	214	11.03	365	23.07	440	39.50	1 432	48.46	**2 451**	**122.06**
	Habitat total	**706**	**36.39**	**747**	**47.22**	**516**	**46.32**	**1 810**	**61.25**	**3 779**	**191.18**
Bushveld	**CTD**	**68.9**		**63.7**		**78.6**		**154.5**			**365.74**
Browser											
Tragelaphus scriptus	Bushbuck	18	0.26	55	0.86	29	0.37	39	0.25	**141**	**1.75**
Sylvicapra grimmia	Grey duiker					1	0.01	2	0.01	**3**	**0.02**
Giraffa camelopardalis	Giraffe							5	0.03	**5**	**0.03**
Tragelaphus strepsiceros	Greater kudu	838	12.15	512	8.04	1824	23.20	925	5.99	**4 099**	**49.38**
Oreotragus oreotragus	Cape klipspringer					5	0.06			**5**	**0.06**
	Browser total	856	12.42	567	8.90	1 859	23.65	971	6.28	**4 253**	**51.26**
Intermediate-feeder											
Aepyceros melampus	Impala	4	0.06	179	2.81	41	0.52	114	0.74	**338**	**4.13**
Tragelaphus angasii	Nyala	2	0.03	41	0.64	580	7.38	6	0.04	**629**	**8.09**
	Intermediate-feeder total	6	0.09	220	3.45	621	7.90	120	0.78	**967**	**12.22**

(Table 5.1 continue)

		Spring		Summer		Autumn		Winter		Total	
		n	**n/CTD**	**N**	**n/CTD**	**n**	**n/CTD**	**n**	**n/CTD**	**n**	**n/CTD**
Grazer											
Connochaetes taurinus	Blue wildebeest	6	0.09					1	0.01	**7**	**0.1**
Redunca fulvorufula	Mountain reedbuck	502	7.28	170	2.67	316	4.02	223	1.44	**1 211**	**15.41**
Hippotragus niger	Southern sable antelope	49	0.71	10	0.16	94	1.20	37	0.24	**190**	**2.30**
Damaliscus lunatus *	Tsessebe	13	0.19	13	0.20					**26**	**0.39**
Phacochoerus africanus	Warthog	2	0.03	21	0.33	12	0.15	17	0.11	**52**	**0.62**
Kobus ellipsiprymnus *	Waterbuck	2	0.03							**2**	**0.03**
Ceratotherium simum	Southern white rhinoceros	38	0.55	4	0.06	1	0.01	16	0.10	**59**	**0.73**
Equus quagga	Plains zebra	9	0.13	195	3.06	16	0.20	48	0.31	**268**	**3.71**
	Grazer total	621	9.01	413	6.48	439	5.59	342	2.21	**1 815**	**23.30**
	Habitat total	**1 483**	**21.52**	**1 200**	**18.84**	**2 919**	**37.15**	**1 433**	**8.96**	**7 035**	**86.74**
	Grand Total (All habitats)	**4 960**	**102.00**	**7 931**	**147.07**	**6 355**	**126.57**	**8 015**	**138.58**	**27 261**	**514.22**

*n = number of observations; n/CTD = number of observations per camera trap days; * = new record of species that was recorded to practice geophagy*

Table 5.2. *Hierarchically-nested linear models used to compare geophagy site visitation rate (ln-transformed) across habitats, seasons, and diet niches (BR = browser, IM = intermediate-feeder, GR = grazer). The covariate n_i represents relative abundances of species sampled at each reserve.*

n	r^2	*df*	*F*	Effect	SS	MS	*df*	*F*
Across all four habitats								
1026	0.442	48, 977	16.150***	Habitat	553.824	184.608	3	108.264***
				n_i	99.748	99.748	1	58.497***
				Habitat / Season	291.038	24.253	12	14.223***
				Habitat / Season / Diet	128.087	4.003	32	2.347***
Sites within Loskop Dam NR								
401	0.228	22, 378	5.081***	Site	7.268	7.268	1	4.170*
				Site / Season	110.831	18.472	6	10.599***
				Site / Season / Diet	76.707	5.114	15	2.934**

n = number of observations; *df* = degrees of freedom; SS and MS = sum of squares and mean squares, respectively; Significance: *** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$

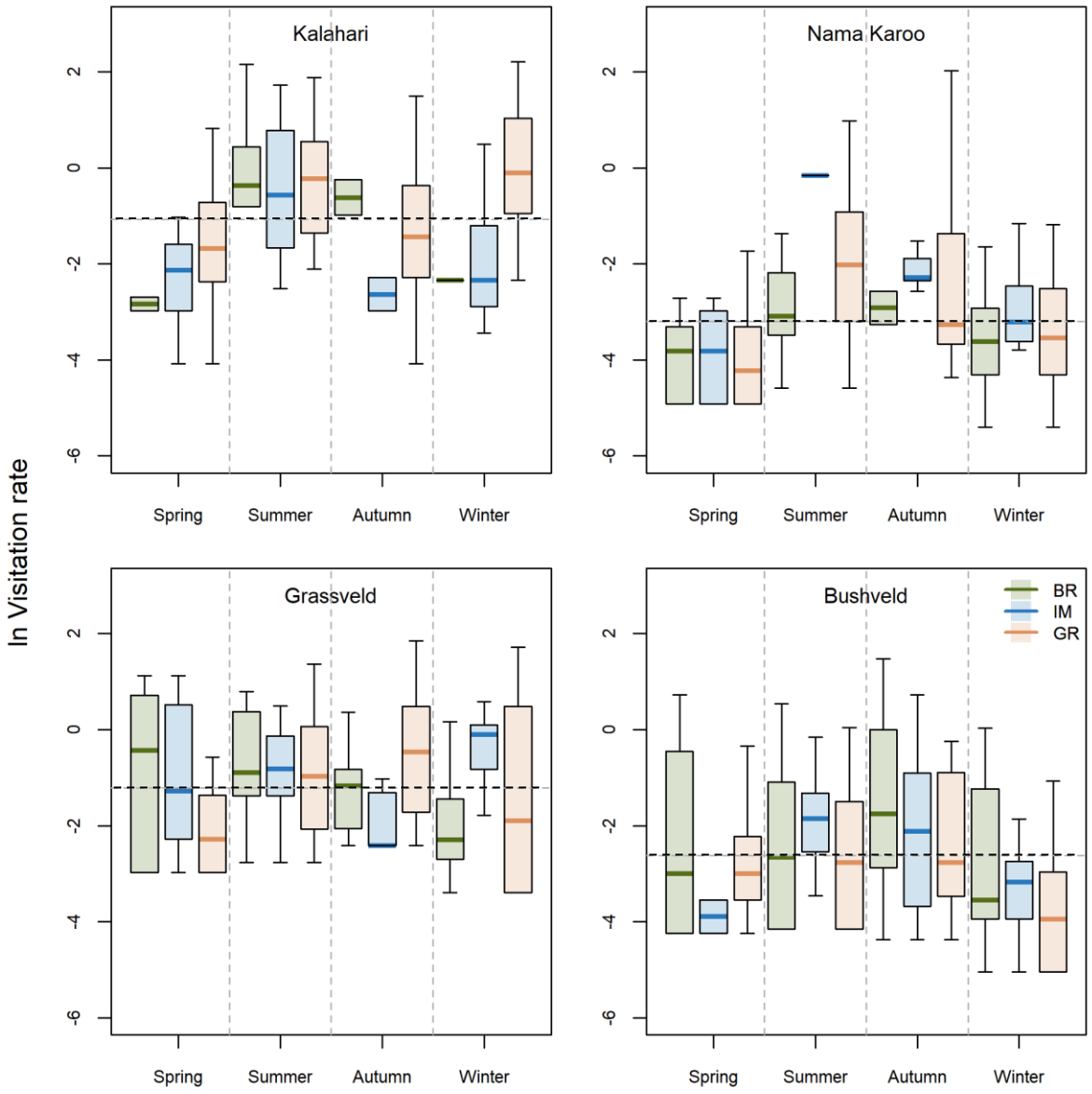

Figure 5.1. *Comparison of geophagy site visitation rates (ln-transformed) across the four habitats, and four seasons, in this study. Stippled horizontal lines indicate habitat means. Horizontal lines in the boxes are medians, boxes themselves are interquartile ranges, and whiskers are ± 1.5 of 75th and 25th percentiles, respectively. BR = browsers, IM = intermediate-feeders, and GR = grazers.*

In the Kalahari, the highest ρ, summed across six species recorded there, was found for the summer and winter months (67.96 and 63.73 records per CTD, respectively), followed by spring (41.63/CTD) and then autumn (21.16/CTD). These differences were significantly different when comparing summer with spring and autumn ($p < 0.001$ and 0.01, respectively), and winter with spring ($p = 0.02$), irrespective of diet niche; lack of statistical difference between either winter or spring with autumn is likely because only a small number of species ($n = 3$) were recorded in autumn. At species level, gemsbok (*Oryx gazelle*), a grazer, totalling 151.33/CTD, were consistently the most abundant recorded in this habitat, peaking during winter (55.18/CTD). This was followed by mixed-feeding springbok (*Antidorcas marsupialis*) (totalling 21.8/CTD) and browsing eland (*Taurotragus oryx*) (14.74/CTD); red hartebeest (*Alcelaphus buselaphus*), kudu (*Tragelaphus strepsiceros*) and steenbok (*Raphicerus campestris*) were recorded infrequently. However, there were no statistically significant differences between ρ across diet niches ($p > 0.05$), suggesting species' visitation rates occurred in proportion to their relative abundances (note the significant effect of n in Table 5.2). Yet, the issue of abundance is probably more nuanced than this interpretation would imply because, for example, ρ for eland was low in all seasons except summer, during which time it exceeded that of springbok. This issue is dealt with in greater detail below.

At Tussen-die-Riviere Nature Reserve in the Nama Karoo habitat, where overall ρ was lower than in other habitats, as many as 13 species were recorded to consume soil, and eight of these were recorded during each of the four seasons (Table 5.1). In contrast with the Kalahari, the highest ρ was found in autumn (total 21.95/CTD), followed by summer (13.02/CTD), whereas ρ in winter (4.31/CTD) and spring (2.46/CTD) was significantly lower ($p < 0.0001$ to <0.01). However, pairwise *post hoc* tests for the nested Diet niche term showed that these seasonal differences were only significant amongst grazers, whereas ρ for browsers and intermediate-feeders remained similar, and low, throughout the seasonal cycle (<1/CTD, except for springbok which peaked in autumn at 2.05/CTD). Amongst grazers, black wildebeest (*Connochaetes gnou*) (cumulative ρ 10.55/CTD), gemsbok (9.41/CTD), plain's

zebra (*Equus quagga*) (9.16/CTD), and to a lesser extent red hartebeest (3.27/CTD) dominated the sample, with black wildebeest, plain's zebra, and red hartebeest peaking in autumn (8.05, 7.98, and 2.21/CTD, respectively), and gemsbok peaking in summer (8.36/CTD).

In the Grassveld habitat, where ρ was similarly high compared with the Kalahari, most animals were recorded during the dry winter (61.25/CTD), followed by summer (47.22/CTD), autumn (46.32/CTD), and finally spring (36.39/CTD; Table 5.1). These seasonal variations were much smaller than in other habitats, and consequently not significantly different from each other (p = 0.069 to 0.999; Fig. 5.1). Of the 13 species recorded here, grazer species (122.06/CTD), specifically plain's zebra (74.45/CTD) and sable antelope (*Hippotragus niger*) (37.77/CTD) dominated during all four seasons. In contrast to the general pattern in the Grassveld, these two species showed substantial seasonal variations and, consequently, the seasonal change in grazer ρ was statistically significant (p = 0.018). The number of plain's zebra steadily increased from spring (2.78/CTD) to summer (7.65/CTD), autumn (26.66/CTD) and reached the highest number during the winter (37.36/CTD). Following a relatively low frequency of visits to the geophagy site by sable antelope in spring (5.46/CTD), attendance to the geophagy site reached a peak during the summer (12.52/CTD), and then showed a steady decline towards autumn (10.68/CTD) and winter (9.10/CTD). Other grazer species visited geophagy sites only occasionally (ρ < 5/CTD). Seasonality was also evident amongst intermediate-feeding impala (*Aepyceros melampus*), peaking in spring (17.63/CTD), thereafter decreasing in the summer (9.04/CTD) and autumn (1.53/CTD) before visiting more frequently again in winter (6.94/CTD), and browsing kudu which peaked in summer (14.29/CTD) and visited less often in other seasons (4.76 to 6.96/CTD). These seasonal patterns in impala and kudu were, however, not statistically significant (p > 0.05), due to large seasonal overlaps in ρ (Fig. 5.1).

In the Bushveld habitat, represented here by data from Loskop Dam Nature Reserve, geophagic activity peaked in autumn (37.15/CTD), was relatively high during spring

(21.52/CTD) and summer (18.84/CTD), and significantly lower during winter (8.96/CTD; $p <$ 0.0001 to <0.01; Table 5.1). This habitat differs from the others in this study mainly because it comprises a larger woody vegetation component. Accordingly, browsers were more prevalent here than elsewhere, in fact dominating the sample, reaching a maximum cumulative ρ in autumn (23.65/CTD) and a minimum in winter (6.28/CTD). By contrast, grazer activity was much lower than that of browsers, and with a different seasonal pattern, peaking during spring (9.01/CTD) and summer (6.48/CTD), and dropping significantly during autumn (2.21/CTD; $p = 0.034$). Intermediate-feeders only had cumulative $\rho > 1$/CTD in summer (2.81 for impala) and autumn (7.38 for nyala (*Tragelaphus angasii*)).

5.3.2 Accounting for Relative Abundance

Not surprisingly, the frequency occurrences of different species at geophagy sites were related to their relative abundances (n_i) in the four habitats studied (Table 5.2; $B = 4.061 \pm 0.531$, $t = 7.648$, $p < 0.0001$). As discussed above, accounting for this effect meant that differences in ρ across diet niches were seldom significant: in fact, *post hoc* tests revealed no statistically significant differences in ρ across diet niches within any one season in a particular habitat ($p = 0.0524$ to 0.999). However, grouping species this way, i.e., according to diet niche, potentially obscures differences in activity of species with different nutritional or physiological needs. Indeed, descriptive statistics suggested that even amongst diet niches, species-level responses to seasonality differed, for example between grazing black wildebeest and gemsbok in the Nama Karoo, or between intermediate-feeding nyala and impala in the Bushveld.

By plotting relative visitation rates (ρ^*) as a function of relative abundance at each habitat showed that although species generally plotted close to the 1:1 lines, some notable exceptions occurred (Fig. 5.2). Eland in the Kalahari, black wildebeest, zebra and gemsbok in Nama Karoo, sable and zebra in the Grassveld, and kudu and nyala in Bushveld, all appeared to have frequented geophagy sites more often than expected based on their abundances at

each site. By contrast, warthog were recorded relatively infrequently in the Nama Karoo, and impala in the bushveld also frequented geophagy sites less often than expected.

5.3.3 Within-habitat Variation

Analysis restricted to the Bushveld habitat, facilitating a comparison between two types of lick sites, revealed that significant spatial variations in ρ occurs even within a single habitat type (Site effect in Table 5.2). Here, there was a clear pattern of higher ρ at the Erosion type licks than Mountain Slope sites ($F_{1, 378} = 4.170$, $p = 0.042$; Fig. 5.3). However, there was also a significant seasonal effect ($F_{6, 378} = 10.599$, $p < 0.0001$), with ρ being lower in winter than in other seasons ($p < 0.0001$ to 0.049) mirroring the overall pattern for the Bushveld. The drop in geophagic activity in winter was larger at the Mountain slope sites, with the overall outcome being that the difference between the two types of sites was only significant in winter ($p < 0.01$).

In terms of specific diet niches, while the overall effect was statistically significant ($F_{15, 378} = 5.114$, $p < 0.001$), no differences were found between diet niches within each site type and season. A seasonal pattern was evident amongst grazers, at least at the Mountain slope sites, where ρ was higher in summer than winter ($p < 0.01$).

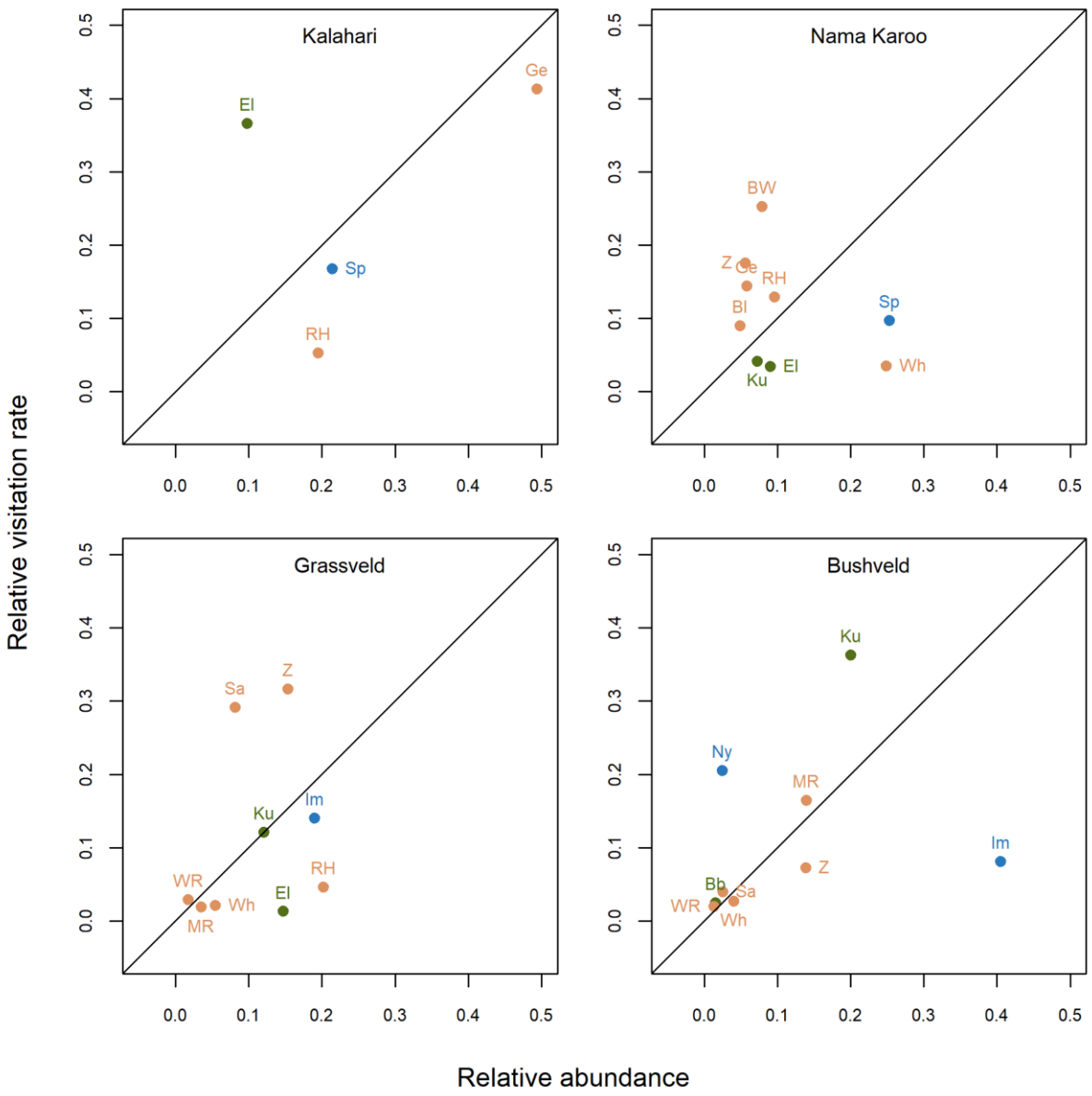

Figure 5.2. *Relationship between geophagy site visitation rate and relative abundances of mammalian herbivores, around 1:1 lines (black diagonals) at the four habitats sampled. Species above the 1:1 line visited sites more frequently than expected relative to their abundance, and vice versa for species below the line. Colours correspond with diet niches displayed in Fig. 1: green = BR (Bb = bushbuck, El = eland, Ku = kudu), blue = IM (Im = impala, Ny = nyala, Sp = springbok), orange = GR (Bl = blesbok, BW = black wildebeest, Ge = gemsbok, RH = red hartebeest, MR = mountain reedbuck, Sa = sable, Wh = warthog, WR = white rhino, Z = zebra).*

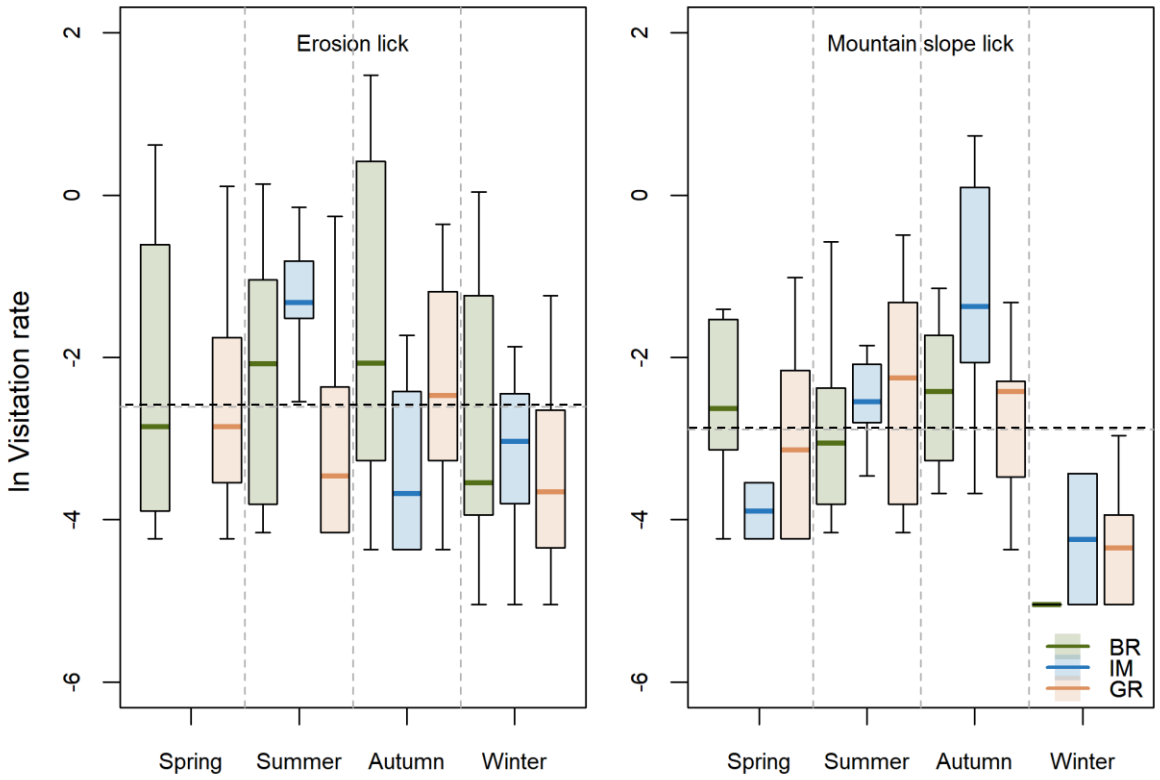

Figure 5.3. *Comparison of geophagy site visitation rates of mammalian herbivores (ln-transformed) across two sites at Loskop Dam Nature Reserve ('Bushveld" in Fig. 1), and four seasons, in this study. Stippled horizontal lines indicate habitat means. Horizontal lines in the boxes are medians, boxes themselves are interquartile ranges, and whiskers are ± 1.5 of 75th and 25th percentiles, respectively. BR = browsers, IM = intermediate-feeders, and GR = grazers.*

5.3.4 Activity Times

Activity times at geophagy sites were generally concentrated during daylight hours, either in the mornings after sunrise or in the evenings before sunset (Fig. 5.4). There were relatively few occurrences between the hours 20:00 and 05:00, and when these did occur, they were mostly the secondary visit of species that showed bimodal activity. Variation in activity hours could not, for the most part, be explained by variance across habitats or seasons (Table 5.3), although the lack of statistical significance could reflect low statistical power associated with relatively small number of data points distributed across the habitat and seasonal groups (n = 71, and for secondary peaks in bimodal cases n = 28). For example, despite the global model being non-significant (p = 0.078), active hours did appear to be earlier in summer than in winter (*post hoc* $p < 0.01$).

More notable differences in activity hours emerged between species, evinced by the estimates of temporal niche overlap between group pairs. Overlap was smaller than 0.5 for the majority (n = 323 of a total 492 pairs, about two-thirds) of pairs, and only the bushveld habitat had an overall mean approaching this level (Fig. 5.5). A linear model confirmed a significant effect of habitat on these data ($F_{3, 476} = 9.332$, $p < 0.0001$), and that overlap in the bushveld was, on average, above levels recorded for the Kalahari ($p = 0.032$) and Nama Karoo ($p < 0.0001$). There were also changes in overlap across seasons (Habitat X Season interaction $F_{9, 476} = 3.652$, $p < 0.001$), but only in Nama Karoo where average overlap was less in summer and winter than in autumn ($p < 0.0001$ and 0.023). Thus, for the most part, temporal niche overlap was relatively low throughout, indicating that temporal niche separation was mainly occurring between species within particular habitats.

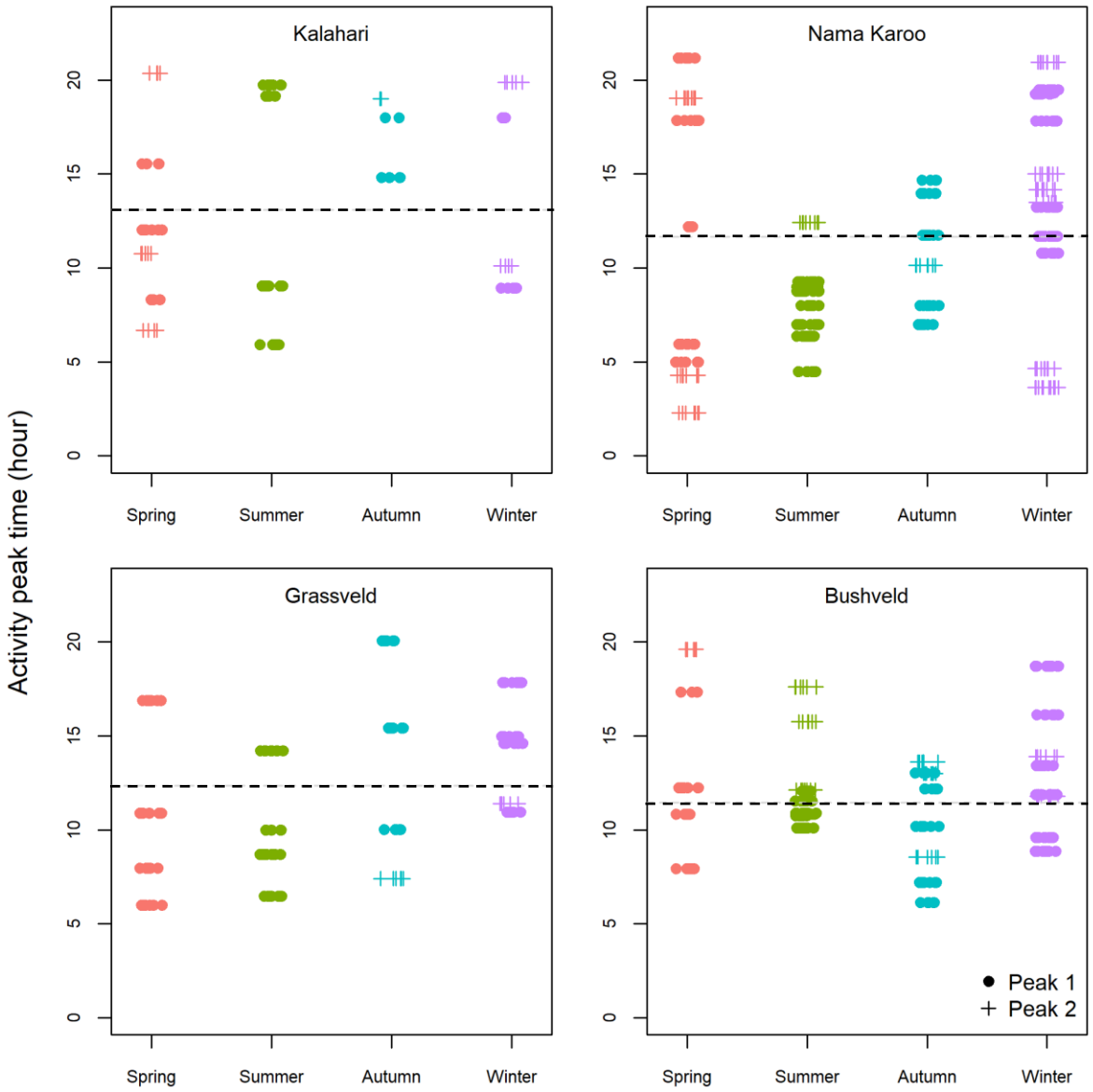

Figure 5.4. *Peak activity times (density means) of mammalian herbivores at geophagy sites in different habitats and seasons. Each symbol represents a species: circles = mean of the largest density, crosses = means of the second density for cases where bimodal activity patterns emerged (>30 % probability of occurring within the second density function). Stippled horizontal lines indicate habitat means (first peak only).*

Table 5.3. *Crossed linear models used to compare geophagy site activity times of mammalian herbivores throughout the day across habitats and seasons.*

N	r^2	*df*	*F*	Effect	SS	MS	*df*	*F*
Peak activity time								
71	0.3192	15, 55	1.719	Habitat	52.003	17.334	3	1.046
				Season	211.556	70.519	3	4.255*
				Habitat X Season	180.735	20.082	9	1.212
Secondary peak activity time								
28	0.2701	12, 15	0.463	Habitat	93.902	31.301	3	0.828
				Season	24.206	8.069	3	0.213
				Habitat X Season	95.586	15.931	6	0.421
Activity time overlap								
492	0.1233	15, 476	4.462***	Habitat	1.704	0.568	3	9.158***
				Season	0.354	0.118	3	1.904
				Habitat X Season	2.035	0.226	9	3.644**

n = number of observations; *df* = degrees of freedom; SS and MS = sum of squares and mean squares, respectively; Significance: *** $p < 0.0001$, ** $p < 0.001$, * $p < 0.01$, + $p = 0.074$

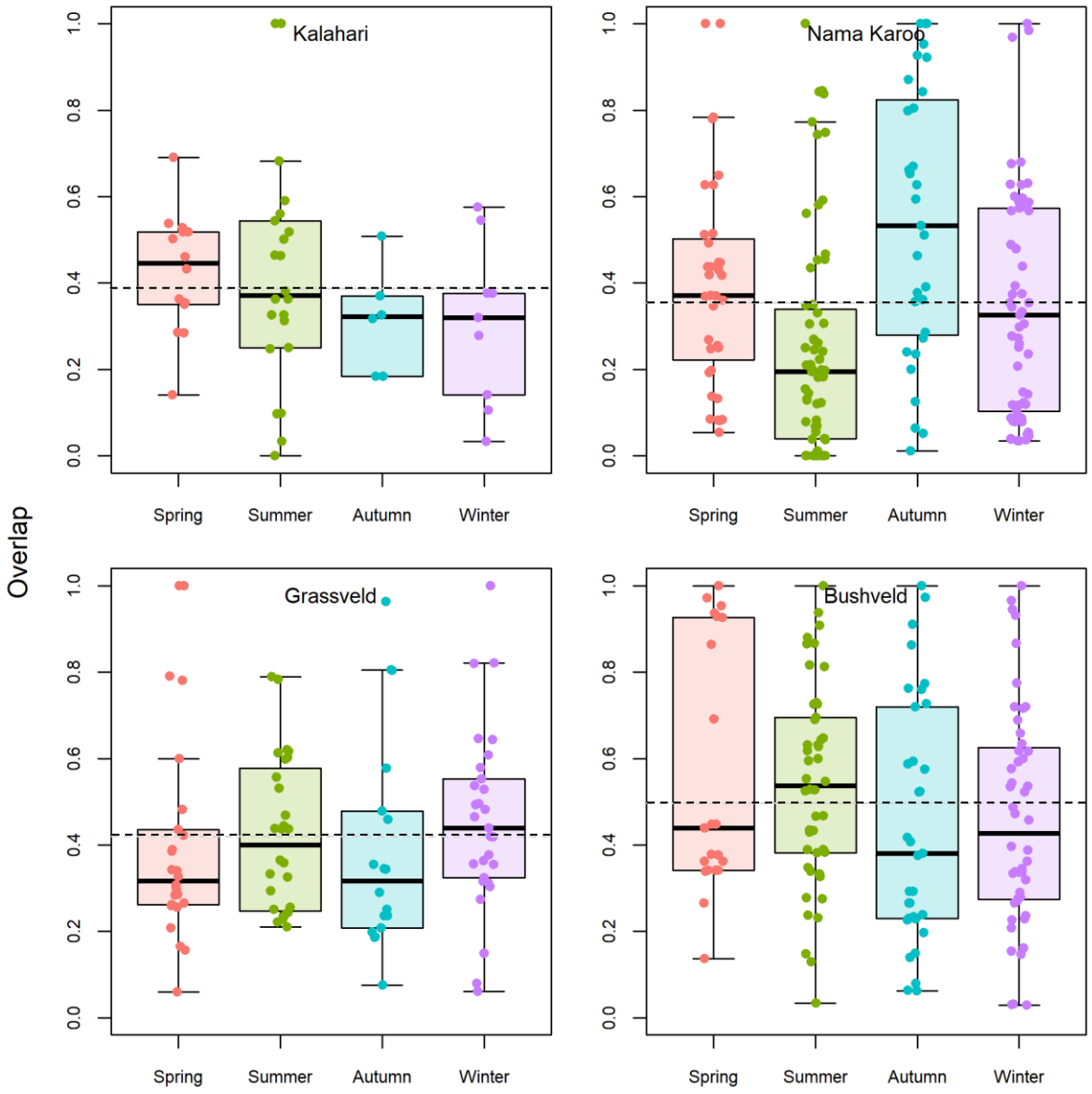

***Figure* 5.5.** *Overlap in activity times between mammalian herbivore species pairs (symbols) in each habitat and season. Stippled horizontal lines indicate habitat means. Horizontal lines in the boxes are medians, boxes themselves are interquartile ranges, and whiskers are ± 1.5 of 75th and 25th percentiles, respectively.*

5.3.5 Sex Ratios

Females clearly dominated geophagy site visits (Fig. 5.6). Out of 23 542 sexed individuals, 17 780 (75.5 %) were female. There were clearly different female:male sex ratios across habitats, with high percentages of females in the Kalahari and Grassveld (85.3 and 84.9 %, respectively), less in the Bushveld (67.2 %), and in the Nama Karoo the sex distribution was more-or-less even (47.2 % females) (χ^2 = 2 146.478, *df* = 3, $p < 0.0001$).

There were also seasonal trends, albeit that patterns were not consistent across habitats: female:male ratios in the Kalahari decreased from winter through summer, autumn, and spring; in the Nama Karoo the descending sequence was spring, autumn, summer, winter; and in the Bushveld summer, winter, spring and finally autumn (χ^2 = 190.486, 358.030, and 234.978, respectively; *df* = 3, $p < 0.0001$). Because of these differences, it was necessary to include the Habitat X Season interaction term in the GLMM used to evaluate the patterns formally (see below). In the Grassveld, however, no seasonal trends were evident (χ^2 = 6.102, *df* = 3, $p = 0.107$). Therefore, data for Grassveld amongst dummy variables used in the GLMM were zeroed.

For the most part, the GLMM supported interpretations based on visual inspection of trends in Fig. 5.6. The fixed effects Habitat and Season were significant (see non-overlapping 95% CIs in Table 5.4). Focusing on the parameters for the interaction terms, the low female:male ratios observed in spring were significantly different from other seasons; however, summer and autumn, while intermediate between spring and winter, did not differ from each other. Similarly, in the Nama Karoo, parameter estimates revealed significantly higher female:male ratios during spring than summer, with winter having the lowest (autumn female:male ratios did not differ from those of spring). In the Bushveld, however, all seasons had overlapping parameter estimates, except for spring which had higher female:male ratios. It appears that the seasonal changes shown in Fig. 5.6 for the Bushveld are influenced also by changes in species composition – a random effect included in the GLMM.

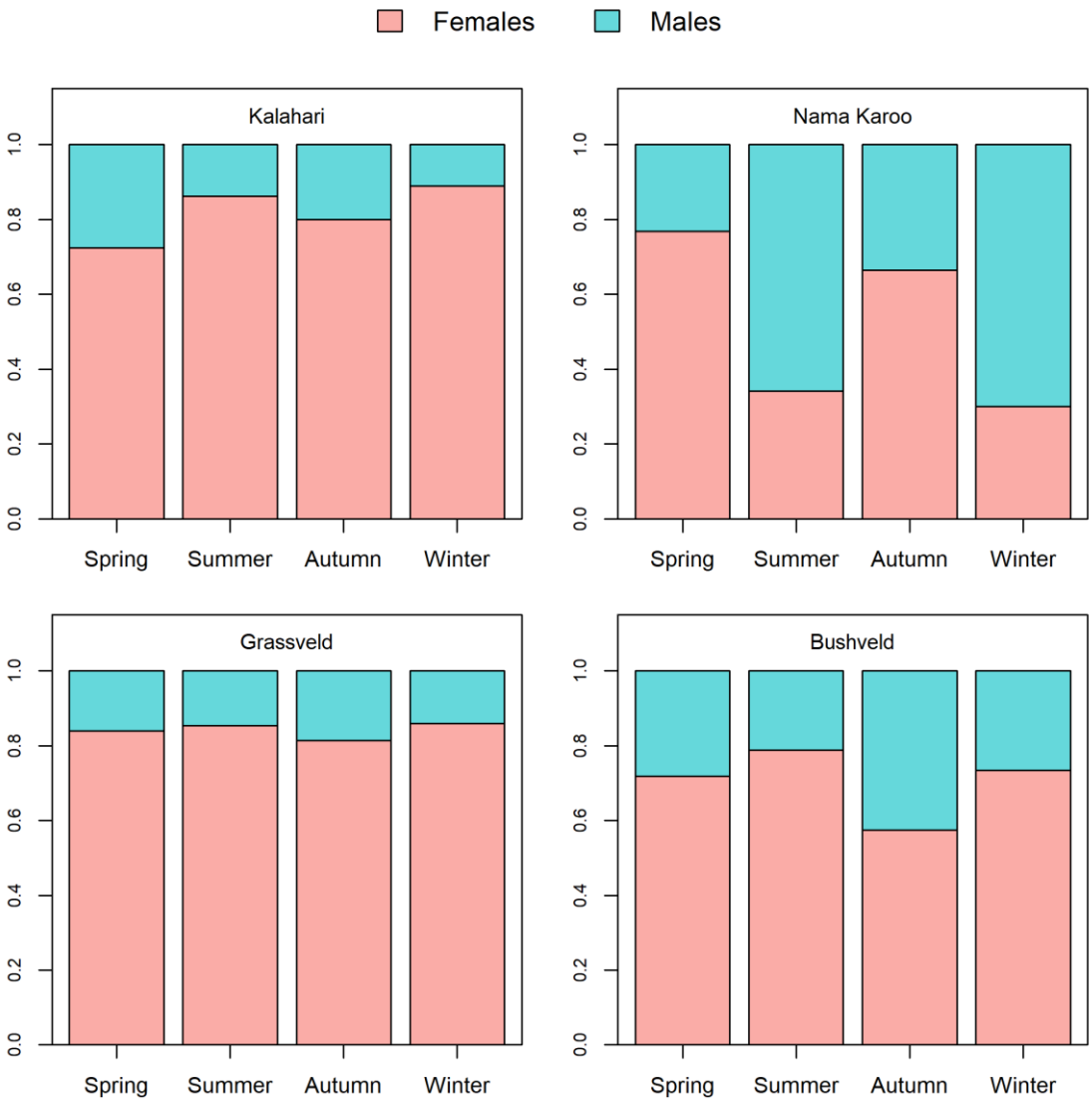

Figure 5.6*. Frequency occurrences of mammalian herbivore females and males that engaged in geophagy (expressed as proportions of the total) during different seasons in four habitats.*

Table 5.4. *Parameter estimates (with 95% confidence intervals, CI, in parentheses) derived from a GLMM comparing female:male ratios of mammalian herbivores across habitats and seasons. Counts and percentages for both sexes within habitats and seasons are shown to assist interpretation (see also Fig.5.6).*

Parameter	Estimate (95% CI)	Females (%)	Males (%)
Intercept	-1.695 (-2.224 to -1.167)		
Summer	0.133 (-0.169 to 0.436)		
Autumn	0.694 (0.354 to 1.033)		
Winter	0.343 (0.075 to 0.611)		
Kalahari	-0.294 (-0.648 to 0.060)		
Nama Karoo	0.283 (-0.128 to 0.695)		
Bushveld	1.716 (1.447 to 1.985)		
Grassveld X Spring	zeroed	575 (83.9 %)	110 (16.1 %)
X Summer	zeroed	564 (85.3 %)	97 (14.7 %)
X Autumn	zeroed	345 (81.4 %)	79 (18.6 %)
X Winter	zeroed	1413 (85.9 %)	231 (14.1 %)
Kalahari X Spring	zeroed	650 (72.4 %)	248 (27.6 %)
X Summer	-0.854 (-1.200 to -0.507)	4025 (86.2 %)	645 (13.8 %)
X Autumn	-1.138 (-1.533 to -0.742)	971 (79.9 %)	244 (20.1 %)
X Winter	-1.487 (-1.808 to -1.165)	3325 (89.0 %)	412 (11.0 %)
Nama Karoo X Spring	zeroed	215 (76.8 %)	65 (23.2 %)
X Summer	1.272 (0.827 to 1.717)	362 (34.1 %)	700 (65.9 %)
X Autumn	0.352 (-0.133 to 0.837)	531 (66.4 %)	269 (33.6 %)
X Winter	1.969 (1.526 to 2.413)	174 (30.1 %)	405 (69.9 %)
Bushveld X Spring	zeroed	1034 (71.8 %)	406 (28.2 %)
X Summer	-0.945 (-1.311 to -0.579)	910 (78.8 %)	245 (21.2 %)
X Autumn	-0.557 (-0.929 to -0.185)	1671 (57.4 %)	1239 (42.6 %)
X Winter	-0.690 (-1.011 to -0.368)	1015 (73.4 %)	367 (26.6 %)

5.4 Discussion

5.4.1 Visitation Frequency

In addressing the first and second objective of this chapter, the clear difference in frequency of geophagy, observed between habitats as well as across seasons, indicated a variation in the proximate stimuli that triggered geophagy. Animals ate significantly more often soil in the Kalahari and Grassveld than in the Bushveld habitat whereas in the Nama Karoo, animals ate significantly less often compared with any of other habitats in the study.

Although all habitats in the study area had grass as a component, it occurred in different species composition as well as in percentage of coverage. The Kalahari is generally referred to as an arid savanna (Van Rooyen and Van Rooyen 1998) where, according to the description of savannas by Bourliére and Hadley (1983), the grass stratum is continuous and occasionally interrupted by tree and shrub species. Therefore, large mammalian herbivores, specifically grazers, consume soil more in habitats where grass is the predominant plant cover, than in the Bushveld with more trees or the Nama Karoo with a complex mixture of grass and dwarf karroid shrubs. The occurrence of dissimilar plant species with different nutritional values, might therefore be an explanation for the observed variation in geophagy between habitats. According to McDowell (1985) as well as Suttle (2010), the mineral content of plants is affected mostly by the mineral composition of the soil in which they grow and furthermore, different plant parts differ in nutritional values (Owen-Smith and Novellie 1982). In addition to this, climatological differences especially rainfall patterns, undoubtedly contribute to the variations in phenology across different habitats and seasons (Suttle 2010).

The Kalahari, the only habitat in this study where animals had almost unlimited freedom to find nutrition by migrating, was the habitat where most animals (194.48/CTD) engaged in geophagy. This was also the only habitat where literature on nutrient levels, and fluctuations thereof, in forage across seasons could be obtained. Various studies on the nutritional value of plants of the Kalahari, including Van Hoven et al. (1984), Tolsma et al. (1987) and Stapelberg et al. (2008) indicated seasonal fluctuations of nutrients for several tree and grass

species. In general, browse species contain higher concentrations of crude protein than grass species (Minson 1990; Lukhele 2002; Stapelberg et al. 2008). In a study on seasonal fluctuations in selected plant species which included three woody and two grass species, commonly utilised by springbok in the Kalahari, Stapelberg et al. (2008) reported that although the crude protein content was in general above the level which is required by African ungulates, the diet of springbok, an intermediate-feeder, in the south-western Kalahari appeared to be phosphorus deficient. Both crude protein and phosphorus content of the browse and grass species reached a minimum during the cold dry season in the Kalahari (Stapelberg et al. 2008). On the other hand, the content of Ca peaked during the cold-dry season in browse species, whereas that of grasses remained low throughout the year. Although Stapelberg et al. (2008) reported that the Ca:P ratio of plant species with excess of calcium is unhealthy for ruminants, springbok, an intermediate feeder, were recorded to ingest soil especially during the summer and winter months.

The supplement of Ca could therefore not be the primary motivation for the ingestion of Ca rich soil in the Kalahari by springbok as concluded in Chapter 3. However, only eland were recorded to ingest soil above their relative abundance, and although they consumed soil during all the seasons (with a total of 14.39/CTD), summer (13.01/CTD), when Ca levels were the lowest in browse species (Stapelberg et al. 2008), was the season when they visited geophagy sites the most. The supplementation of Ca, at least during the summer, might therefore be the driver for geophagy among eland. The buffering capacity of carbonates as found in calcite, is important in neutralising the increased acidity of the rumen, which usually occurs with the transition from fibrous winter forage to lush spring growth during spring (Ayotte et al. 2008). In the Kalahari grazers consumed soil at high frequencies during all the seasons with a peak observed during winter. The low Ca content of grass during all the seasons (Stapelberg et al. 2008) might therefore indicate that grazers consume soil for the purpose of supplementing a Ca deficient diet.

For browsers, geophagy might also play a significant role in detoxification of secondary plant products. Plant secondary metabolites, such as tannins, affect browsing ruminants in South African savannas negatively especially during the late summer (Cooper and Owen-Smith 1985). Tannins are generally regarded as inhibitory to the growth of microorganisms (McSweeney et al. 2001). Thus, tannins might reduce the effectiveness of fermentation and degradation of plant tissues in the rumen of large mammalian herbivores, which depend on microbial symbionts for part of their energy needs (Cooper and Owen-Smith 1985). Several studies (e.g., Johns 1986; Gilardi et al. 1999; Dominy et al. 2004; Ta et al. 2018; Pebsworth et al. 2019) mentioned the detoxification role of ingested soil, containing clay minerals. Although browsers consumed soil during all the seasons at all four study sites, geophagy peaked during the summer in both the Kalahari (13.04/CTD) and Grassveld (15.11/CTD). In the Bushveld however, the peak season of soil ingestion for browsers was during autumn (23.65/CTD). One explanation for the peak time of geophagy in the Bushveld might be that temperatures in this habitat remain high even during the autumn months, followed by a moderate winter. Deciduous and semi-deciduous trees and shrubs there do not shed their leaves until the end of autumn. Plants in the Bushveld habitat therefore have and extended growing phase, and might have high plant secondary metabolites at high levels till late in autumn. Another possibility might be that during autumn, browsers are forced to expand their diet breadth to incorporate plants that they would usually avoid during spring and summer (Owen-Smith and Cooper 1989, O'Reagain and Grau 1995, Owen-Smith 2002). Therefore, browsing herbivore species would potentially increase their geophagy as the increased intake of minerals would help neutralise this seasonal increase in plant secondary compounds. This however should be investigated further. In the Nama Karoo, where browsers consumed soil at a far lower frequency (0.10 – 1.06/CTD) than in any of the other habitats, almost the same frequency of geophagy was observed during winter (1.06/CTD) and summer (1.04/CTD). This observation might also be explained by plant secondary compounds. In summer, new growth tends to have high levels of chemical defence (but also high levels of crude protein), while in winter, the food incorporated into the diet contains high levels of secondary compounds. This

result might however, be explained by the low visitation rate of browsers to geophagy sites that are too low for statistical detection of patterns like seasonality.

The supplementation hypothesis of geophagy implies that animals should engage in geophagy when availability of plant nutrition is at its lowest level. In a southern African context, this coincides with the colder dry seasons of autumn (March to May) and winter (June to August). Peak activity times during these seasons were observed among grazers in the Kalahari (Winter; 55.58/CTD), Nama Karoo (autumn; 19.80/CTD) and Grassveld (winter; 48.46/CTD). However, with frequencies the lowest of any habitat, the peak season when grazers visited geophagy sites in the Bushveld was during the spring (9.01/CTD). Practising geophagy during spring might benefit grazers by contributing to the buffering effect of salivary bicarbonate to neutralize rumen acidity (Brady and Weil 1999), which increase during the transition from a fibrous winter forage to lush growth in spring time (Ayotte et al. 2006). Another possible explanation for geophagy during spring and summer might be a strategy to supplement minerals that were lost in sweat or urine, and that could not be replenished by forage. In comparison between erosion and mountain slope geophagy sites in the Bushveld habitat, the higher frequency of animals that visited the erosion licks compared with the mountain slope sites, might merely be an indication of the easier access and therefore less energy that is needed to visit the lower lying sites.

In the remaining habitats, Kalahari, Nama Karoo and Grassveld, grazers that ingested soil mainly during the autumn and winter, might have received other benefits from soil ingestion. Grasses have a higher neutral detergent fibre (NDF) content, the structural components of plant cells, than browse which are more lignified than grass (Hummel et al. 2006). The fact that larger herbivores generally feed on plant species of lower quality is well documented (e.g., Owen-Smith 1988; Codron et al. 2007; Müller et al. 2013). According to Clauss et al. (2009), fibre digestibility is dependent on particle size and digesta retention time, and a longer passage time of food particles seems to be adaptive for grazing ruminants (Hummel et al. 2006). A few studies reported on the advantage of clay minerals in the diet of

animals, whereby the passage rate is slowed down for better utilisation of feed nutrients. By adding clay, with strong colloidal properties that absorb water rapidly like bentonite, to the diet of chickens (Cosialls et al. 1992; Damiri et al. 2010) and sepiolite, a hydrated magnesium aluminium silicate, to that of calves (Elitok and Başer 2016), increased fermentation time with positive effects on body weight gain as well as the prevention of diarrhoea was observed. According to Caton et al. (1999), the selection of soils which is high in finely divided clay particles for ingestion, may be a strategy of orangutans to extend the retention time of digesta in the colon, which increases fermentation time. Similarly, grazers therefore, benefit from a slower retention time of ingested fibre. The rate, and therefore the extent of digestion of structural carbohydrates of plant cells, which are degraded by microorganisms in the rumen (Zhang et al. 2007), determine the nutritive value of ruminant feeds (Andrés et al. 2005).

In all the habitats and across all seasons, in total more grazers engaged in geophagy than browser and intermediate feeders combined, even after accounting for variations in abundances of the species representing these feeding guilds. In the results of relationships between geophagy site visitation rate and relative abundances of species (*vide* Fig. 5.2), grazers were observed to consume soil more than their relative abundance in the Nama Karoo and Grassveld, and even in the more wooded Bushveld (mountain reedbuck), albeit to a lesser extent. In Kalahari, gemsbok eat soil surprisingly less frequently than expected, given their high abundances. An explanation for this result might be that there are many pans in the area, and gemsbok might visit other similar geophagy sites which were not monitored, but this would require further study to quantify.

5.4.2 Activity Times

Large mammalian herbivores engaged in geophagy mainly in the daylight hours in all habitats (third objective). This reflected the general diurnal activity patterns of mammalian herbivores. Wu et al. (2018) hypothesised that extant mammalian herbivores have evolved to be diurnal in order to avoid carnivores, and that mammalian predators have shifted their activities toward nocturnality. As many predators favour hunting near waterholes (Bailey 1993;

Van der Meer et al. 2012), such areas that are visited by animals on a regular basis can be regarded as 'landscapes of fear', as described by Laundré et al. (2001; 2010). In a lowland rain forest in Amazonian Ecuador, Link et al. (2010) concluded that white-bellied spider monkeys (*Ateles belzebuth*) and red howler monkeys (*Alouatta seniculus*) spent long periods at the geophagy site before going to ground to ingest soil, suggesting that licks are indeed perceived as risky by these primates. Additionally, Link and Fiore (2013) found that subgroup size reached its maximum specifically during the period of lick visitation. A greater increase in size of subgroups with higher fusion rates of white-bellied spider monkeys also formed two hours before arriving at the geophagy site in comparison with matched time windows on non-visiting days (Link and Fiore 2013). Like waterholes, geophagy sites are located at specific areas in a landscape, and the same principles of landscapes of fear, which apply to waterholes, are therefore relevant to geophagy sites. The preference to visit geophagy sites mainly during the daytime, can therefore be explained by the inherent fear of predators during the darker hours of the day. This also explained the earlier visits in the day during summer as opposed to the winter times when the sun rises later.

According to Wu et al. (2018), the diel activity patterns observed between different species of ungulates, may have evolved as a compromise between factors such as predation and competition. The explanation for the notable differences in hours of activity observed between species might therefore be two-fold. Firstly, the risk of predation might influence decisions made by herbivores when to visit geophagy sites. By visiting geophagy sites at the same time, or shortly after other herbivore species, animals might minimise the predation risk and thereby reduce the perception of a landscape of fear. Herd forming species usually visited the geophagy sites within a group, and thereby benefited from the presence of conspecifics to scan the surroundings and thus detect an approaching predator (the many eyes many ears principal as suggested by Pulliam 1973). A further advantage to visit geophagy sites in groups might be that each individual had a lower risk of being preyed upon because of the "dilution effect" (Hamilton 1971; Dehn 1990). According to Creel et al. (2014), grouping is a proactive

response to the use of dangerous habitats in African ungulate communities, while vigilance is a reactive response to information about predation risk on a finer scale. Smith and Cain (2009) could not establish any relationship between herd size and vigilance in impala but reported that vigilance of each individual in a herd decreased with increasing density of the herd. The effects of predation risk are reduced by forming herds of mixed-species (Stears et al. 2020). As illustrated by Schmitt et al. (2014), benefits of dilution and detection is only to the advantage of species if these species in the mixed-species herds share a common predator. Although only sporadically, mixed herds of similar body sized animals such as impalas and mountain reedbuck as well as kudu and sable antelope did form at geophagy sites in the Bushveld habitat (see Appendix B, Fig.S5).

At geophagy sites in this study, animals were usually in close proximity of each other. However, specifically at the Main Lick and Kloppersкloof, many instances were recorded where animals, although in close vicinity of each other, were still vulnerable to predation as their heads were completely inside the concave cavities of the mined-out area (Fig. 5.7). Nine instances, of which only three were during night-time, were recorded where leopards (*Panthera pardus*) visited geophagy sites in the Bushveld habitat. It has been documented that diel activity between carnivores and their prey might be partially or exclusively synchronised (Harmsen et al. 2011). Whether the activity times of potential prey species at geophagy sites influenced this usually nocturnal predator (Mugerwa et al. 2017) to be cathemeral is uncertain. At one occasion, a leopard, the main predator in the Loskop Dam Nature Reserve, was sniffing (Fig. 5.8 A) at the Main Lick site only 37 min before kudu engaged in geophagy at the same place (Fig. 5.8 B). At these lick sites, several instances were recorded where ungulates visited geophagy sites with allospecific animals. Apart from forming mixed herds with similar body sized herbivores, animals also visited geophagy sites when primates, chacma baboons (*Papio ursinus*) and vervet monkeys (*Chlorocebus pygerythrus*), visited the geophagy sites (Fig. 5.9), although not always. Schmitt et al. (2016) found that there is a vigilance benefit among zebra that associated in mixed herds with giraffe.

As many animals react on alarm calls made by other species (Kitchen et al. 2010), animals that engaged in geophagy with primates in the vicinity, might have the benefit of an early warning system without spending energy on vigilance themselves. In addition to this, alarm calls may also function to deter predators (Hasson 1991; Caro 1995; Isbell and Bidner 2016). The benefit of feeding with vocal “watchdogs”, such as primates, can only be achieved when primates, which are diurnal (Skinner and Chimimba 2005), are active.

Figure 5.7. *Camera trap images of mountain rhebok (A) and sable antelope (B) engaged in geophagy at Main Lick (Loskop Dam Nature Reserve, Bushveld habitat with heads inside concave cavities. (Source: HJB Butler©).*

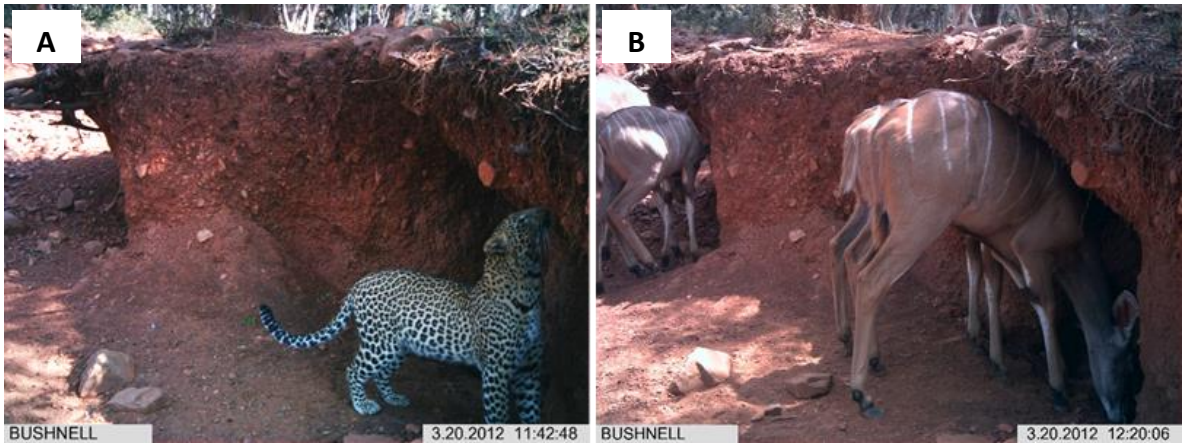

Figure 5.8. *Camera trap images of a leopard sniffing (A) and kudu feeding on soil shortly after that (B) at the Main Lick geophagy site at Loskop Dam Nature Reserve (Bushveld habitat). (Source: HJB Butler©).*

Figure 5.9. *Camera trap images of nyala (A and B), impala (C), and kudu feeding at geophagy sites in the presence of primates at the Kloppersklоof (A and B) and Main Lick (C and D) geophagy sites at Loskop Dam Nature Reserve (Bushveld habitat). (Source: HJB Butler©).*

If anti-predator behaviour is a main driver for the forming of mixed herds, one would expect that such overlap in visits to geophagy sites between species would be more noticeable in the Kalahari, where cheetah, leopard, and lion are the main predators. The relatively low overlap between species in the Kalahari can be explained by the low numbers of large mammal species (only six) which were recorded to visit geophagy sites. Furthermore, the large open pan area, with no opportunity for an ambush by predators, might also have an effect as competition for the mineral resource, rather than reduced vigilance obtained from mixed herds, might be a key factor. As part of their anti-predator behaviour, many animals have been recorded to move to open areas during night-time including Angolan giraffe (*Giraffa giraffa angolensis*) (Burger et al. 2020) and impalas (Riotte-Lambert et al. 2013). In the Central Kalahari Game Reserve, also in Botswana and similar to the habitat of the present study, Selebatso et al. (2017) reported that blue wildebeest herds also remained in pan habitats with clear visibility during the night. The low overlap in visits to geophagy sites between species during daylight hours in the Nama Karoo and Grassveld, might be as a result of the absence of predators in both these game reserves.

Secondly, reducing competition between species might influence the decision of animals to visit geophagy sites at different times. The larger overlap between species observed in the Bushveld, where 15 different species were recorded to visit geophagy sites, potentially resulted in a higher level of competition between species. On the other hand, the Kalahari where only six species were recorded, had the lowest overlap between species at the geophagy sites. At waterholes, Hayward and Hayward (2012), also found that a high degree of overlap existed between herbivores, even though species had different ‘peak’ drinking times. Although several instances were recorded where different species engaged in geophagy simultaneously, bouts of visits to geophagy sites were usually species-specific. A clear pattern of hierarchy at the geophagy sites was observed between ungulate species that consumed soil. In general, large bodied species dominated small ones, males dominated females, and adults dominated younger individuals. Apart from body size, the possession of

weaponry such as horns, also seems to play a role in dominancy. As an example, it was observed that at Willem Pretorius Game Reserve (Grassveld), female impala, that do not have horns, left the geophagy site (Fig. 5.10 A) when zebra, with a much bigger body size than impala, approached to feed on soil (Fig. 5.10 B). After the feeding session of zebra, which lasted for about 18 minutes, the impala returned to the geophagy site (Fig. 5.10 C). However, on another occasion, where an adult impala male, equipped with horns, entered the geophagy site where zebra were present, the male impala dominated the zebra by chasing them away (Fig. 5.11). This clearly is an indication that visitation frequencies by species or sex, was also influenced by the presence of more dominant or submissive species or sexes.

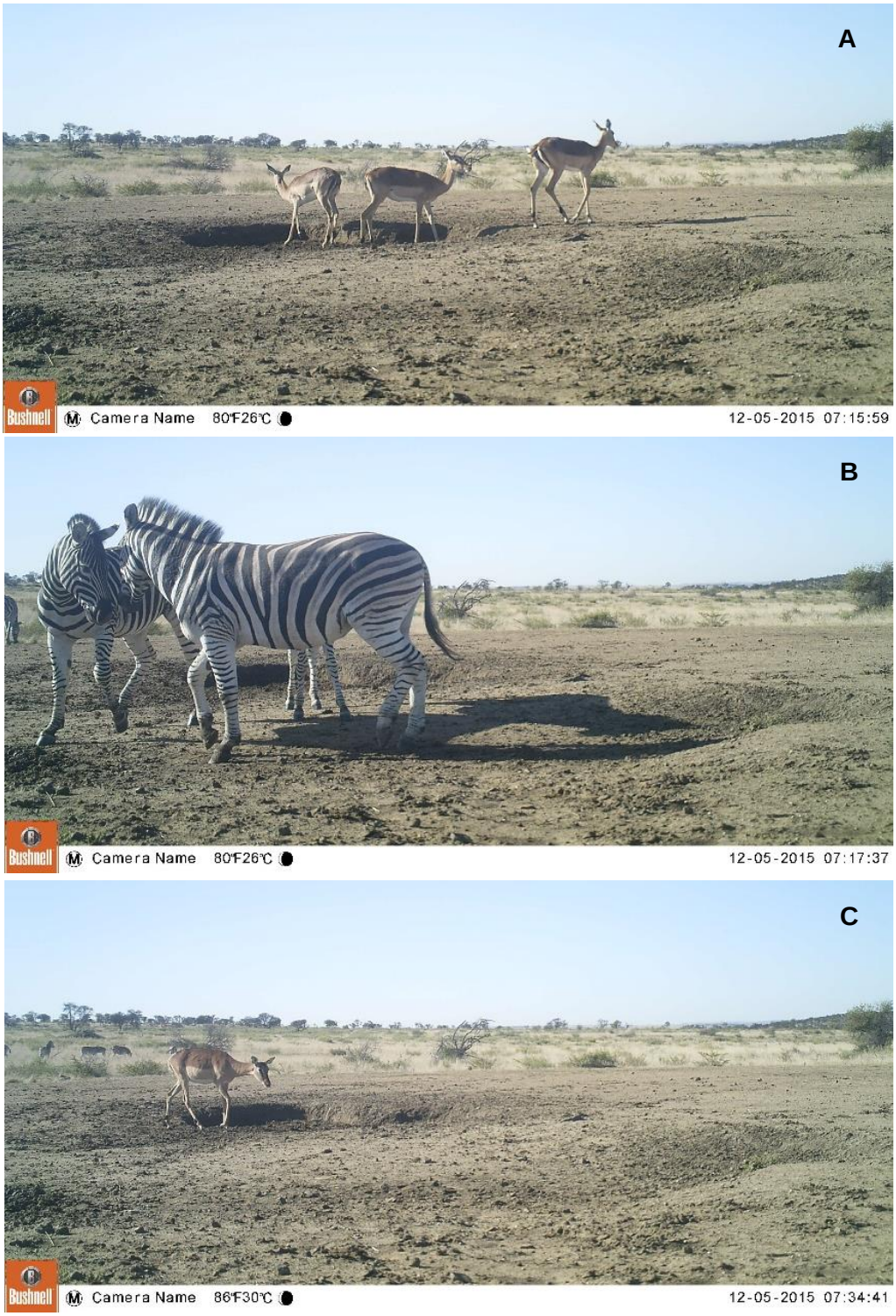

Figure 5.10. *A sequence of camera trap images of female impala (A) at the geophagy site at Willem Pretorius Game Reserve (Grassveld habitat) that left the site when zebra approached (B) but revisited the geophagy site when the zebra left (C). (Source: HJB Butler©).*

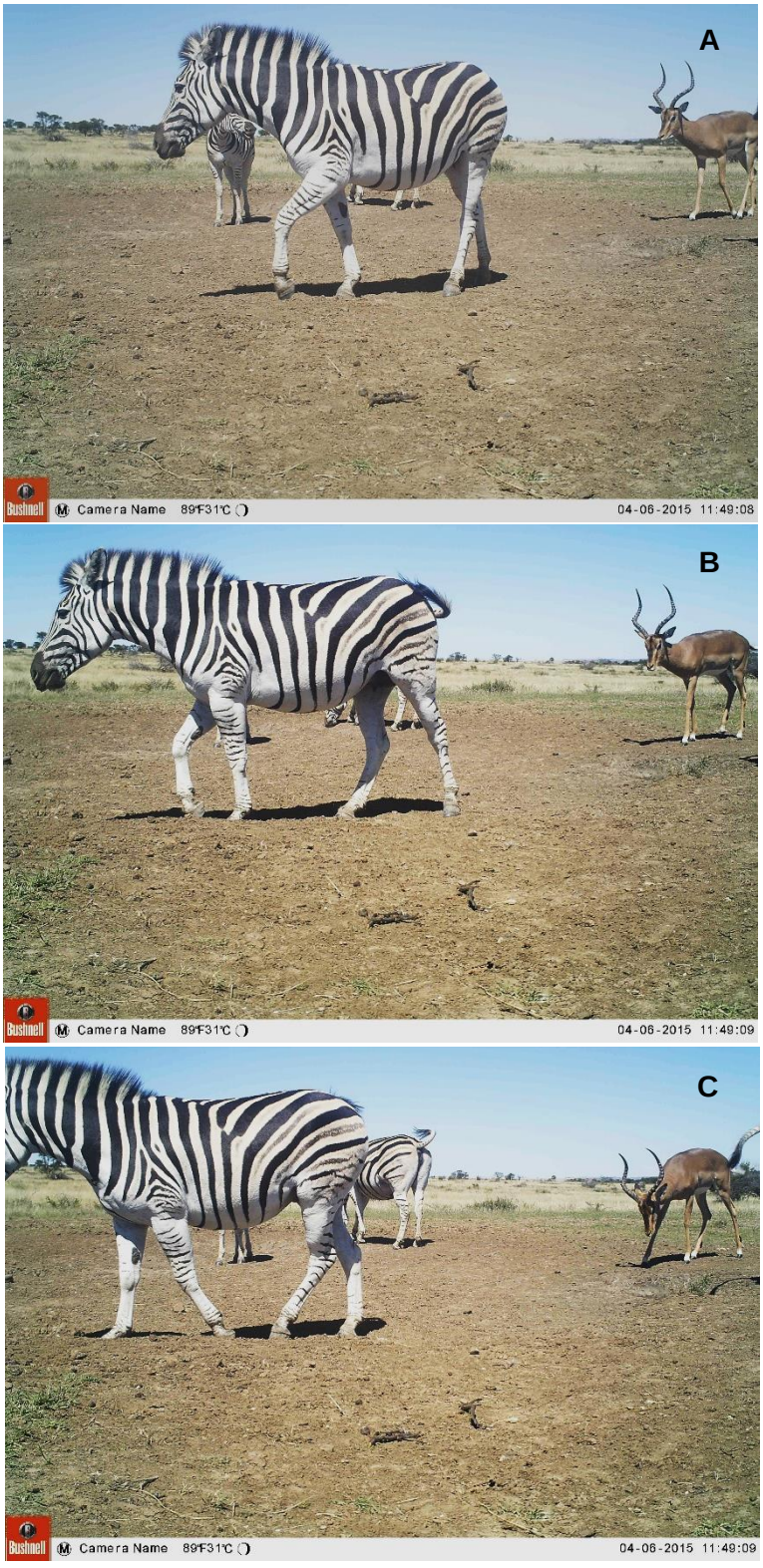

Figure 5.11. *A sequence of camera trap images at Pretorius Game Reserve (Grassveld habitat) of a male impala approaching the geophagy site (A, B) occupied by zebra which left after an angle-horn offensive display (Estes 1991) by the impala (C). (Source: HJB Butler©).*

5.4.3 Sex Ratios

Although skewed sex ratios in the different habitats might have influenced the results, the clear dominancy of females that visited geophagy sites is clear evidence of the nutritional demands on the different physiological needs of females. Admittedly, as stated by McDowell (1985), the requirements of ruminant nutrition are complex and variable. The nutritional demands for female ungulates during times of pregnancy and lactation is well documented. According to McDowell (1985) particularly Na, is required after fertilisation and during lactation. Geophagy was also linked to pregnancy and lactation times among bats (Voigt et al. 2008), chacma baboons (Pebsworth et al. 2011) elephants (Holdø et al. 2002), sika deer (Ping et al. 2011), and sambar deer (*Cervus unicolor*) (Matsubayashi et al. 2007). However, if geophagy is an indication of higher nutritional demands, in this study it seems that females, except for those in the Nama Karoo, had a higher demand to supplement their diet throughout the year than males, and not only during times of pregnancy and lactation.

Offspring of ungulates are born at a time of optimal availability of nutrition to support the maternal demands (Parker et al. 2009; Ogutu et al. 2014). This means that birth peak should be synchronised with the early growing season shortly after the start of the first rain. However, according to Zerbe et al. (2012), the time of birth might rather be an indication of good body condition before time of conception. According to Parker et al. (2009), the peak time of conception for ungulates is during autumn, when both males and females have accumulated substantial fat reserves through the summer. Therefore, nutritional demands on the body of females are throughout the year, and not only during times of pregnancy and lactation. This might explain the year-round high levels of geophagy observed among females.

5.5 Conclusions

Seasonal and periodic differences of geophagia between diet niches and sexes across habitats is a clear indication that there is no single, universal explanation for geophagy. In this study, large mammalian herbivores, specifically grazers, consumed soil more in habitats where grass is the predominant plant cover than in the Bushveld with more trees, or the Nama Karoo with a complex mixture of grass and dwarf karroid shrubs. In general, browsers preferred to consume soil mainly during summer months, although in the Bushveld the highest frequency of geophagy was observed during autumn. In the three semi-arid habitats, Kalahari, Nama Karoo and Grassveld, grazers frequently consume soil during the autumn and winter months, but in the Bushveld habitat, the peak visitation to geophagy sites was during spring. No clear pattern of peak seasonality for soil ingestion was observed for intermediate feeders. It seems therefore that seasonality of geophagy is linked to the diet of large mammalian herbivores, and therefore differs between habitats that offer varying relative abundances of a species' staple food. To fully understand these differences in the prevalence of geophagy between habitats, nutritional analyses of forages might elucidate the conundrum.

Although some species showed a bi-model pattern of geophagy during the day, most visits to geophagy sites occurred during daylight hours. This indicated an inherent perception of landscapes of fear, similar to that at waterholes. The consecutive nutritional demands on the different reproductive states of females, might be an explanation for the high frequencies of females that were observed to engage in geophagy in this study. Therefore, it seems that mammalian herbivores in different habitats engaged in geophagy as a result of seasonal nutritional demands and can be linked to food preferences in their diet as well as availability of nutritional food sources.

5.6 References

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Chapter 6: Conclusions and future research

6.1 Conclusions

Herbivores require nutrients to sustain all physiological functions on a daily basis. These nutrients can come from a variety of sources and can be obtained from water, energy, protein, vitamins, and minerals (McDowell 1985). The species and composition of plants, growth stage and maturity of the plant, the type of soil, as well as climate and seasonal conditions are important factors that influence the mineral intake of such animals (McDonald et al. 2011). Optimal foraging theory as described by Stephens and Krebs (1986), predicts that animals should apply foraging tactics whereby they balance maximum energy (nutritional) gains while reducing energetic losses associated with resource acquisition. The concept of optimal foraging theory is however more nuanced than merely the selection of specific food sources. In this context, optimizing means balancing maximum energy (nutritional) gains while reducing energetic losses associated with resource acquisition. The intentional ingesting of soil, geophagy, is a widespread behaviour among many animals and has been documented for various animal species including humans. Enzootic geophagy has been observed in many parts of the world and in climates ranging from temperate, to dry, wet, arctic and montane areas (Kreulen and Jager 1984).

An investigation into the behavioural aspects of geophagy among large mammalian herbivores in different habitats, where animals compete not only for forage but also for soil minerals, will elucidate both the biophysical factors that stimulate this behaviour, as well as the role of geophagy in resource partitioning and multispecies coexistence. The goal of this study was to investigate and compare the frequency occurrence of geophagy amongst different large mammalian herbivores species distributed over a spatio-seasonal gradient. This includes a comparison across four different habitat types within the central interior of southern Africa, namely (in descending levels of aridity) Kalahari, Nama Karoo, Grassveld, and Bushveld.

Differences in conditions mean that each represents a distinct habitat type (see Chapter 2), which allows for subsequent study of spatial patterns in geophagy amongst herbivores. Although geophagic soil across the four diverse habitats share some common physicochemical properties (see Chapter 3), several differences do occur. Based on the results of this study, it is unlikely that soil colour is the principal stimulus for geophagic behaviour amongst mammalian herbivores as claimed by some studies (e.g., Mahaney and Krishnamani 2003). Herbivores were found to avoid surface soil, but preferred digging to eat at a constant depth. In general, animals consume soil with lower quantities of quartz, and this might be one explanation for the preference to consume soil at a specific depth (see Chapter 3). Although geophagic soils have in general lower fractions of sand and higher clay contents, animals prefer to establish geophagy sites in soil with low bulk density where soil is not compacted. The volume of coarse fragments in the geophagic soil however do not play a major role, as animals consume soil with very low coarse fragments, as seen in the Kalahari habitat, but even in soil with relatively high amounts of coarse fragments as evident from the geophagy sites in the Bushveld habitat. It is furthermore concluded that high soil CEC values are not necessarily a prerequisite for geophagic soil. In this study, even soil with moderate CEC, representing a wide range of pH levels, were consistently consumed by herbivores.

Although several studies have debated the environmental and behavioural factors underlying geophagy (e.g., Mahaney and Krishnamani 2003, Young et al. 2011), herbivores appeared to ingest soil deliberately for different reasons across the four study areas (see Chapter 5). In the more arid habitats like the Kalahari, Nama Karoo and to a lesser extent Grassveld, the main reason for geophagy was interpreted as supplementation of Ca. However, the behaviour was also driven by secondary benefits in the form of salt (Halite) or other essential minerals mainly Fe, Mg, K, Mn, P, Cr, Co, Zn and Mo. In addition to Ca, animals supplement their nutritional needs, specifically Na, Mg, Mn, Co and Mo by eating soil. In the Nama Karoo animals ingest soil rich in Na, Fe, K, Co and Zn. The presence of kaolinite, although at low quantities, might relieve animals of gastric disorders. The craving for salt

seems not to be the driving force behind geophagia in the Grassveld habitat. Rather, geophagic soil from this habitat supply animals, apart from Ca, mainly with essential minerals including Mg, Mn, Cr, Co and Zn. In agreement with Stephenson et al. (2011), the occurrence of kaolinite in all the geophagic soils in the Bushveld habitat indicated that animals might consume this soil for relief of gastric disorders, since this habitat mainly includes browser species that are subjected to high secondary plant compounds in their diets. The benefits of nutritional supplements of essential elements cannot, however, be discarded. Geophagic soil from the Main Lick site within the Bushveld can supplement Mg, Mn, Ca, Na, P, Cr, Zn and probably Se. At another Bushveld site, Renosterhoek, animals can obtain Fe, Mg, Mn, Na, Cr, Co, and Zn, while ingesting soil from Zaagkuil can supplement their diets with Mn, Cr, and Mo. Although Ca seems to be of least importance at the Kloppersкloof geophagy site, Co and Zn were also identified to be a possible reason why animals ingest soil from that specific site. The occurrence of the iron-containing clays, hematite and ilmenite, in all the geophagy sites in the Bushveld habitat, might be an important indication to the role of Fe in the stimulus of geophagia in the Bushveld habitat. However, only at Renosterhoek, Fe seems to be the driving factor that attracts animals to this geophagy site. However, the bioavailability of iron from these geophagy sites needs to be determined to confirm this. It seems therefore that large mammalian herbivores, that are free to roam over large areas, do not ingest soil for the main purpose of mineral or element supplementation, rather they practice geophagy as a form of self-medication against gastric disorders. In small confined areas however, such animals obtain scarce nutrients from geophagy sites or may even find relief of gastric ailments.

The analyses of clay-containing dung pellets seem to contribute to the understanding of geophagy. The supplementation role of geophagy, at least for some chemical elements, was clearly illustrated with this method. However, this method also highlighted that the deliberate ingestion of soil might even deprive animals from certain elements. Furthermore, analyses of clay-containing dung pellets indicated the protective function of geophagy. Consuming soil that is high in clay content, also bind heavy metals such as Pb which can be

harmful to the animal. Consuming soil clearly also assist in the eradication of at least eggs of parasites in the elementary canal of animals. In agreement with Krishnamani and Mahaney (2000), geophagic earth might prevent larger pathogens such as geohelminths from colonizing hosts. Although the specific action is unclear and should be investigated further, a possible explanation for this might be that the abrasive action of the soil destroys these eggs or that the constrain of respiration of parasites, as suggested by Young et al. (2011) might eliminate these eggs. Another possibility might be that soil that is high in element concentrations, influence the osmotic pressure and might desiccate the parasite eggs in the digestive tracks of animals. A secondary advantage to this is that less parasite eggs are expelled by dung and therefore possible parasite infections at geophagy sites and elsewhere sites are reduced.

Seasonal and periodic differences of geophagia between diet niches and sexes across habitats is a clear indication that there is no single, universal explanation for geophagy. In this study, large mammalian herbivores, specifically grazers, consumed soil more frequently in habitats where grass is the predominant plant cover than in the Bushveld with more trees, or the Nama Karoo with a complex mixture of grass and dwarf karroid shrubs. In general, browsers preferred to consume soil mainly during summer months, although in the Bushveld the highest frequency of geophagy was observed during autumn. A possible explanation might be that during autumn and winter, browsers are forced to expand their diet breadth to incorporate plants that they would usually avoid during spring and summer (Owen-Smith and Cooper 1989, O'Reagain and Grau 1995, Owen-Smith 2002). Therefore, browsing herbivore species would potentially increase their geophagy as the increased intake of minerals would help neutralise this seasonal increase in plant secondary compounds.

In the three semi-arid habitats, Kalahari, Nama Karoo and Grassveld, grazers frequently consume soil during the autumn and winter months, but in the Bushveld habitat, the peak visitation to geophagy sites was during spring. No clear pattern of peak seasonality for soil ingestion was observed for intermediate feeders. It seems therefore that seasonality of geophagy is linked to the feeding niche of large mammalian herbivores, and therefore differs

between habitats that offer varying relative abundances, and perhaps nutritional value, of a species' staple food. To fully understand these differences in the prevalence of geophagy between habitats, nutritional analyses of forages might elucidate the conundrum.

Although some species showed a bi-model pattern of geophagy during the day, most visits to geophagy sites occurred during daylight hours. This indicated an inherent perception of landscapes of fear, similar to that known to occur when animals congregate at waterholes. The consecutive nutritional demands on the different reproductive states of females, might be an explanation for the high frequencies of females that were observed to engage in geophagy in this study.

6.2 Future research

As mentioned in previous chapters, there are still unanswered questions around geophagy, especially concerning large mammalian herbivores. To fully understand differences in the prevalence of geophagy between habitats, simultaneous nutritional analyses of forages is likely to be essential. In addition, understanding the diet preferences of the different herbivore species and proportion of their diet comprised of the different plant species will also elaborate on the reason and seasonality of geophagy. Linked to this, in order to clarify on the protective role of geophagy, a detailed study on the seasonality of secondary plant metabolites, especially amongst plant species which are preferred by browsers within a given landscape, should also be of high importance. This type of multi-faceted approach would help explain how species that exploit different components of the resource, i.e., browse and grass, differentially benefit from geophagy.

The assimilation of heavy metals as a result of geophagy, mentioned in chapter 3, is a matter of concern and should be investigated. During culling programs of reserves, bovids should be harvested at geophagy sites to analyse digestive tracts including amount of soil consumed, assimilation of chemical elements from the soil, the prevalence of parasites, as well as physiological parameters of animals that have been witnessed to consume soil. The

carcasses of harvested animals that were confirmed to practice geophagy, might also provide data on the negative effects of soil eating such as tooth wear. An image from a camera trap at the Main Lick (Loskop Dam Nature Reserve) clearly showed an abscess on the lower jaw of a kudu calf (Fig. 6.1). Whether this was due to geophagic behaviour is unclear. However, geophagy might cause infections during teething in diphyodont animals.

This study, in particular through analyses of camara trap data, highlighted some specific questions that can help guide future research. Firstly, how the behaviour of ingesting soil is established in an individual animal remains a mystery. One possible explanation is that such behaviour is learned through operant conditioning (associative learning) which is then reinforced by a reward in one way or another. On several occasions it was noticed that animals drink muddy water from shallow geophagy sites that have been filled with rainwater (Fig. 6.2). However, in these incidents, geophagy sites were already well established and it could be that such animals merely visited these sites because of conditioning. However, drinking muddy water, especially in drier areas and during times of drought when water sources start to decline, might be an initial trigger that onsets the behaviour to ingest soil. On the other hand, several incidents in this study were photographically captured where adult females, accompanied by juvenile offspring, consumed soil. On one occasion, a gemsbok calf was clearly suckling from the mother (Fig.6.3 A), and less than two minutes later the same calf was recorded to be consuming soil (Fig. 6.3 B). Borruso et al. (2021) mentioned that baby lemurs (*Indri indri*) still carried by the mother also ate soil after the mother started to ingest soil. This indicates that the behaviour of geophagy might be learnt behaviour which is socially transmitted to especially younger individuals. However, a personal observation was made of an orphaned springbok calf (two months old) and that was still bottle fed with cow milk, which ate soil from a flower garden. This on the contrary suggest that the behaviour of geophagy might have an internal stimulus. Clearly the onset of geophagy is still a conundrum with many questions that need to be answered.

Figure 6.1. *A kudu calf with an abscess (inside yellow circle) on the lower jaw (A and B) engaging in geophagy (B) at the Main Lick site at Loskop Dam Nature Reserve. (Source: HJB Butler©).*

Figure 6.2. *A blue wildebeest (A) and mountain reedbuck (B) drinking muddy water from a rain-filled geophagy site at Loskop Dam Nature Reserve. (Source: HJB Butler©).*

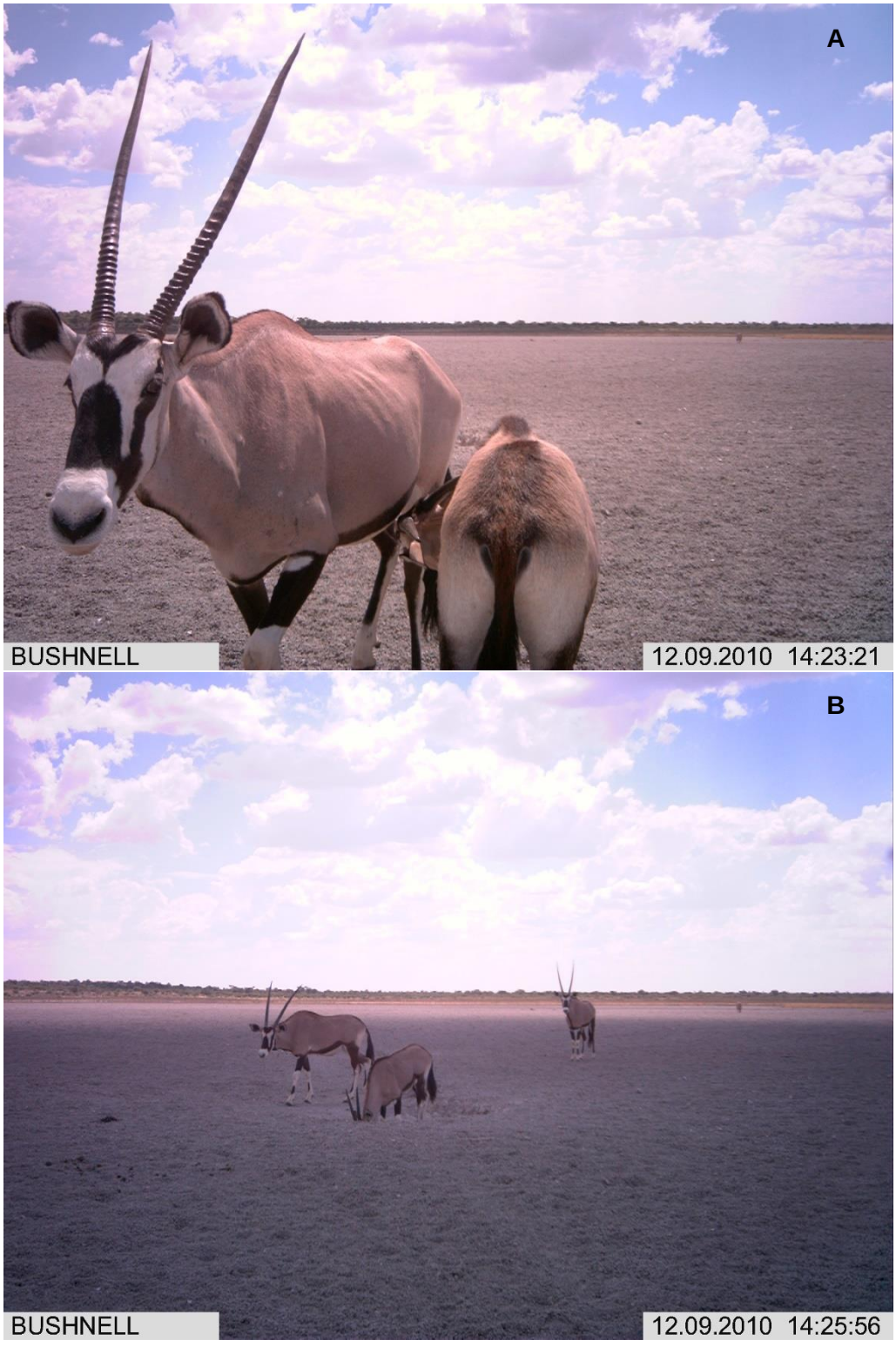

Figure 6.3. *A juvenile gemsbok calf at Jack's Pan (Kalahari) suckling from its mother (A) and shortly after that, engaged in geophagy (B). (Source: HJB Butler©).*

Geophagy is a widespread behaviour amongst terrestrial vertebrates, but remains both counter-intuitive and poorly-understood. For herbivores, a conundrum is that the costs of soil ingestion are high, indeed they may intuitively even be deemed higher than the potential gains. Soils are low in nutrients, other than minerals whose availability for digestion and tissue synthesis is questionable and, as mentioned above, play a prominent role in abrasive wearing of teeth. This latter effect is especially important because excessive tooth wear is expected to reduce fitness, not only in terms of survival/longevity, but because the lowered nutritional status of such animals reduces lifetime reproductive potential. Simultaneous analyses of an individual's tooth wear status, body condition, and rate/intensity with which it practiced geophagy, coupled with an improved understanding of the overall benefits of geophagy, are needed so that this trade-off can be modelled and parameterized empirically.

6.3 The importance of the protection and conservation of geophagy sites

At the end of the Pleistocene, mammoths (*Mammuthus primigenius*) of Northern Eurasia experienced chronic mineral hunger because at that time, there was a considerable expansion of acidic and acidic gley (a sticky waterlogged soil lacking in oxygen, typically grey to blue in colour) geochemical landscapes, resulting in a drastic deficiency of Ca, Mg, Na, P, I, Co, Cu, Se, Zn and other vital chemical elements (Leshchinskiy 2015). The change in habitat was closely associated with the drastic replacement of favourable Ca-Mg-Na landscapes with acidic and acidic-gley ones which reached maximum range by the end of the Pleistocene, and are still the predominant landscape in most of Northern Eurasia today (Leshchinskiy 2015).

Based on studies by Leshchinskiy (2015) on the remains of extinct mammoths found in beast solonetzs (the Russian term for a ground surface area characterized by a high content of certain macro- and micro-elements) lacustrine-alluvial localities of Russia, Poland and the Czech Republic, obvious signs of skeletal diseases occurred. He found that mammoths suffered from osteoporosis (a condition in which bones become weak and brittle), osteofibrosis (loss of calcium from the bones, causing them to become fragile), osteomalacia (softening and bending of bones), arthrosis (a type of arthritis that occurs when flexible tissue at the ends of

bones wears down), as well as other joint diseases. These studies emphasized that articular surfaces of extremity bones in some individuals appeared to be damaged and mutilated by these diseases with osteoporosis observed in 90 percent of specimens in separate collections and concluded that acute mineral starvation became widespread in mammoths and other large mammals (Leshchinskiy 2015). Consequently, mammoths became extinct due to geochemical stress arising from deep abiotic changes in ecosystems as they most likely received insufficient amounts of essential chemical elements. As a result, significant trauma in the animals, which suffered sprains and fractures, even at very low loads and mammoths with broken limbs or spines could not find food in sufficient quantities and could not follow the herd and consequently died quickly or were hunted by predators (Leshchinskiy 2015).

Specific mammoth "cemeteries" of the late Pleistocene as well as the frequent presence of mineral substances in the gastro-intestinal tracts of mammoth carcasses and their coprolites, sometimes reaching 90 percent of their mass, is evidence of the vulnerability to mineral starvation of mammoths and only rare beast solonetz landscapes could have served as geochemical oases where the large herbivores could satisfy their mineral hunger (Leshchinskiy 2015). Furthermore, Leshchinskiy (2015) noted rarefaction (the lessening of density of tissue, especially of nervous tissue or bone) in all age groups including infant mammoths, which indicated that the onset of diseases began in the prenatal period, since females suffered from mineral starvation.

Despite the negative effects that geophagy might have on animals such as energy spend to find and travel to these sites (Wiles and Weeks 1986; Klein and Thing 1989; Stephenson et al. 2011), attracting predators and therefore increasing predation risk (Henshaw and Ayeni 1971; Moe 1993; Rawson and Bach 2011; Fack et al. 2020), increasing likelihood of transmission of disease and parasites (Henshaw and Ayeni 1971; Abrahams and Parsons 1996; Pebsworth et al. 2012), as well as exposure to uptake of toxicological contaminants in the soil (Rich and Talent 2009; Kutalek et al. 2010), excessive tooth wear (Barker 2005; Martinelli et al. 2013), and blockage of the alimentary canal (Mushi et al. 1998;

Abutarbush and Petrie 2006; Melendez et al. 2007; Jegede et al. 2016; Niinistö and Sykes 2021), animals over a broad spectrum of taxa still practice this behaviour of ingesting soil deliberately.

All of the above emphasizes the importance of access to resources of minerals during times when sufficient minerals cannot be obtained from natural food sources. Geophagy sites must therefore be preserved and incorporated into management plans. The fact that animals visit these sites regularly on a daily basis, construction of hides close to geophagy sites might even serve similar functions as waterholes to attract ecotourists.

6.4 References

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Appendix A

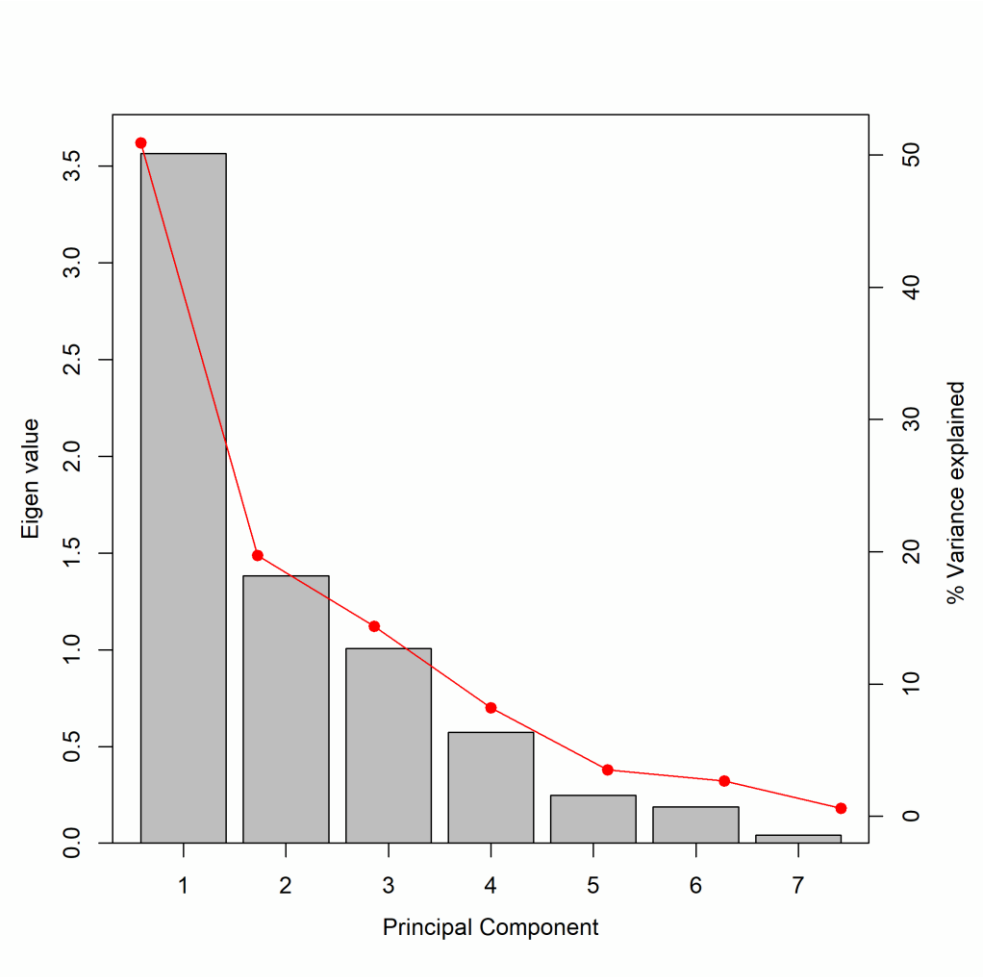

Figure S1. *Scree plot of eigen values (bars) and their explained % variance (line) of major elements in geophagic soil at four habitats in the study area.*

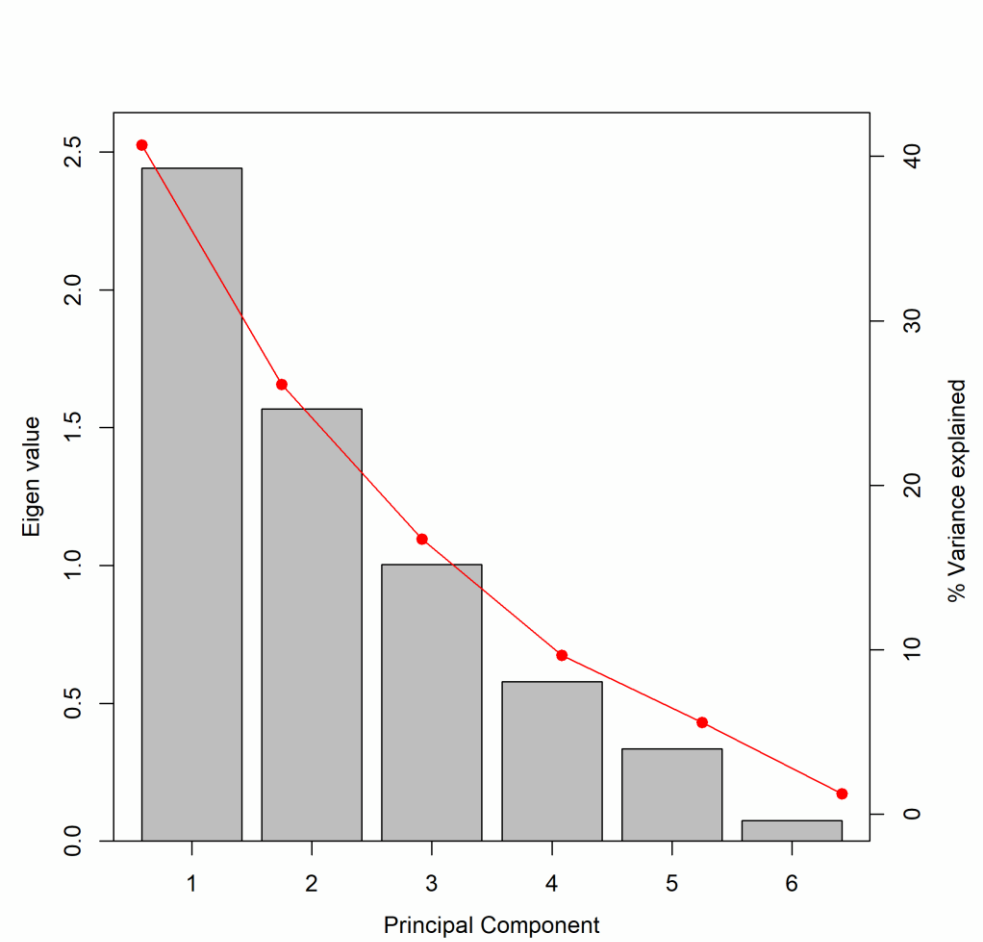

Figure S2. *Scree plot of eigen values (bars) and their explained % variance (line) of trace elements in geophagic soil at four habitats in the study area.*

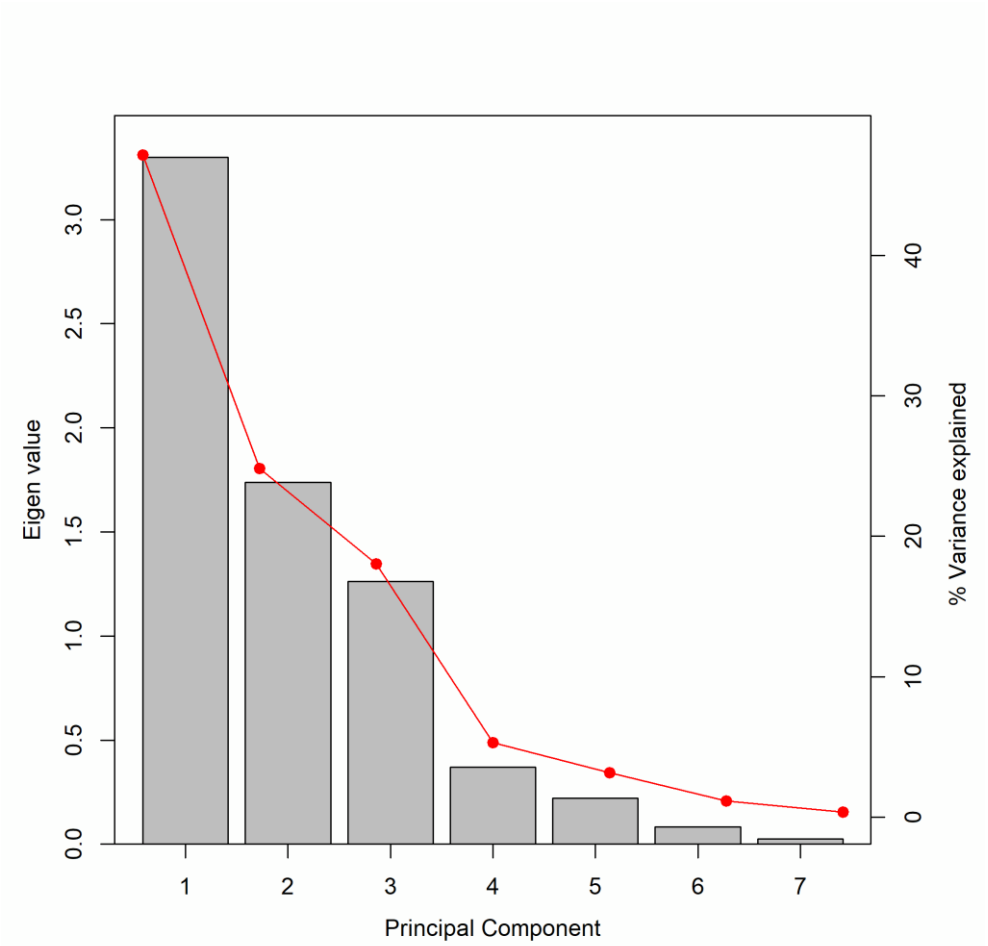

Figure S3. *Scree plot of eigen values (bars) and their explained % variance (line) of major elements in geophagic soil at Loskop Dam Nature Reserve.*

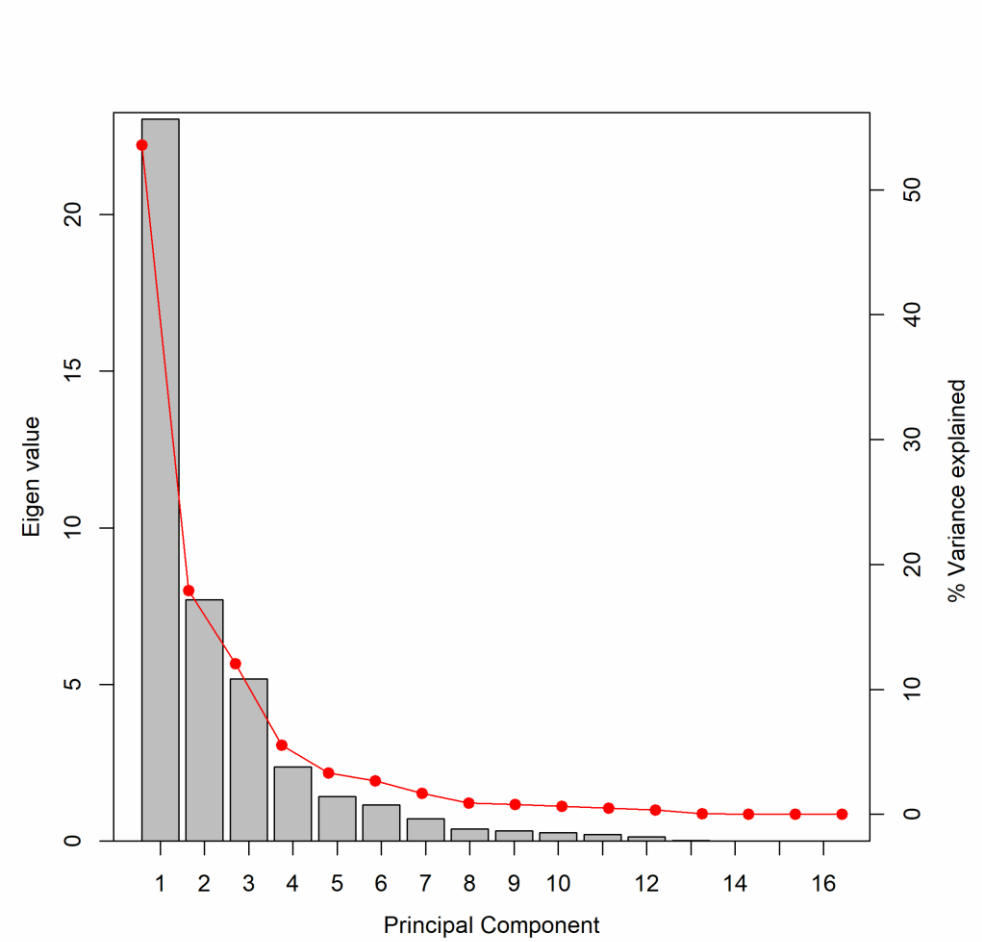

Figure S4. *Scree plot of eigen values (bars) and their explained % variance (line) of trace elements in geophagic soil at Loskop Dam Nature Reserve.*

Table S1. *Primary and secondary mineral concentrations (%) of X-Ray diffraction (XRD) analyses in geophagic soil in the four habitats of the study area.*

		Mineral																		
Habitat	**Soil profile**	**Anatase**	**Andalusite**	**Ankerite**	**Bassanite**	**Calcite**	**Clinopyroxene**	**Glauberite**	**Goethite**	**Gypsum**	**Halite**	**Hematite**	**Ilmenite**	**Kaolinite**	**Muscovite**	**Orthoclase**	**Plagioclase**	**Quartz**	**Sepiolite**	**Serpentine**	**Smectite**
Kalahari	Top			8	5	27		-			1						2	41	16		
	Middle 1			11	8	29		-			6						-	32	14		
	Feeding depth			21	-	35		9			9						-	12	14		
	Control			8	4	25		3			5						-	42	13		
Nama Karoo	Top	8				2						-		9	15			66			
	Middle 1	7				2						-		9	15			67			
	Feeding depth	8				3						-		9	15			65			
	Control	5				-						3		6	10			76			
Grassveld	Top					3	17			3						7	17	53			
	Middle 1					2	20			3						3	19	53			
	Feeding depth					2	20			-						6	19	53			
	Control					5	18			-						10	17	50			
Bushveld																					
Main Lick	Top	10	-						-			8		21	23	-	19	19			-
	Middle 1	-	-						-			7		19	19	16	15	-			24
	Middle 2	-	8						-			-		17	18	17	16	-			24
	Feeding depth	-	-						6			-		19	17	13	12	15			18
	Control	10	-						-			8		21	23	-	19	19			-

(Table S1 continue)

Habitat	Soil profile	Mineral																		
		Anatase	Andalusite	Ankerite	Bassanite	Calcite	Clinopyroxene	Glauberite	Goethite	Gypsum	Halite	Hematite	Ilmenite	Kaolinite	Muscovite	Orthoclase	Plagioclase	Quartz	Sepiolite	Serpentine	Smectite
Renosterhoek	Top					5						1	-	9	19	11	11	44		-	
	Middle 1					9						1	-	10	18	12	9	41		-	
	Feeding depth					-						5	5	12	16	12	10	40		-	
	Control					-						4	4	-	15	4	-	63		10	
Zaagkuil	Top					8						1	2	5	19	11	11	43			
	Middle 1					8						1	2	8	19	11	9	42			
	Feeding depth					6						5	5	10	19	10	7	38			
	Control					6						4	4	6	15	6	7	52			
Kloppersklоof	Floor						4					8	7	25	22	-		34			
	Cave						-					8	8	24	21	7		32			
	Control						7					3	8	23	23	9		27			

Dominant mineral (>50%), Major mineral (20-50%), Minor mineral (10-19%), Accessory mineral (2-9%), Trace mineral (< 2%), Not present (-)

Anatase TiO_2	Andalusite $Al_2(SiO_4)O$	Ankerite $Ca(Fe^{2+},Mg)(CO_3)_2$	Bassanite $Ca(SO_4) \cdot 0.5H_2O$
Calcite $CaCO_3$	Clinopyroxene $(Ca,Na,Mg,Fe,Al,Ti)_2Si_2O_6$	Glauberite $Na_2Ca(SO_4)_2$	Goethite $FeO(OH)$
Gypsum $CaSO_4 \cdot 2H_2O$	Halite $NaCl$	Hematite Fe_2O_3	Ilmenite $Fe^{2+}TiO_3$
Kaolinite $Al_2(Si_2O_5)(OH)_4$	Muscovite $KAl_2(Si_3AlO_{10})(OH)_2$	Orthoclase $K(AlSi_3O_8)$	Plagioclase $NaAlSi_3O_8$/ $CaAl_2Si_2O_8$
Quartz SiO_2	Sepiolite $Mg_4(Si_6O_{15})(OH)_2 \cdot 6H_2O$	Serpentine $Al_2Si_2O_5(OH)_4$	Smectite $(Na,Ca)_{0.33}(Al,Mg)_2(Si_4O_{10})(OH)_2 \cdot nH_2O$

Table S2. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil at Jack's Pan in the Kalahari Wildlife Management area.*

		Geophagic soil			Control
Depth (cm)		**0-5**	**15-30**	**60-80**	**60-80**
Major elements (Weight %)	SiO2	59.77	52.61	48.21	94.42
	TiO2	0.18	0.19	0.15	0.15
	Al2O3	2.62	2.86	2.30	1.99
	Fe2O3	1.23	1.56	1.21	1.20
	MgO	12.84	15.91	17.98	0.43
	MnO	0.05	0.06	0.05	0.01
	CaO	20.92	23.62	24.74	0.09
	Na2O	1.49	2.09	3.62	0.02
	K2O	0.33	0.37	0.39	0.85
	P2O5	0.29	0.30	0.22	0.01
Loss on ignition		0.28	0.43	0.46	0.24
	Total	**99.99**	**99.98**	**99.33**	**99.41**
Trace elements (mg/kg)	V	59	59	74	11
	Cr	12	13	12	13
	Co	2	3	3	2
	Ni	8	8	7	5
	Cu	12	12	12	4
	Zn	27	27	24	8
	As	3	6	7	-
	Br	10	18	23	1
	Rb	26	26	26	23
	Sr	2204	2269	2594	17
	Y	7	6	6	3
	Zr	6	<1	1	70
	Nb	<1	<1	<1	2
	Mo	2	4	6	0
	Ag	10	9	9	6
	Cd	<1	<1	<1	4
	Sn	1	<1	1	5
	Ba	171	166	152	153
	Pb	<1	<1	<1	4
	Th	5	5	6	1
	U	28	28	33	1

Table S3. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil at Tussen-Die-Riviere Nature Reserve.*

		Geophagic Soil			Control
Depth (cm)		**0-5**	**5-15**	**15-30**	**15-30**
Major elements (Weight %)	SiO2	58.90	49.80	39.90	79.20
	TiO2	0.57	0.62	0.54	0.65
	Al2O3	9.70	9.30	13.08	6.66
	Fe2O3	24.12	32.05	37.40	8.50
	MgO	0.40	0.46	0.40	0.10
	MnO	0.13	0.11	0.07	0.11
	CaO	0.68	0.65	0.41	0.11
	Na2O	0.26	0.42	0.37	0.10
	K2O	1.56	2.42	2.85	1.57
	P2O5	0.03	0.05	0.03	0.04
Loss on ignition		2.78	3.98	4.98	2.96
	Total	**99.94**	**99.40**	**98.94**	**101.88**
Trace elements (mg/kg)	Sc	11	10	13	7
	V	70	69	73	77
	Cr	362	230	210	450
	Co	19	22	25	24
	Ni	31	48	65	42
	Cu	19	17	12	22
	Zn	109	121	145	92
	As	16	14	16	16
	Rb	165	169	178	85
	Sr	12	23	27	15
	Y	32	30	37	28
	Zr	402	421	256	405
	Nb	14	12	12	14
	Mo	<1	<1	<1	<1
	Ba	385	392	415	276
	Pb	9	8	9	9
	Th	16	19	19	15
	U	7	5	8	5

Table S4. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil as well as kudu dung clay pellets at Willem Pretorius Game Reserve.*

		Geophagic soil			Control	Kudu dung
Depth (cm)		**0-5**	**5-15**	**15-30**	**15-30**	
Major elements (Weight %)	SiO_2	60.79	59.05	57.85	68.95	62.04
	TiO_2	0.70	0.71	0.68	0.63	0.65
	Al_2O_3	10.66	11.28	10.88	9.05	11.01
	Fe_2O_3	6.91	7.41	7.31	5.68	3.43
	MgO	3.93	4.11	4.26	3.15	0.95
	MnO	0.17	0.22	0.28	0.14	0.06
	CaO	5.37	5.71	7.24	4.16	1.25
	Na_2O	1.07	1.02	1.06	1.20	0.36
	K_2O	0.98	0.92	0.95	1.11	2.39
	P_2O_5	1.79	1.04	1.05	0.05	0.26
Loss on ignition		7.47	8.35	8.17	5.62	17.45
	Total	**100**	**99.82**	**99.73**	**99.74**	**99.79**
Trace elements (mg/kg)	Sc	19	26	17	18	10
	V	172	184	174	140	100
	Cr	316	340	330	264	48
	Co	38	44	42	32	27
	Ba	426	423	406	389	471
	Ni	91	100	97	74	26
	Cu	45	50	45	33	20
	Zn	46	52	55	43	53
	As	14	12	14	15	16
	Br	5	5	4	3	<1
	Rb	41	41	39	45	89
	Sr	114	109	112	110	109
	Y	21	21	22	20	28
	Zr	226	198	193	276	242
	Nb	7	8	7	8	11
	Pb	12	11	12	12	<2
	Th	5	6	5	6	15
	Mo	<1	<1	<1	<1	<1
	U	-	-	-	-	7

Table S5. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil as well as Kudu and impala dung clay pellets at Main Lick in Loskop Dam Nature Reserve.*

		Geophagic soil				Control	Kudu dung	Impala dung
Depth (cm)		**0-40**	**40-60**	**60-80**	**80-140**	**80-140**		
Major elements (Weight %)	SiO_2	39.20	42.50	43.67	45.42	45.78	43.62	32.07
	TiO_2	12.46	5.23	3.42	1.54	1.63	1.29	1.34
	Al_2O_3	9.82	14.36	15.74	16.62	15.25	18.39	17.70
	Fe_2O_3	21.41	19.63	19.21	9.73	12.42	12.44	13.60
	MgO	1.31	1.82	1.95	8.15	7.42	0.13	0.11
	MnO	0.22	0.16	0.18	0.18	0.14	1.08	0.58
	CaO	9.52	10.31	9.86	10.93	11.26	3.57	2.93
	Na_2O	2.82	2.06	2.85	3.65	3.62	0.02	0.01
	K_2O	1.41	1.48	0.91	0.70	0.84	2.24	1.22
	P_2O_5	0.12	0.18	0.14	0.26	0.12	0.22	0.51
Loss on ignition		1.52	2.09	1.86	2.50	1.41	16.50	29.70
	Total	**99.81**	**99.82**	**99.79**	**99.68**	**99.89**	**99.50**	**99.77**
Trace elements (mg/kg)	Sc	30	30	33	11	12	31	41
	V	53	229	203	86	93	224	322
	Cr	52	45	40	62	71	87	7
	Co	24	28	25	14	18	60	78
	Ni	45	57	61	20	42	94	53
	Cu	36	152	185	21	36	127	143
	Zn	49	131	152	680	542	114	98
	As	5	4	5	34	31	28	18
	Se	<1	<1	<1	<1	<1	-	-
	Rb	41	75	79	140	145	126	58
	Sr	46	56	48	155	160	69	67
	Y	26	28	35	25	26	35	29
	Zr	195	199	197	245	254	232	207
	Nb	<1	12	11	17	17	10	9
	Mo	<2	4	<2	<2	<2	-	-
	Ba	551	451	458	590	617	552	324
	Pb	47	13	9	98	98	-	-
	Th	5	4	6	12	11	12	13
	U	<1	<1	3	3	4	7	<3

Table S6. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil as well as kudu dung clay pellets at Renosterhoek in Loskop Dam Nature Reserve.*

		Geophagic soil			Control	Kudu dung
	Depth (cm)	**0-5**	**15-20**	**40-50**	**40-50**	
Major elements (Weight %)	SiO2	64.21	57.14	55.48	69.11	44.34
	TiO2	2.03	2.34	2.57	1.26	1.59
	Al2O3	11.68	12.02	14.66	9.91	17.80
	Fe2O3	9.39	13.74	14.08	7.40	13.44
	MgO	0.65	0.68	0.80	0.32	1.15
	MnO	0.14	0.21	0.18	0.11	0.11
	CaO	0.64	0.67	0.36	0.39	0.76
	Na2O	0.27	0.86	0.74	0.05	0.13
	K2O	2.75	2.84	2.13	1.93	2.31
	P2O5	1.33	1.16	0.05	0.08	0.21
Loss on ignition		6.80	8.27	7.32	8.94	17.09
	Total	**99.89**	**99.93**	**98.27**	**99.50**	**98.93**
Trace elements (mg/kg)	Sc	27	25	25	11	34
	V	267	274	280	155	282
	Cr	147	152	153	212	150
	Co	49	58	52	39	71
	Ni	43	36	40	31	86
	Cu	241	227	236	65	185
	Zn	128	133	139	115	137
	As	32	36	36	23	31
	Rb	117	121	118	122	104
	Sr	41	38	42	29	59
	Y	52	49	51	47	45
	Zr	432	389	373	442	234
	Nb	18	18	18	18	11
	Mo	<1	<1	<1	<1	<1
	Ba	516	524	535	605	491
	Pb	<2	<2	<2	<2	<2
	Th	22	23	23	21	15
	U	4	4	4	5	6

Table S7. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil as well as kudu dung clay pellets at Zaagkuil in Loskop Dam Nature Reserve.*

		Geophagic soil			Control	Kudu dung
Depth (cm)		**0-5**	**15-20**	**40-50**	**40-50**	
Major elements (Weight %)	SiO_2	43.10	44.46	59.92	51.92	36.12
	TiO_2	1.83	1.84	1.26	1.78	2.43
	Al_2O_3	18.72	17.69	18.13	20.33	20.72
	Fe_2O_3	13.87	14.63	11.02	15.05	19.19
	MgO	1.32	1.25	0.22	1.53	0.62
	MnO	0.12	0.16	0.14	0.14	0.25
	CaO	1.09	1.19	0.08	0.67	0.69
	Na_2O	0.84	0.25	0.07	0.52	0.07
	K_2O	2.14	2.16	1.72	1.23	1.40
	P_2O_5	0.16	0.17	0.07	0.02	0.41
Loss on ignition		16.61	14.39	6.06	6.12	17.59
	Total	**99.81**	**98.18**	**98.69**	**99.31**	**99.49**
Trace elements (mg/kg)	Sc	33	30	22	24	48
	V	229	203	155	163	377
	Cr	40	45	76	54	75
	Co	23	21	20	21	28
	Ni	57	57	42	45	71
	Cu	150	152	95	92	176
	Zn	152	131	125	127	181
	As	4.8	3.7	3.9	3.7	4.8
	Se	<1	<1	<1	<1	<1
	Rb	42	75	150	146	99
	Sr	10	10	14	14	34
	Y	28	35	64	63	34
	Zr	84	199	427	367	255
	Nb	12	18	22	21	15
	Mo	3	4	4	<2	<2
	Cs	12	12	14	14	17
	Ba	321	338	354	346	468
	Pb	9	13	33	27	19
	Th	4	6	20	18	6
	U	<1	<1	6	3	<1

Table S8. *Soil chemistry (X-Ray Fluorescence) of major (% weight) and trace (mg/kg) elements of geophagic soil as well as nyala dung clay pellets at Kloppersklоof in Loskop Dam Nature Reserve.*

		Floor	Cave	Control	Nyala dung
Depth (cm)		**0-10**	**0-10**	**0-10**	
Major elements (Weight %)	SiO_2	43.49	41.71	40.39	39.94
	TiO_2	3.14	2.44	3.14	2.18
	Al_2O_3	19.40	21.26	20.82	21.66
	Fe_2O_3	19.41	19.22	21.53	16.49
	MgO	0.56	0.63	0.63	0.44
	MnO	0.15	0.18	0.27	0.15
	CaO	0.84	0.72	0.36	0.71
	Na_2O	0.02	0.06	0.10	0.01
	K_2O	0.98	1.38	1.76	0.95
	P_2O_5	0.14	0.15	0.17	0.24
Loss on ignition		11.64	12.75	11.56	17.13
Total		**99.77**	**100.50**	**100.73**	**99.90**
Trace elements (mg/kg)	Sc	52	56	68	51
	V	425	480	560	388
	Cr	141	196	167	12
	Co	55	75	53	86
	Ni	68	102	68	70
	Cu	203	284	325	210
	Zn	152	219	190	145
	As	16	40	31	35
	Rb	87	149	115	81
	Sr	75	29	28	26
	Y	30	53	43	56
	Zr	201	316	300	354
	Nb	10	15	16	17
	Mo	<1	<1	<1	-
	Ba	538	535	694	354
	Pb	<2	<2	<2	-
	Th	11	24	17	21
	U	<3	<3	<3	4

***Table S9**. Results of principal component analyses (PCA) of major elements in geophagic soil of four habitats in the study areas.*

PC	Lambda	% Explained	Cumulative % variance	Major elements (factor loadings)						
				CaO	Fe2O3	K2O	MgO	MnO	Na2O	P2O5
1	3.5634	50.9052	50.9052	-0.5013	0.3443	0.4382	-0.4998	0.1717	-0.3981	-0.0211
2	1.3811	19.7299	70.6351	0.0130	0.2219	0.0090	0.0209	-0.6165	-0.0667	-0.7520
3	1.0066	14.3806	85.0157	-0.1699	-0.6006	-0.0088	0.0093	-0.4857	-0.5505	0.2670
4	0.5742	8.2024	93.2181	0.2279	0.3208	0.6252	0.2588	-0.4139	0.1521	0.4391
5	0.2465	3.5212	96.7393	-0.1893	-0.5732	0.4823	-0.2102	0.0090	0.5534	-0.2290
6	0.1870	2.6717	99.4111	-0.2700	0.1799	-0.4235	-0.4801	-0.4279	0.4294	0.3427
7	0.0412	0.5889	100.0000	-0.7477	0.0875	-0.0702	0.6388	0.0106	0.1420	0.0085

***Table S10**. Results of principal component analyses (PCA) of trace elements in geophagic soil of four habitats in the study areas.*

PC	Lambda	% Explained	Cumulative % variance	Trace elements (factor loadings)					
				Co	Cr	Cu	Mo	Se	Zn
1	2.4416	40.6940	40.6940	-0.5334	-0.4888	-0.2908	0.4951	0.3827	0.0217
2	1.5670	26.1175	66.8114	0.3790	-0.3561	0.6362	0.1244	0.3725	0.4130
3	1.0029	16.7149	83.5263	-0.1655	0.1448	-0.3547	-0.4135	0.1747	0.7901
4	0.5791	9.6523	93.1786	0.1073	0.2851	-0.0809	-0.2692	0.8227	-0.3889
5	0.3351	5.5845	98.7631	0.1587	0.6501	-0.0666	0.6980	0.0849	0.2307
6	0.0742	1.2369	100.0000	-0.7126	0.3306	0.6114	-0.0935	0.0140	0.0127

Table S11. *Results of principal component analyses (PCA) of major elements in geophagic soil of the Bushveld habitat.*

PC	Lambda	% Variance	Cumulative % variance	Major elements (factor loadings) CaO	Fe2O3	K2O	MgO	MnO	Na2O	P2O5
1	3.2986	47.1232	47.1232	0.5092	0.1061	-0.4591	0.4545	0.0599	0.5047	-0.2321
2	1.7388	24.8399	71.9632	0.0389	-0.7067	0.1214	0.3150	-0.5601	0.1139	0.2418
3	1.2625	18.0351	89.9983	-0.2024	-0.0257	-0.3620	-0.1318	-0.4926	-0.2665	-0.7045
4	0.3710	5.3003	95.2986	0.4195	0.4030	0.0949	-0.4710	-0.5821	0.1828	0.2419
5	0.2219	3.1696	98.4683	-0.2235	0.2205	-0.6481	0.2015	-0.1396	-0.3141	0.5679
6	0.0824	1.1777	99.6460	0.1958	-0.5215	-0.4540	-0.6274	0.2755	0.0740	0.0927
7	0.0248	0.3540	100.0000	-0.6587	0.0750	-0.0911	-0.1444	-0.0769	0.7237	0.0403

Table S12. *Results of principal component analyses (PCA) of trace elements in geophagic soil of the Bushveld habitat.*

PC	Lambda	% Variance	Cumulative % variance	Trace minerals (factor loadings) Co	Cr	Cu	Mo	Se	Zn
1	3.6287	60.4789	60.4789	-0.5023	-0.4842	-0.4185	0.3585	0.4493	0.0877
2	1.2653	21.0888	81.5677	0.1234	-0.0823	0.3408	0.4309	0.1796	-0.8025
3	0.5202	8.6698	90.2375	-0.0486	0.1247	-0.4393	-0.6699	0.3028	-0.4987
4	0.3352	5.5863	95.8237	-0.1978	0.3763	-0.5512	0.3630	-0.5726	-0.2363
5	0.2080	3.4666	99.2904	0.3589	0.6005	-0.1951	0.3169	0.5730	0.2091
6	0.0426	0.7096	100.0000	-0.7497	0.4910	0.4170	-0.0700	0.1343	0.0040

Appendix B

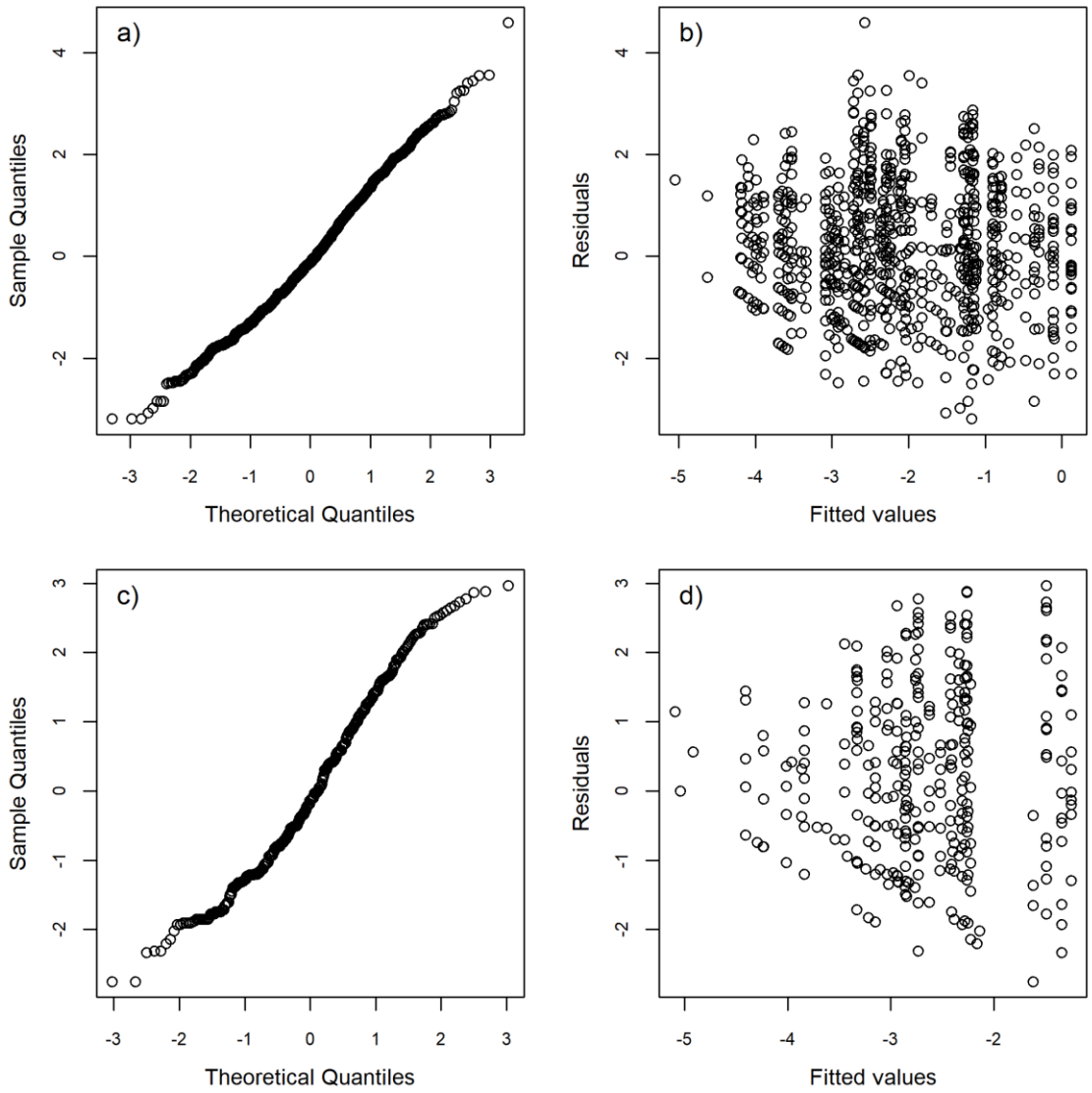

Figure S1. *Diagnostic plots of residuals for the two linear models used to compare geophagy site visitation rates amongst the four habitats (top row) and between sites at Loskop Dam (bottom row). The normal probability plots – in particular the first – suggest distributions at least approaching normality. More importantly, the residuals show no obvious pattern over model-fitted values (right hand column) and the various predictor variables (not shown), indicating homoscedasticity.*

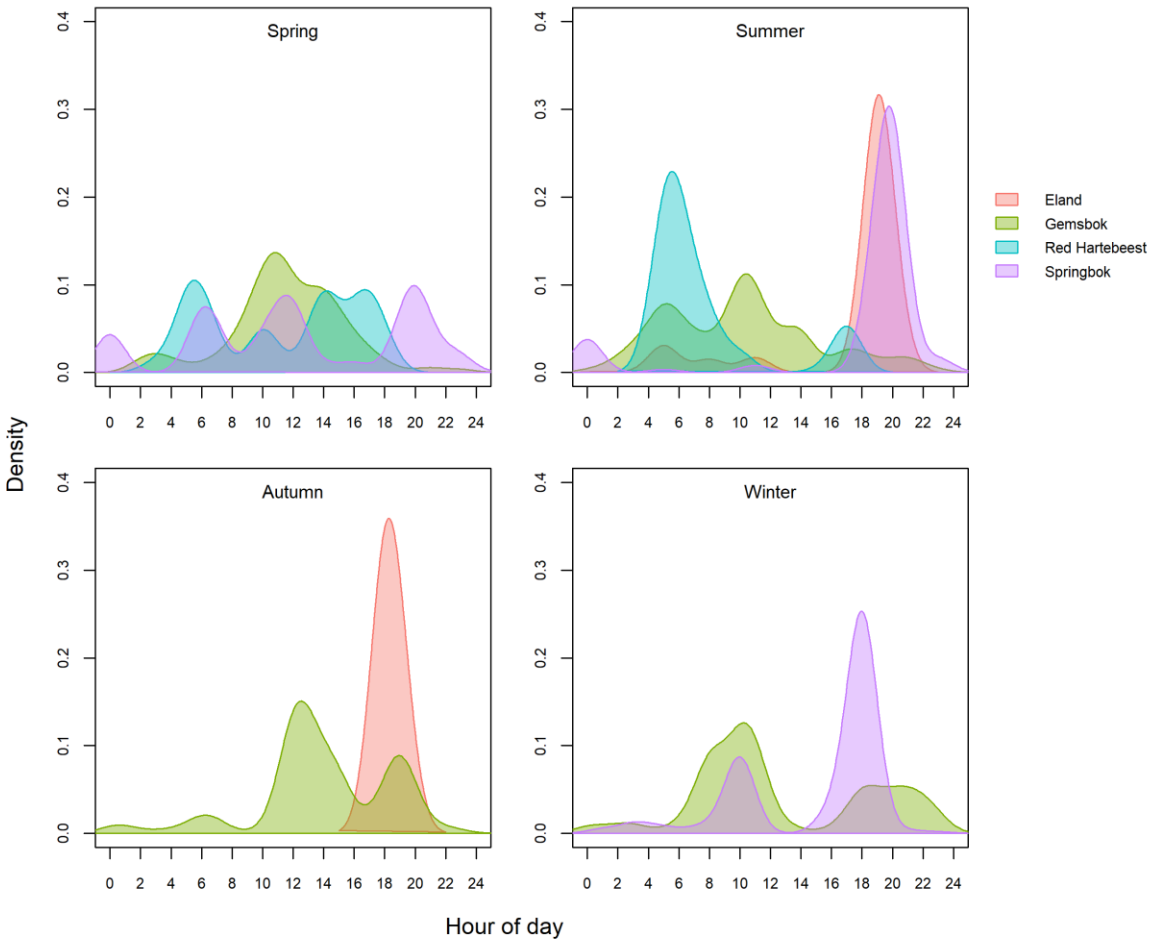

Figure S2. *Daily geophagy activity times of herbivores across different seasons in the Kalahari. Not in accordance with analyses above, but for visual consistency, density estimates are plotted using bandwidth = 1.*

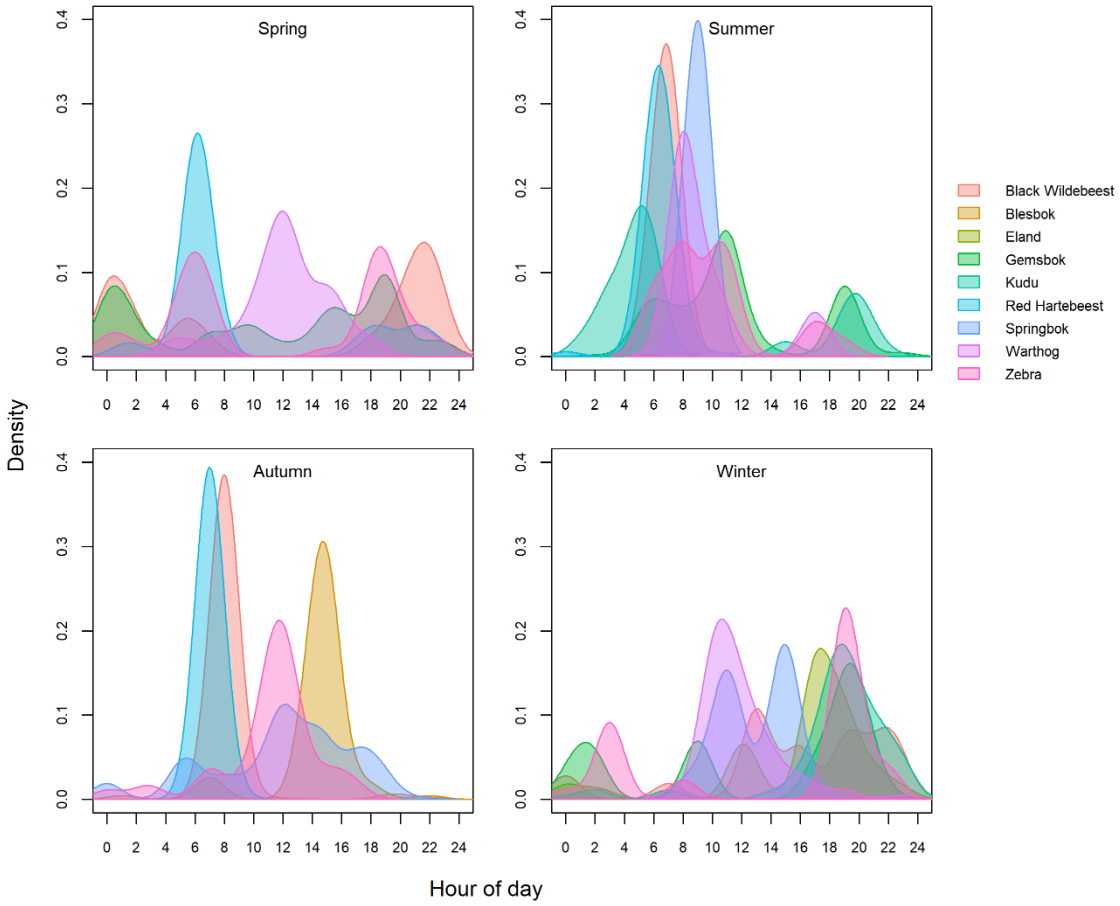

Figure S3. *Daily geophagy activity times of herbivores across different seasons in the Nama Karoo (Tussen-die-Riviere Game Reserve). Not in accordance with analyses above, but for visual consistency, density estimates are plotted using bandwidth = 1.*

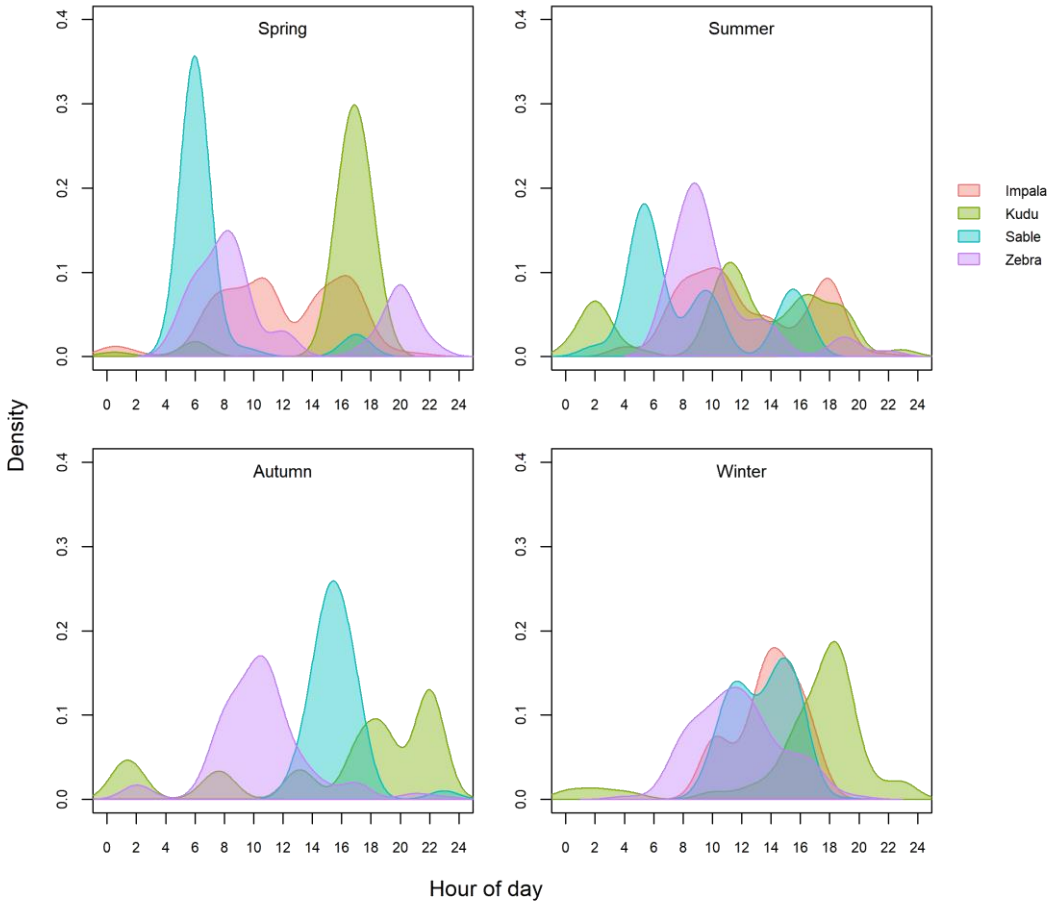

Figure S4. *Daily geophagy activity times of herbivores across different seasons in the Grassveld (Willem Pretorius Game Reserve). Not in accordance with analyses above, but for visual consistency, density estimates are plotted using bandwidth = 1.*

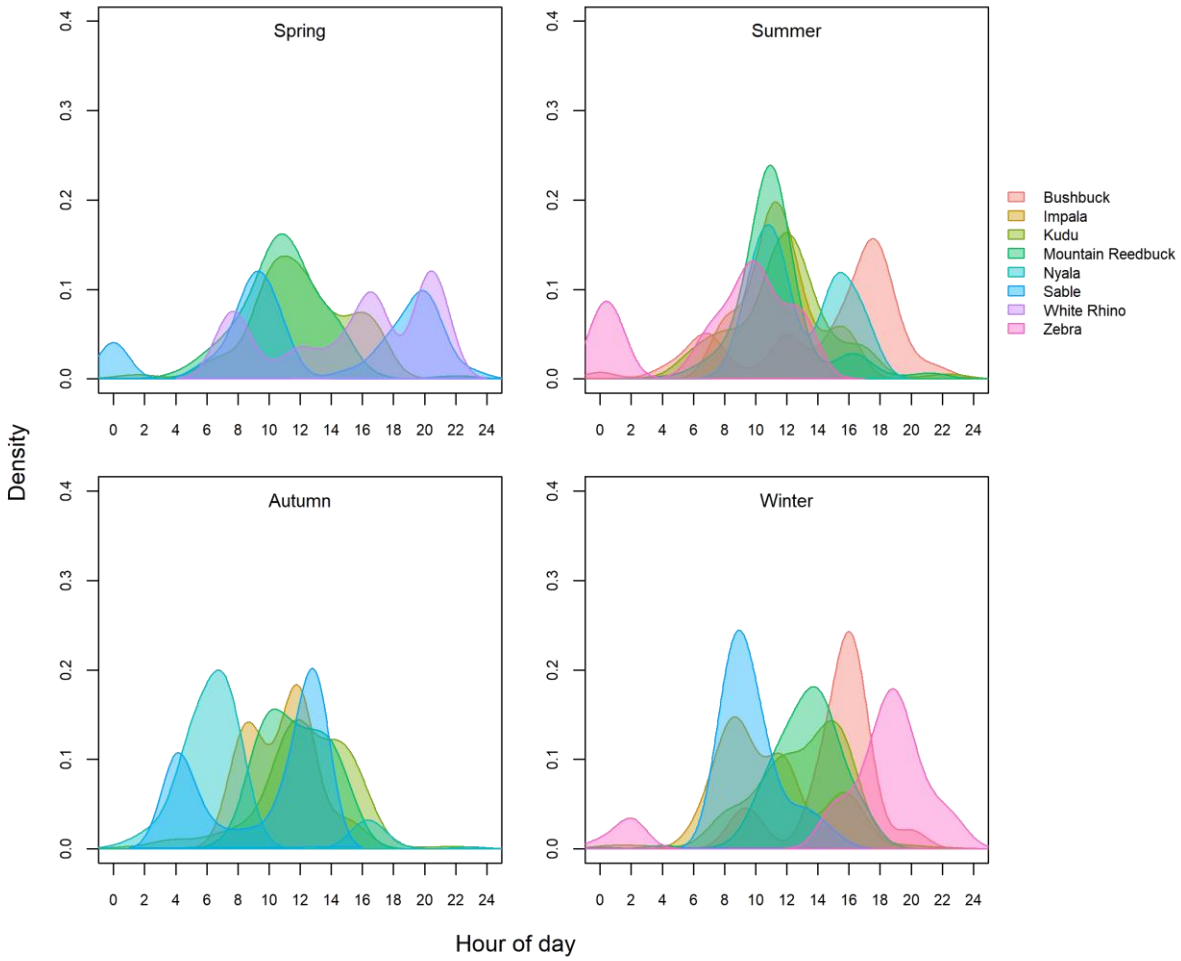

Figure S5. *Daily geophagy activity times of herbivores across different seasons in the Bushveld habitat (Loskop Dam Nature Reserve). Not in accordance with analyses above, but for visual consistency, density estimates are plotted using bandwidth = 1.*