Bones and ecology in the Southern African Rift Valley: Implications for our understanding of human evolution



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This work is dedicated to my family.

My parents, Adriano Isac Mathe and Puresa Simone Ngomane,

my fiancée, Norina Carlos de Jesus Francisco Vicente,

my siblings, Admiro Mathe, Ronaldo Mathe, and Dulce Mathe,

my sister-in-law, Natasha Alberto, and

my nephew and niece, Dinis Mulhanga and Adrielly Mathe, respectively.

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ABSTRACT

The fossil evidence for human evolution in open-ground African ecosystems is primarily found in river and lake deposits of the East African Rift Valley. Palaeontological and archaeological samples in these settings constitute evidence used to make inferences about past environments, biological evolution, and cultural beginnings. However, important questions remain about how well our palaeontological collections represent the animals that lived in those ancient landscapes and the ecology of those settings. The factors that control the density and distribution of bones in modern sedimentary landscapes shed light on the variables that control the density and distribution of fossils in palaeontological and archaeological sites. Those ancient sites are geologically like the diverse Rift Valley landscapes in Gorongosa National Park in Mozambique. Therefore, this thesis explores bones and ecology in a southern African ecosystem to enhance our understanding of human evolution in Rift Valley open-ground landscapes. Chapter One provides an introduction and overview of neotaphonomy in Africa: the ecological and palaeoecological implications of modern bone assemblages in open-ground environments. Chapter Two explores the 'Bones of Gorongosa: Establishing Live-Dead Fidelity in a Complex African Ecosystem'. The results of this chapter lead to the estimation that more than 50% of vertebrate species in palaeoenvironments are not present in palaeontological and archaeological assemblages, but from those recorded, the species diversity and abundance from the assemblages reflect the diversity and abundance of the ancient living community. Chapter Three explores the 'Ecological Influences on Bone Deposition in the Rift Valley Landscapes of Gorongosa National Park, Mozambique'. The results revealed that higher bone deposition occurs closer to roads and farther from low energy water sources like lakes and pans (water marshes). These findings also indicate that faunal fossils may have accumulated further away from water sources. Chapter Four examines the ecology of primate carcass distribution in the eastern Rift Valley landscapes of GNP, and its results revealed that

primate carcasses are more frequently found near rivers, while non-primate carcasses tend to accumulate further away. The results further indicate that primate bone abundance differs significantly from that of other mammals, with the higher densities of primate bones observed in the annually flooded landscapes rather than in non-annually flooding landscapes. These findings suggest that the limited records of primates at palaeontological sites like the Mursi Formation do not necessarily reflect the lack of primates in these ancient ecosystems; such patterns may instead reflect ecological factors—particularly the role of water sources—influencing bone deposition and preservation. Chapter five returns to a human evolution perspective by reviewing the reflection of palaeontological and archaeological assemblages in the ancient mammal communities in African open-ground landscapes, and also explores the implications of modern bone survey researches, presented in this thesis, for our perception of palaeontological and archaeological site formation, and to address issues of hominin palaeoecology in rift valley settings analogous to those where our ancestors evolved.

STATEMENT OF AUTHORSHIP

This document follows the integrated thesis format. Chapter One will be submitted to *Frontiers in Mammal Science, section Evolution, Anatomy and the Paleosciences* in August 2025. Chapter Two will be submitted to the *American Journal of Biological Anthropology* in September 2025. Chapters Three and Four are in preparation for submission as research papers to *Current Anthropology* and a special issue in the journal *Primates*, respectively. All these chapters result from collaborations with my supervisors, colleagues, and external researchers who have contributed to the development and execution of the studies. I am responsible for the work presented in each chapter, including conceptualisation, methodological design, data collection and analysis, interpretation and visualisation of results, and writing up. For Chapter Two, I directed the osteological data collection in the park, and I shared responsibility for primary data collection during fieldwork with my supervisors, Susana Carvalho and René Bobe, as well as members of the Paleo-Primate Project Gorongosa, interns and external researchers in Gorongosa, including Kaitlyn Gaynor and Meredith Palmer (camera trap data) and Marc Stalmans (biennial aerial surveys). For Chapters Three and Four, the same osteological data used in Chapter Two and environmental data collected by the science team as part of biodiversity monitoring were utilised. For all chapters, I benefited from computational support and manuscript revisions provided by co-authors. These chapters (except for chapter 5) have been written in the first-person plural in preparation for their submission to journals as collaborative research papers. The submitted and published work conducted during my DPhil programme the related and unrelated to the thesis can be found in the appendices of this thesis (Appendix B).

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LIST OF ABBREVIATIONS

ANP - Amboseli National Park

EARS - Eastern Africa Rift System

GLM - Generalised Linear Model

GNP - Gorongosa National Park

JM - Jacinto Mathe

LTA - Long Term Agreement

MNI - Minimum Number of Elements

MNI - Minimum Number of Individuals

NB - Negative Binomial Model

NDVI - Normalized Difference Vegetation Index

NIR- Near-infrared

RAI- Relative Abundance Index

VNP - Virunga National Park

Chapter One. Neotaphonomy in Africa: the ecological and palaeoecological implications of modern bone assemblages in open-ground environments

Bones actively accumulating on modern landscapes alongside living vertebrates present a unique source of ecological information. Some studies have shown a correlation between the taxonomic composition of the bones and the living communities they come from, but how closely do these bones capture ecological variables such as species richness and relative abundance of species in the living community? What are the key biases in bone assemblages relative to the living communities they come from? Answers to these questions are relevant to the monitoring of modern ecosystems and for our understanding of biases in the fossil record, issues within the scope of neotaphonomy. Here we review neotaphonomic studies in African open-ground landscapes focused on the relationship between osteological assemblages and living communities, and on the variables that drive bone deposition, preservation, and distribution across these landscapes. Some studies have reported a significant correlation between the diversity of species documented in bone assemblages and those in the living community (live-dead fidelity), but some of these studies were conducted in anthropogenically disturbed landscapes and lacked information documenting events between the animal's death and skeletonisation. To push further the field of neotaphonomy, it is necessary to implement new methodological approaches, such as: 1) combining osteological surveys and carcass monitoring, 2) using camera trapping to document the living community and to monitor the fate of carcasses, 3) using comparable data-collection methods that allow for inter-site comparisons, 4) evaluating key ecological variables such as water features, predator presence, vegetation type, and road proximity in analyses of bone deposition and carcass distribution, 5) monitoring

carcasses systematically from the moment of death until burial, and 6) using data from radio-collars deployed on predators to maximise the chances of locating fresh kills. Understanding current gaps and adopting novel methodological approaches will improve our interpretation of live-dead fidelity, with implications for our understanding of fossil bone assemblages and palaeoecology.

1.1. Introduction

Bone assemblages accumulating on modern land surfaces alongside living vertebrates present a unique source of data about environments, ecology, and population dynamics (Western and Behrensmeyer, 2009). These bone assemblages also hold important lessons for our understanding of palaeoenvironmental and palaeoecological reconstructions based on fossil samples (Behrensmeyer and Hill 1980). Yet, as noted by Kidwell a decade ago, "death assemblages have been a severely underexploited source of biological data" (Kidwell 2015:4923). In this review, our main question is: how closely do modern bone assemblages in African open-ground landscapes reflect the taxonomic richness, relative abundance, and environmental conditions of the broader ecosystems producing them? This question is often posed in terms of live-dead fidelity (Kidwell 2007, 2013; Lockwood and Chastant 2006; Miller 2011; Miller et al. 2014; Pyenson 2010, 2011). The question of live-dead fidelity focuses on the first stages of the taphonomic cycle: the transition of organic remains from the biosphere to the lithosphere (Efremov 1940). Here we use the term 'neotaphonomy' to refer to bone taphonomy with a focus on processes before the burial of organic remains (Behrensmeyer and Kidwell 1985) (See Figure 1-1).

Studies of neotaphonomy or actualistic taphonomy in Africa were pioneered by researchers seeking to understand fossil bone accumulations at hominin sites. Speculations about the role of hominins, tools, and hunting in creating the fossil assemblages found in Plio-Pleistocene South African caves (Dart 1949, 1957) led C.K. Brain to undertake pioneering work on modern bone accumulations (Brain 1967, 1969; Charles Kimberlin Brain 1981, 1981). The study of taphonomic processes in relation to human evolution gained momentum in the 1970s and 1980s with the publication of key works based on actualistic studies in modern African landscapes (Behrensmeyer 1978; Blumenschine 1986b; Hill 1975, 1984; Shipman 1975, 1981).

Following a major conference sponsored by the Wenner-Gren Foundation in 1976, the publication of the edited book *Fossils in the Making* (Behrensmeyer and Hill 1980) marked a turning point in the study of African taphonomy.

Our focus on African neotaphonomy aims to improve our understanding of fossil assemblages as tools for the reconstruction of past habitats. Although some neotaphonomic studies have reported positive correlations between modern mammals and their osteological remains (live-dead) (Western and Behrensmeyer 2009), important questions remain. How accurately do bone assemblages capture the relative abundance and diversity of species in the living community across different open-ground landscapes in African ecosystems? What are the key biases in bone samples relative to the living vertebrates? What methodological problems and key gaps remain to be addressed? What locations in Africa could be targeted for future neotaphonomic studies?

To address these questions, we review neotaphonomic studies that assess species abundance and diversity in natural vertebrate communities based on modern bone assemblages from open-ground landscapes in Africa (excluding caves). We then explore: i) the primary ecological factors influencing bone deposition within the taphonomic cycle across various African landscapes, ii) key biases in bone assemblages compared to living vertebrate communities, iii) methodological challenges and knowledge gaps, and iv) potential locations for future neotaphonomic research in Africa. Finally, we propose tentative answers and suggest concrete methodological steps for conducting new empirical studies to further test how accurately modern faunal assemblages reflect the abundance and diversity of living vertebrate communities. This discussion is relevant to our use of modern bone assemblages as a crucial source of biological data and for our understanding of palaeoecological reconstructions based on fossil bones.

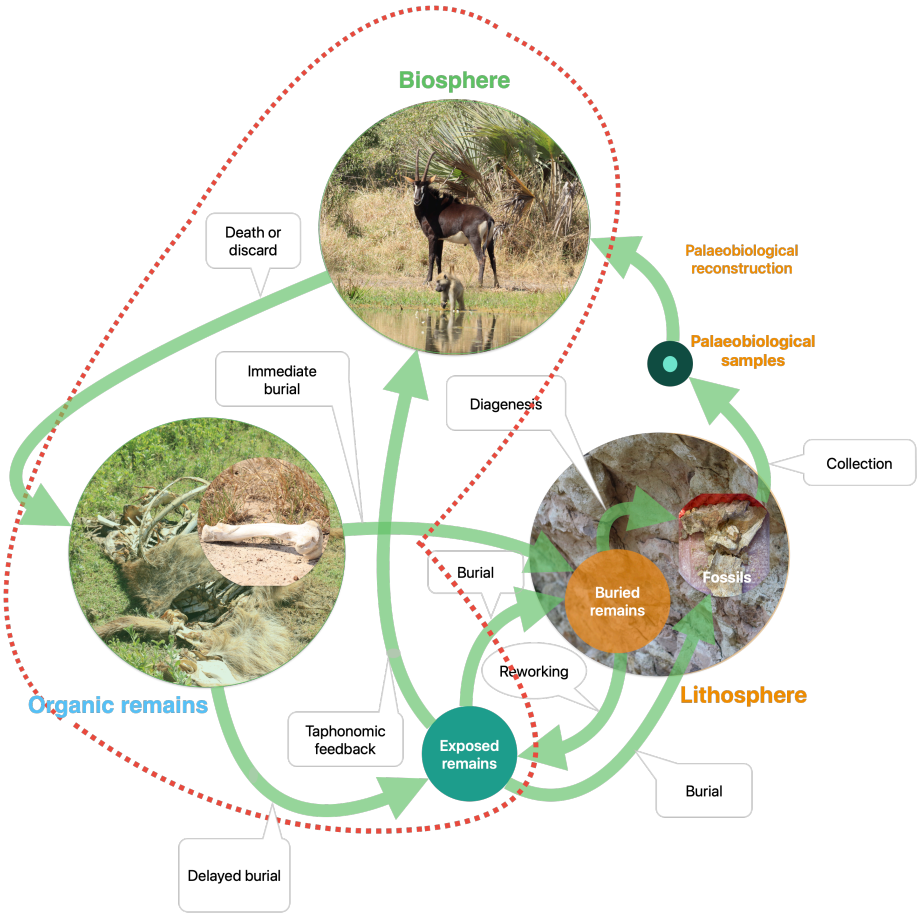


Figure 1-1. The taphonomic cycle, adapted from Behrensmeyer et al. (2000). The taphonomic cycle illustrates various routes taken by the dead or discarded organic remains, depicting their fate as either being recycled (destroyed) or preserved. The red dashed line represents the pre-burial processes (neotaphonomy) that are the focus of this review.

1.2. Bone deposition and live-dead fidelity across modern landscapes

Most fossil evidence for early hominin evolution has been found in Africa (Alemseged 2023; Haile-Selassie, Melillo, and Su 2016; Leakey and Walker 2003; Reynolds and Bobe 2022; White 2002), as is the contextual evidence used to interpret early hominin behaviour, palaeoecology, and palaeoenvironments (Behrensmeyer 2006; Bonnefille 2010; Cerling et al. 2011; Potts 2007; Reynolds and Bobe 2022). Thus, neotaphonomic studies addressing issues of early hominin evolution have focused on bone assemblages in different African habitats (Behrensmeyer 1993; Blumenschine 1986b, 1986a, 1989; Brain 1967; Tappen 1995; Western

and Behrensmeyer 2009). One of the fundamental questions asked in these studies is whether bone assemblages capture the relative abundance and taxonomic richness of species in the living community across different African ecosystems. This question can be approached with studies of bone deposition and live-dead fidelity, i.e., assessing osteological collections in relation to the living community they come from. These studies can help identify biases in our interpretations of palaeontological records and their context. In this section, we first discuss key studies of bone deposition and live-dead fidelity carried out in African open-ground landscapes (excluding caves) focusing on mid- and large-sized vertebrates and then live-dead fidelity and palaeoenvironmental reconstruction focusing on small mammals. Figure 1-2 shows the geographic locations of neotaphonomic studies conducted in across open-ground African ecosystems (for more details, see Table S 1-1).

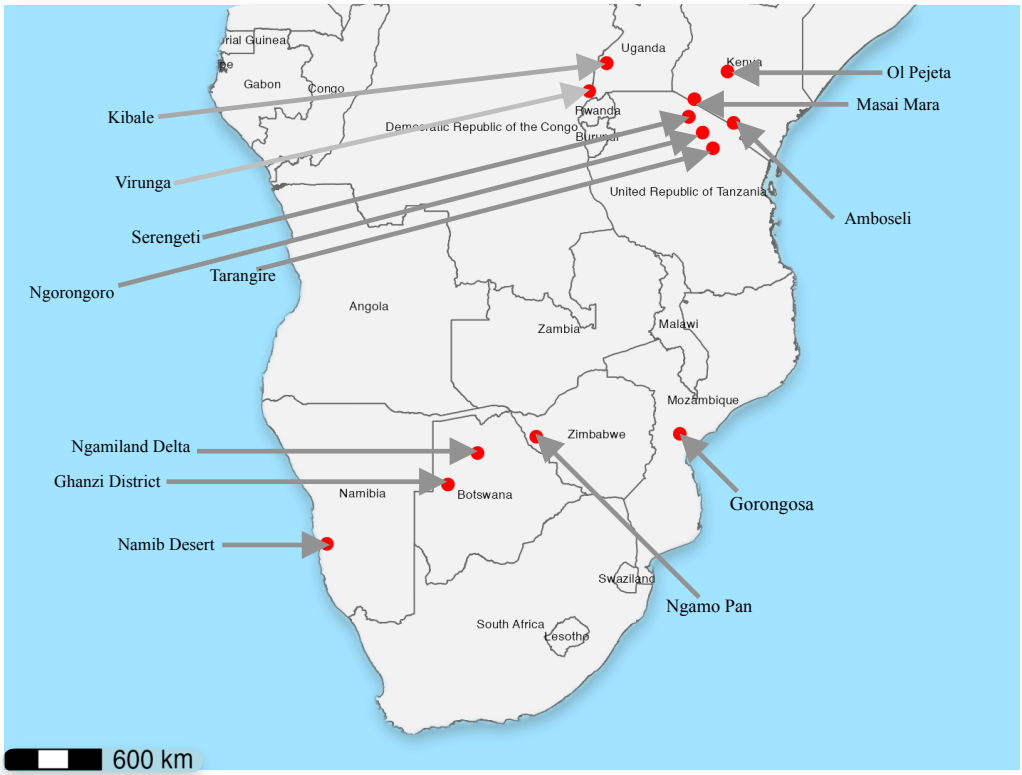


Figure 1-2. Red dots indicate sites where neotaphonomic open-ground studies of natural bone accumulations have been conducted in eastern and southen Africa (See also Table S 1-1).

1.2.1. Bone deposition and live-dead fidelity of mid- and large-sized vertebrates

Studies of bone deposition and live-dead fidelity of bone assemblages relative to the living community in African ecosystems were pioneered by Behrensmeyer and colleagues at Amboseli National Park in Kenya (Behrensmeyer 1993; Behrensmeyer and Miller 2012; Behrensmeyer, Western, and Boaz 1979; Western and Behrensmeyer 2009), and Tappen in Virunga National Park in the Democratic Republic of Congo (Tappen 1992, 1995). To investigate how the vertebrate living community is represented in bone assemblages, Behrensmeyer and colleagues surveyed 96 straight-line transects across six habitats covering 1.5% of the total Amboseli basin area (Behrensmeyer, 1993; Behrensmeyer et al., 1979). Later, in 2002, the number of transects was reduced to 44 lines (Western and Behrensmeyer 2009). The protocol otherwise remained the same across years, with lines of 30 to 100 m in width. Lines were walked until the bone collection reached 20 individuals or a habitat boundary was reached (whichever came first). Additionally, small plots of 10x10m to 50x50m placed along the transect were intensively surveyed to locate small vertebrate bones and help correct for observer bias (Behrensmeyer et al. 1979). During transects, data was collected on bone elements present, taxon, relative age at death, weathering stage, damage type, degree of burial, and articulation state to estimate a minimum number of individuals and species richness. Weathering stages were used to group specimens into different windows of time (i.e., 1964-1969, 1970-1976, 1993-1998, 1999-2004) for subsequent analysis (Behrensmeyer 1993; Western and Behrensmeyer 2009). In Amboseli, it is estimated that most bones decomposed beyond recognition within 10 to 15 years after first deposition (Behrensmeyer 1978). Also, species weighing less than 15kg were under-represented in these assemblages, which suggests that species with lower body mass may be systematically underrepresented in palaeoecological reconstructions of areas analogous to modern-day Amboseli (Behrensmeyer 1993;

Behrensmeyer et al. 1979). Behrensmeyer and colleagues noted that the strength of the live-dead relationship at Amboseli varies across years and habitats. For instance, the live-dead correlation from 1964 to 1969 (0.903) was stronger than from 1999 to 2004 (0.450) (Figure 1-3). Morever, the correlation in swamp areas (0.130) is weaker than in the plains (0.756) (Figure 1-4). Thus, the timing of bone collections and the habitats of bone surveys have an impact on live-dead assessments. Nevertheless, a key conclusion of this work is that bone assemblages track changes in habitats over time as well as the dynamics of mammal populations (Western and Behrensmeyer 2009).

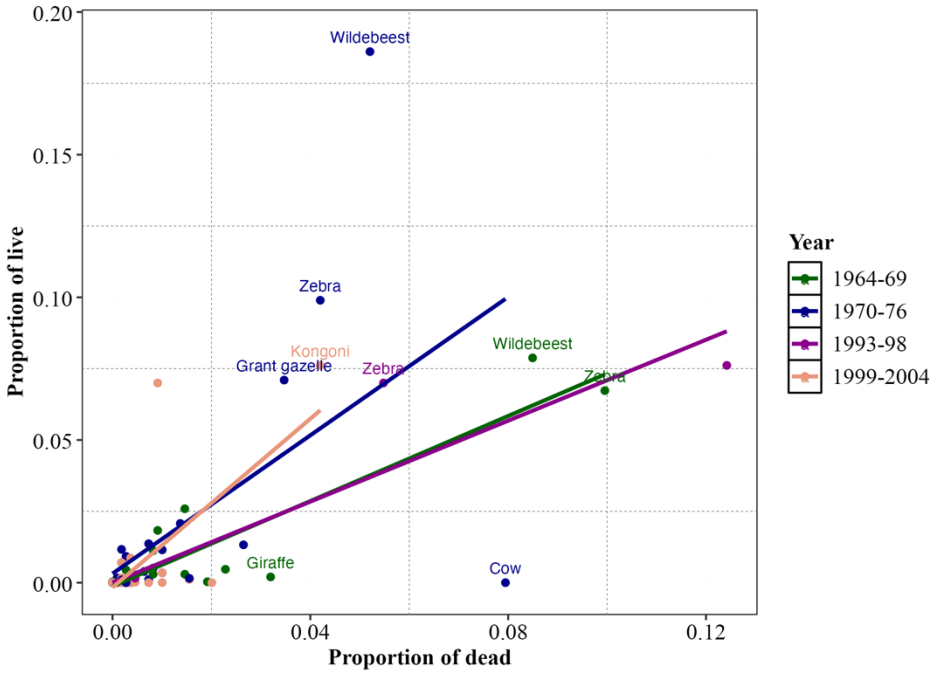


Figure 1-3. Correlation between the proportions of live-dead mammals from Amboseli NP in five-year intervals. Figure drawn with data from Western and Behrensmeyer (2009).

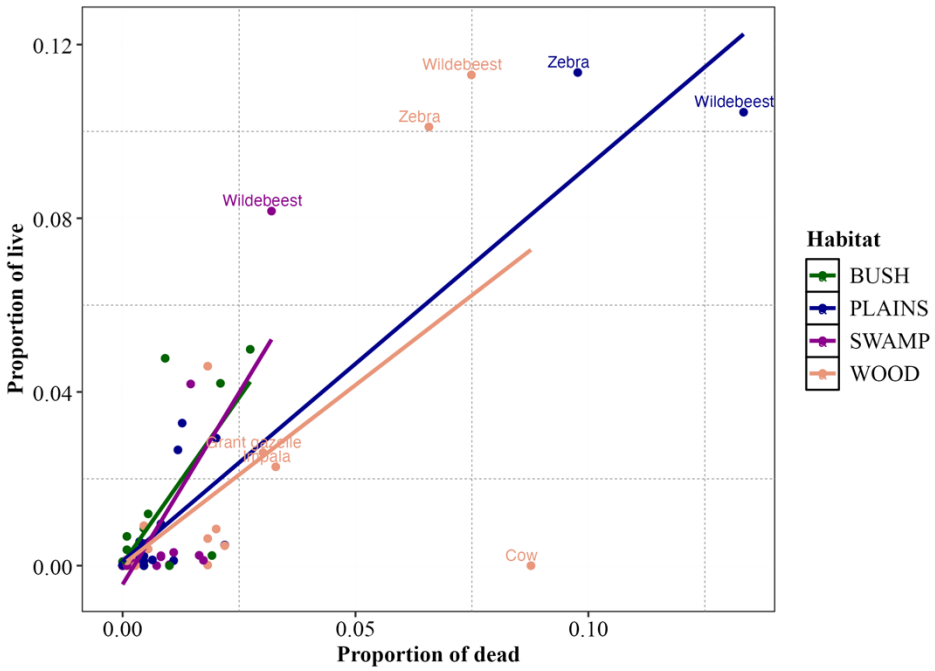


Figure 1-4. Correlation between the proportion of live-dead mammals from Amboseli NP in four main habitats. Figure drawn with data from Western and Behrensmeyer (2009).

The systematic bone documentation in Amboseli also included avian species (Behrensmeyer, Stayton, and Chapman 2003). Bird species are an important component of modern vertebrate communities, but their bones, filled with air cavities, are fragile and often fragmentary (Behrensmeyer et al. 2003). Understanding the taphonomy of modern bird remains will help our interpretations of fossil assemblages with extinct avifauna (Olson 1985, 1999). Behrensmeyer and colleagues noted that Amboseli bird bones, except for the ostrich, decay faster than bones of adult mammals (Behrensmeyer et al. 2003). This may explain why few bird bones of advanced weathering stages are present in the fossil record. Despite the low representation of birds in the Amboseli bone assemblages, analyses of diet, body weight, and habitat indicate that bird bones do provide an adequate representation of general habitats occupied by the living avian community in the basin. This suggests that avian remains are important for palaeoecological reconstructions and for tracking habitat changes in the fossil record (Behrensmeyer et al. 2003).

Another important study focusing on modern mammal bone deposition was carried out by Tappen at Virunga National Park in the Democratic Republic of the Congo (Tappen 1992, 1995). Tappen's aim was to assess the implications of modern bone deposition for our understanding of palaeontological site formation. Tappen recorded the minimum number of elements (MNE) for mammal species using transect lines of variable dimensions across different types of habitat (see Figure 1-5) (Tappen 1995). A comparison of dietary categories among mammals and their relative abundance highlights the ecological differences between the Virunga and Amboseli areas targeted by the bone surveys (see Figure 1-5). Both areas are dominated by grazing mammals, but Amboseli has a greater proportion of browsers and mixed feeders. However, it should be noted that the Virunga bone surveys were limited to the savanna parts of the park, not to the entire Virunga region, which hosts a great diversity of habitats.

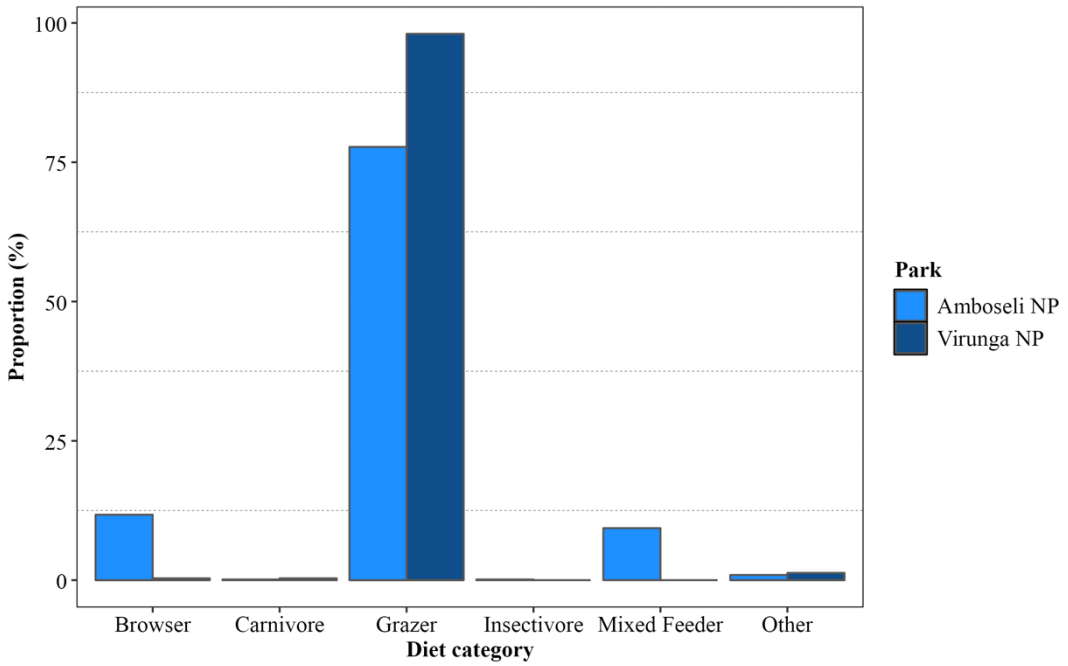


Figure 1-5. Minimum Number of mammal species per diet categories recorded in Virunga NP and Amboseli NP using data from Tappen (1992) and Western and Behrensmeyer (2009).

Tappen's research assessed the influence of environmental variables in bone deposition using 34 transects across four different habitats within the savanna landscapes (Plateau,

Southern Plateau, Riverine and Lake margin zones) and revealed that bone deposition in Virunga NP is not uniform (Tappen 1992, 1995). The Plateau is an open grassland with a high abundance of kob and reedbuck, while the Southern Plateau is more wooded, supporting fewer kob and reedbuck and with abundant waterbuck, warthog, and hippopotamus presence due to the proximity to rivers and lakes. The Riverine zone has a high density of trees and bushes, with the Semliki River actively eroding sediments. The Lake zone consists of sandy beaches, cliffs, and slopes, with vegetation ranging from bare ground to dense bushes. Bone deposition was higher in open grasslands (Plateau) compared to mixed, wooded, and closed environments such as the Riverine and Lake margins where bone accumulation is lower (see Figure 1-6). This indicates that topography and vegetation affect bone accumulation (Tappen 1995). As with the findings from Amboseli, bone distribution in Virunga NP was not always uniform along transects. Sometimes the distribution was random: bones in different habitats have comparable chances of being recorded (Tappen 1995).

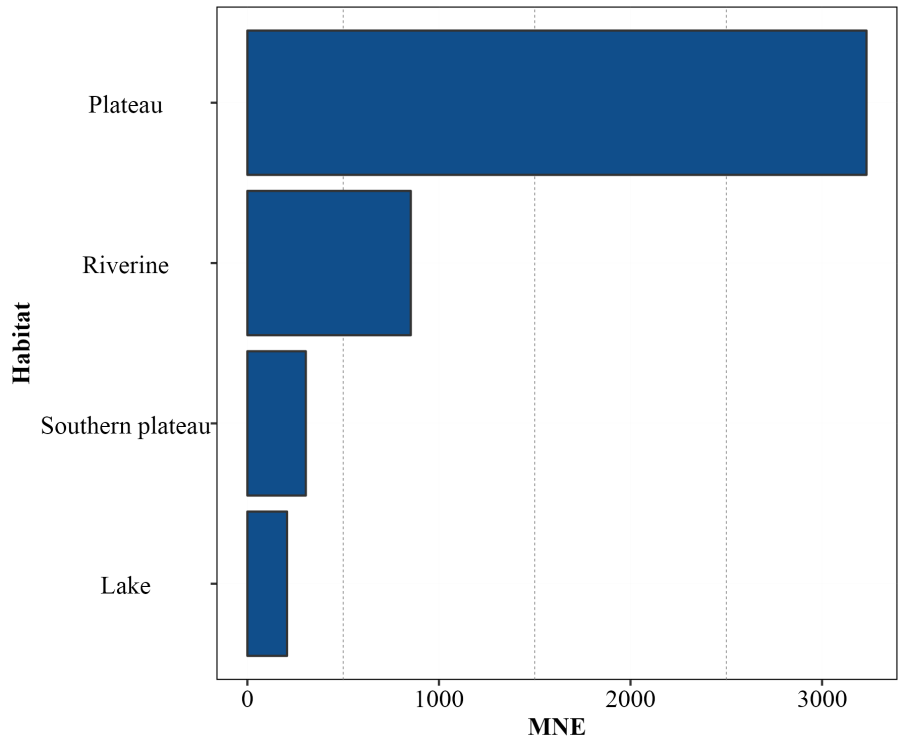


Figure 1-6. Minimum Number of elements (MNE) across main habitats of Virunga NP with data from Tappen (1995).

1.2.2. Live-dead fidelity using small mammals

Vertebrate bones, regardless of size and species provide important information about past environments and site formation (Behrensmeyer et al. 1979; Reed 2007, 2011; Western and Behrensmeyer 2009). Small mammals are a key component of modern and past animal communities and, although sometimes neglected, they are fundamental to refine palaeoecological reconstructions (Avery 2001; Denys 1987; Manthi and Winkler 2020; Reed and Geraads 2012; Wesselman 1984; Winkler 2003) and to understand the fossil record of mammals of small body mass (Terry 2010). Rodents, for instance, are frequently consumed by owls and their remains are later regurgitated as pellets (Andrews 1990; Terry 2004), from which we can infer the prey and predator species (Brain 1981; Denys et al. 2018; López and Chiavazza 2020).

Interestingly, pellet remains may capture more small mammal biodiversity (over 60%) than direct survey methods, such as rodent trapping (Reed 2007). From a palaeoenvironmental perspective, the presence of small mammals provides indications of their ecological preferences; the abundance of prey taxa in owl-accumulated assemblages varies across habitats. For example, rodent species inhabiting the semiarid and dry savanna regions of the Serengeti in Tanzania are associated with specific owl roosting sites in plains areas with low precipitation, while those in arboreal habitats are found in semi-open and closed environments such as treed-grassland and grassed-woodland (Reed 2007). Reed also found significant similarities between modern micromammal samples and those obtained from the Laetoli Pliocene fossil sites in the same region and suggests that there is continuity between ancient and modern landscapes in ecosystem structure, influenced by climatic, tectonic, and volcanic factors (Reed 2011).

A study by Linchamps et al. (2021) presented the first combined taxonomic and taphonomic analysis of barn owl (*Tyto alba*) pellets in Botswana. The aim of this study was to examine the accuracy of palaeoenvironmental analyses based on micromammals for this region and to understand the taphonomic processes at play in two distinct environments: the Kalahari Desert and the Okavango Delta. More than 100 pellets from Kalahari Desert and 85 pellets from rural Ngamiland District in the Okavango Delta were collected and analysed. This study found differences in prey composition between samples of the two distinct areas, which further highlights the ecological relevance of barn owls in biodiversity assessments (Linchamps et al. 2021). Although the often-used Gerbillinae/Murinae ratio in some areas, such as North African regions, was found inadequate, the study revealed that ecological indices (Taxonomic Habitat Index and Taxonomic Biome Index) based on the presence/absence and relative frequencies of recorded small mammals were consistent with observed habitats (Linchamps et al. 2021; Stoetzel et al. 2011). Furthermore, the Kalahari pellet assemblage indicates high score for species adapted to deserts and shrublands, whereas the Okavango assemblage presents a higher prevalence of species adapted to flooded grasslands and savannas (Linchamps et al. 2021).

Studies of micromammal assemblages from owl pellets are constrained by owl ecology, roosting behaviour, and dietary preferences. Thus, the integration of behavioural ecology alongside environmental characterisation and taphonomic analyses can provide a strong baseline to illuminate paleoenvironmental reconstructions from owl pellets (Reed 2005).

1.3. Ecological variables and bone deposition in African landscapes

Most organisms do not fossilise as they are affected by multiple intrinsic (e.g. body size, age) and extrinsic (biotic and abiotic) factors involved in taphonomic processes and end up getting 'recycled' back to their environments (Behrensmeyer, Kidwell, and Gastaldo 2000). The answer to the question of how accurately bone assemblages capture the relative abundance and diversity of species in the living community across different open-air landscapes in African ecosystems requires, first and foremost, an understanding of the effect of these factors on the preservation of faunal remains.

Hard tissues pass through many 'filters' during the complex taphonomic cycle (Figure 1-1) before being recycled or becoming fossilised (Behrensmeyer 1978). This cycle, i.e., the potential transition of organic remains from the biosphere to the lithosphere, involves the replacement of organic molecules by minerals such as calcite, siderite, and pyrite, over variable periods that depend on local conditions. This transition may involve immediate burial, recycling, and re-burial with complex feedback mechanisms (Figure 1-1).

In this review we focus on the processes that occur from the animal's death to the pre-burial phase, i.e., before diagenesis can take place (Figure 1-1). In the pre-burial phase, due to various filters that are influenced by ecological factors, there is potential loss of information as the organic remains become more fragmentary, modified or consumed, and less abundant through time. This pre-burial phase of the taphonomic cycle sheds light on interpretations of the fossil record.

Ecological variables play a role from the death of the organism onward with regard possible preservation prior to burial. Key controls of the living community include habitat complexity, anthropogenic activities, social community structure, predator species, resource availability, and specific environmental conditions (Sinclair, Dublin, and Borner 1985). Thus,

ecological variables, such as water, habitat type, predators, herbivores, and decomposers, are important for understanding the community and population dynamics over time (Behrensmeyer 1993). Next, we focus on these ecological variables and their importance for neotaphonomy, particularly on how they affect the interpretation of relative abundance, diversity and ecological fidelity of functional traits based on modern bone assemblages.

1.3.1. Predators and scavengers

The first phase of the taphonomic cycle involves the death of organisms, which may occur through a variety of pathways including predation, disease, malnutrition, accidents, injuries due to intra-specific conflict, or catastrophic events like flooding due to cyclones (Beardmore-Herd et al. 2025; Walker et al. 2023). In African natural ecosystems, the main mammalian predators of larger ungulates are lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and wild dogs (*Lycaon pictus*). These mammalian predators capture prey of body mass ranging from over 550 kg (taken by lions) to as little as 5 kg (at the low end of prey taken by wild dogs) (Hayward and Kerley 2005; Kingdon et al. 2013). Avian predators like owls and eagles also contribute by preying on smaller vertebrates and discarding their remains (Reed 2005). Africa uniquely retains a full guild of stalking, cursorial, and scavenging carnivores (Owen-Smith 2021), with lions dominating in biomass consumption and targeting large grazers (Owen-Smith and Mills 2008), while hyenas exhibit flexible strategies depending on lion presence. Leopards, cheetahs, and wild dogs target smaller or vulnerable prey but have limited impact due to lower densities and wide-ranging habits (Hayward, Henschel, et al. 2006; Hayward, O'Brien, et al. 2006; Hunter, Henschel, and Ray 2013; Mills and Mills 2017; Stein, Fuller, and Marker 2013). Consequently, carcasses and bone accumulations may be dispersed across the landscape, especially from kills by wide-ranging cursorial predators.

In addition to apex predators, modern species such as vultures (Arriaza et al. 2021; Sebastián-González et al. 2021, 2023), or monitor lizards and carrion beetles also offer valuable insights into scavenging behaviours that may contribute to bone accumulations. Smaller prey is typically entirely consumed, while in larger prey, such as buffalo, soft tissues may be left behind with partly intact skeletons (Behrensmeyer and Miller 2012; Stanton and Dodd 1976).

Scavengers are diverse, and their importance has been underestimated in vertebrate food webs (Sebastián-González et al. 2023). The availability and distribution of carrion is a significant food resource for non-predatory vertebrates with a high degree of scavenging behaviour. Scavenging is responsible for the transfers of more energy per link than predation (Wilson and Wolkovich 2011); it is a behaviour that broadens our understanding of food webs, community and population ecology, evolution, biodiversity conservation, and human well-being (Moleón et al. 2015). In African ecosystems, the distribution of animal carcasses, skeletal profiles, and completeness of bones in places like the Serengeti or Ngorongoro are dependent on the abundance and behaviours of scavengers (Blumenschine 1986b, 1989).

1.3.2. Water (rivers, lakes, and pans)

Watercourses, such as rivers and lakes are important factors in bone transportation, deposition and accumulation (Morris 1997; Tappen 1995). Water bodies shape landscapes and the distribution of animal communities. For instance, during the dry season, animals may forage closer to water bodies where they can hydrate and feed on fresh plants maintained by the remaining moisture. Predators strategically follow their prey and use water holes as lower-effort hunting spots, which can explain bone accumulations near rivers and water channels (Hutson 2016). For example, in the modern ecosystem of Gorongosa National Park, central Mozambique, carnivores and some foragers such as elephants (*Loxodonta africana*), Egyptian/large grey mongoose (*Herpestes ichneumon*), and aardvark (*Orycteropus afer*)

occupy habitats relatively close to Lake Urema, a permanent water body, whereas grazers and primates occupy areas further away from the lake (Gaynor et al. 2021). This highlights the importance of accounting for local and seasonal variation in mammal spatial use, and the critical need to combine modern ecology studies with neotaphonomy to assess how bone assemblages are formed.

Rivers also play an important role in carnivores ambushing prey, sometimes resulting in a high accumulation of bones near those water sources (Hutson 2016). This type of bone accumulation also reflects behavioural variation across species among water-dependent animals: wildebeests and zebras, independently of lions' presence, often occur near water holes and pans – which increases the likelihood of finding their remains in those areas (Hutson 2016). However, some species such as buffalos avoid water holes and pans in the presence of lions, perhaps due to different levels of water dependency, which leads to fewer predation events (Hutson, 2016). In a different context, lions ambush prey coming to drink in habitats like riverine and lacustrine woodlands, and hyenas may scavenge less frequently and intensely in wooded riparian settings than in open vegetation settings away from water bodies (Blumenschine 1986b).

1.3.3. Vegetation

Ecologists study variation in species distributions using various methods, from camera traps to regular counting and, more recently, GPS collars (Bouley et al. 2021; Prosekov et al. 2020; Stalmans et al. 2019). NDVI (Normalized Difference Vegetation Index) used in remote sensing is a ratio between red (R) and near-infrared (NIR) values, which correlate with rainfall (Gandhi et al., 2015) and are positively correlated with vertebrate species richness (Oindo and Skidmore 2002). NDVI has been applied to understand vertebrate species distribution and changes in space use across seasons. This index has not yet been examined for its influence on

bone deposition and carcass distribution. However, based on the understanding that occupancy and space use are positively correlated with higher NDVI values—indicating greener landscapes with more available forage (White et al. 2022)—it is likely that NDVI may also affect bone deposition across different ecosystems. Greener environments could potentially host greater bone accumulations where the majority of herbivores graze or feed. In tropical landscapes, trees provide shade for predators to consume their kills and bones may accumulate under the canopy. Some predators, such as leopards, keep their prey on the high branches of trees to avoid competition with terrestrial carnivores like lions. Blumenschine has demonstrated that, in the Serengeti, leopards abandon the carcasses of medium-size ungulates in riparian woodlands, thus providing potential opportunities for scavengers that can access them (Blumenschine et al. 1987). In places like Virunga NP, most bones are accumulated along tree lines, as trees provide shelter for predators to hold their kills (Tappen 1995).

1.3.4. Habitat type

Studies from different habitats (Tappen 1995) also showed that mammal bone collections vary across different habitats. In Virunga NP, the Southern Plateau (one of the four habitats in Tappen's study) had the highest diversity (as measured by the Shannon index) and the largest number of species (richness), while in tree lines (another habitat type in Tappen's study) few species were found in bone surveys (Tappen 1992, 1995). In a pilot study conducted by Mathe and Bobe (2018) in Gorongosa NP, it was also demonstrated that the abundance of mammals varies across different habitats. However, this variation in the bones collected across habitats can also reflect a bias in research efforts or physiognomic features of the landscape. For example, tall grass or dense vegetation makes it difficult to locate bones in some areas, but these habitats may also constitute a limitation for scavengers to find and access a predator's kill, resulting in more complete and less spread-out skeletons (Tappen 1995). We have also

noted that Behrensmeyer's work at Amboseli NP found different degrees of live-dead correlations depending on habitat type (e.g., woodland, bushland, grassland in Figure 1-4 above).

1.3.5. Roads and other anthropogenic features

Analyses of camera trap data has revealed that mammals at Gorongosa NP tend to occur in greater frequency in areas close to the park roads (Gaynor et al. 2021). For example, mixed-feeder ungulates like the impala, *Aepyceros melampus*, have higher population densities in the proximity of roads. This may happen due to roads that are established in locations with a high density of animals in the first place to increase animal visibility for tourists (Gaynor et al. 2021). It is also possible that animals may be attracted to the vegetation that grows near roads and that herbivores use these roads to travel across habitats (Gaynor et al. 2021). It is also possible that a higher circulation of tourists along the roads might make predators avoid those areas and consequently provide a refuge for herbivores. There is still a gap regarding to what extent proximity to roads may bias osteological collection, but these findings suggest that bones are likely to be accumulated near roads and other human infrastructures. However, in some contexts the opposite scenario may occur as the abundance of birds and mammals is negatively associated with proximity to infrastructure, and this negative association is stronger in open compared to closed habitats (Torres, Jaeger, and Alonso 2016).

1.3.6. Soil

The rate of bone weathering also depends on soil types. In Amboseli NP, alkaline soils result in bones being more weathered on the lower surface resting on the soils. This happens because the salt in those alkaline soils crystallises on bone surfaces, resulting in flaking and faster separation between microscopic organic and inorganic components (Behrensmeyer, 1978). Non-alkaline soils may favour bone preservation as bones slightly buried in these soils

are more weathered on their upper than lower surfaces. These findings suggest that bone preservation may vary depending on the salinity and acidity of the soils (Oghenemavwe, Orupabo, and Horsfall 2022). Further documentation of bone preservation across different habitats and soil types in African ecosystems would be valuable.

1.4. Biases in bone assemblages relative to the living communities

Some of the studies discussed here used surface line transects for carcass or bone documentation, and compared results with extant fauna (Western and Behrensmeyer 2009) or with local habitat features (Tappen 1995) to better understand live-dead fidelity, palaeontological and archaeological site formation, and ecological interactions involving ancient hominins (Blumenschine 1986b). Of particular interest are bone surveys in the context of the East African Rift System (EARS) because so much of the early hominin fossil record derives from this context. Thus, Tappen (1992, 1995) conducted her osteological surveys in Virunga NP, in the Western Branch of the EARS, where environments thought to be analogous to those inhabited by early hominins could be found. Some of these studies took place in national parks or natural reserve areas, but, even in these parks, anthropogenic influence can be significant. At Amboseli, for instance, Behrensmeyer recorded the presence of goats (*Capra hircus*), cows (*Bos taurus*), domestic dogs (*Canis familiaris*) and donkeys (*Equus asinus*) (Behrensmeyer et al. 1979; Western and Behrensmeyer 2009).

These bone surveys conducted in African ecosystems (Behrensmeyer 1993; Tappen 1995; Western and Behrensmeyer 2009) have thus aimed to understand the correspondence between osteological samples (dead) and the communities they come from (live) (Behrensmeyer 1993), and how much of the ecology is captured by these assemblages (Tappen 1995). However, an important missing element in these studies is the information spanning from the moment of death (e.g., a predation event) to the skeletonisation of the carcasses. For

instance, the representation of bone elements in bone patches depends on which species have accessed those bones and how much was consumed and left by carcass consumers (Wadley 2020). Therefore, one of the main gaps in these studies is the lack of complete tracking of carcasses from the moment of death to bone burial. Documenting the moment of death (e.g., predation event) and tracking the processes leading to skeletonisation and burial present an opportunity to contribute to taphonomy and enrich our understanding of why certain bone elements are found, how they are dispersed in different habitats, what happens with those missing from bone patches, and who consumes what and when. This information is essential to assess how the living community is reflected in bone assemblages. This is an area in need of further research.

1.5. Methodological issues and gaps in African neotaphonomic research

The discussed research provides fundamental methodological approaches and key findings that serve as the foundation for understanding bone deposition and taphonomic processes in modern African landscapes. However, methodological challenges persist concerning the correspondence of osteological assemblages to the living communities from which they derive. Standardisation of collection and recording methods would allow for broader comparative studies. Additionally, advanced technology could be applied to expand research coverage across various African environments and conditions, including day versus night and dry versus wet seasons, starting from the onset of a killing event (predation or natural death) until complete carcass skeletonisation and burial.

Understanding the representation of the living in the bone assemblages also necessitates considering bone scattering, dispersal patterns, weathering, and other factors affecting bone modification. To fill these gaps, we make some recommendations: i) to investigate the influence

of ecological variables on carcass distribution and bone deposition; ii) to assess the potential application of advanced technologies (e.g., camera traps, GPS trackers, and drones) to more fully capture neotaphonomic processes; and iii) to expand osteological surveys in complex habitats like those inferred for early hominins in Africa.

The application of advanced technology to address these gaps in neotaphonomy will allow for data collection with higher precision and broader coverage of larger areas and capturing detailed variables that would have been impossible to record a few decades ago. For instance, carcass encounters and monitoring can be aided and improved by using GPS collars deployed on carnivores (for biodiversity monitoring). This would be analogous to Blumenschine's method of returning to the locations where carnivores had been seen on a previous day (Blumenschine 1986b). The GPS locations of carnivores throughout the day can be used to check for carcass presence early in the morning, increasing the chance of finding fresh kills and the success of carcass monitoring.

Camera traps, now a commonly available technology, may also significantly contribute to our understanding of bone patch formation and the animals involved in that process by recording all the activities around the carcasses until complete bone dispersal or burial. For example, research by Wadley (2020) has successfully used camera trapping combined with archaeological techniques to monitor all stages of a greater kudu's (*Tragelaphus strepsiceros*) carcass consumption and burial (Wadley 2020). This shows how camera traps can record activities that would be difficult to observe across different habitats and seasons due to limitations of time, access, number of observers, and observer capabilities (e.g., recording activities on the carcasses during the evenings or on different carcasses occurring in different places at the same time). Therefore, camera traps are key complementary tools that can capture interactions and activities in multiple places throughout the day and night, enhancing insights

into bone patch formation. Additionally, drones are becoming popular and useful tools for surveying and monitoring living animal communities (Bushaw, Ringelman, and Rohwer 2019), and they may also be useful for finding carcasses in open habitats and subsequent monitoring.

1.6. Target locations for future neotaphonomic studies in African ecosystem

Further opportunities for the documentation of osteological specimens across diverse landscapes are offered by Gorongosa NP, located at the southern end of the EARS (Tinley 1977). Gorongosa is characterised by diverse, complex, and dynamic landscapes in some ways analogous to those inhabited by early hominins during the Pliocene and early Pleistocene (Bobe and Behrensmeyer 2004; Bobe and Carvalho 2019). Gorongosa has been the focus of a highly successful wildlife restoration project following the devastating effects of the Mozambican Civil War of 1977-1992 (Muala 2016; Stalmans et al. 2019). The park has no livestock, and poaching has been reduced to less than 5% of what was recorded before the restoration project started (Stalmans et al. 2019). Additionally, Gorongosa offers a heterogeneous and dynamic ecosystem comprised of at least 15 different types of landscapes (Stalmans and Beilfuss 2008). From a pilot study by Mathe and Bobe (2018), we also know that there is a strong positive correlation between live and dead mammals ($r = 0.76$), but further research is needed to fully document neotaphonomic processes in the park.

Other possible locations in Africa are Maputo National Park also located in Mozambique, recently proclaimed as UNESCO area, and Okavango Delta, located in Botswana.

Maputo National Park, in the south of Mozambique may also offer an opportunity to study the preservation of the bone remains of species that do not occur in GNP, such as Giraffes and marine species in the shore. These preservation of bone remains in terrestrial and marine

species in the same national park would also be an important contribution to the understanding of the neotaphonomy under different conditions of diverse taxa.

The Okavango Delta, with its vast size and ecological diversity, contributes significantly to the study of osteological preservation because its unique hydrological gradients and fluctuating flooding patterns create varied depositional environments that may directly affect bone deposition and preservation. Permanent swamps and waterlogged floodplains may often promote rapid burial of bone remains, offering an opportunity to study the neotaphonomy in other places in Africa in addition to GNP. The constant shifts in flooding cycles may also contribute to the understanding of how alternating wet and dry conditions influence the mineralization, decomposition, and bone deposition. Furthermore, since the Delta hosts a wide range of fauna, from large mammals to aquatic species, it may provide a natural laboratory for studying taphonomic processes across multiple taxa. Thus, the Okavango Delta's dynamic landscape would offer critical insights into how environmental factors shape the preservation, alteration, and eventual discovery of osteological remains.

1.7. Future research

Modern African ecosystems have been greatly modified from those that existed during our evolutionary past, and none can be said to serve as a perfect analogue of conditions in the Miocene, Pliocene, or Pleistocene. However, some African national parks and other conservation areas provide ecological and environmental elements that can help us understand different stages of our evolutionary history. Thus, Behrensmeyer's long-term work in Amboseli NP in Kenya (e.g., Western and Behrensmeyer 2009), Blumenschine's intensive study in the Serengeti and Ngorongoro ecosystems in Tanzania (Blumenschine 1986a, 1986b), and Tappen's data collection at Virunga NP in the DRC (Tappen 1992, 1995) have laid a foundation for

comparisons with archaeological faunas and further studies of neotaphonomy in open ground landscapes in Africa.

Hutson (2012, 2016) also built on previous research at Ngamo Pan in Hwange NP to provide a robust neotaphonomic baseline that could be used to assess Pleistocene zooarchaeological assemblages. And there is promising research in Ol Pejeta, Kenya, that will likely make an important contribution to neotaphonomy in Africa (Pobiner 2007; Pobiner and Kovarovic 2011). Similarly, Mathe & Bobe (2018) conducted a pilot study of bone distributions in Gorongosa NP, Mozambique, to expand the range of modern analogues explored for taphonomic data sets. These studies offer a baseline to help us understand the formation of palaeontological sites and interpret zooarchaeological remains.

However, these studies also have limitations that may be overcome with further research and new approaches. We make some suggestions: 1) Combining the survey approaches taken by Behrensmeyer and colleagues with those by Blumenschine would capture more comprehensive information about events occurring from the moment of death (e.g., a predation event) to the skeletonisation, dispersal, and burial or destruction of osteological remains; 2) Establishing systematic methods of data collection would enhance comparability across sites and ecosystems; and 3) Using radio and GPS collars deployed on carnivores would facilitate the finding of fresh carcasses and monitoring them after predation events. Further assessments of species known to occur in a landscape but absent from osteological samples are also needed. In this regard, the use of camera traps may lead to the identification of species often missed by faunal surveys (e.g., nocturnal species). Empirical observations of ecological processes in modern landscapes can help answer the question of why some species are common in bone assemblages while others are rare or absent. Table S 1-1 offers a summary of key gaps in

neotaphonomic research in Africa and suggests possible research avenues to move the field forward.

Table 1-1. Summary of key gaps and solutions to be implemented by combining multi-methods approaches and novel field techniques.

Gap	Research avenue
Limited understanding of processes between carcass abandonment and skeletonisation.	Adopt multi-method approaches by integrating (Western & Behrensmeyer, 2009) and (Blumenschine, 1986b) survey methods to capture data comprehensively. This will improve the record of the full process of carcass decomposition and help interpret missing skeleton elements in bone patches.
Inconsistencies in methodological approaches hinder the comparability of data, particularly when studying the representation of living communities in bone assemblages.	Ensure that methodological approaches are standardized, and data can be compared across sites/studies. This will enhance the accuracy in interpreting bone patches formation in relation to the living communities.
Limited use of modern technology in neotaphonomy studies.	Incorporate technologies such as GPS collars for carnivores, camera traps, and drones to enhance precision in data collection. For instance, GPS collars can aid in carcass monitoring, and camera traps to survey areas around carcasses provide information on bone dispersal, while also offering a view of nocturnal activities.
Insufficient studies on the impact of ecological variables on carcass distribution.	Conduct comprehensive studies across mosaic habitats, considering variables like canopy cover, roads, habitat, carnivore distribution, NDVI, soil type, water boundaries, tree lines, and seasonality. Analyse the influence of anthropogenic features on carcass distribution to enhance the predictive accuracy of bone deposition.

1.8. Supplementary materials

Table S 1-1. Research studies conducted in open-ground landscapes in eastern and southern Africa

Study site	Ecosystem	Research goal	Country	Latitude	Longitude	Key references
Namib Desert Research Station	Namib Desert	Hottentot food remains and interpretations of fossil bone assemblages	Namibia	-24.7512	15.2725	Brain (1967, 1969, 1980)
Amboseli National Park	Amboseli ecosystem	Live-dead-fidelity and bone weathering stage	Kenya	-2.6484	37.2613	Behrensmeyer (1978, 1993) Behrensmeyer et al. (2003) Behrensmeyer et al. (1979) Western and Behrensmeyer (2009) Cutler et al.(1999)17/10/2025 11:41:00
Serengeti National Park	Serengeti ecosystem	Implications of carcass availability for hominin scavenging opportunities	Tanzania	-2.3328	34.8336	Blumenschine (1986b)
Ngorongoro Conservation Area	Ngorongoro crater	Carcass availability and early hominid scavenging opportunities	Tanzania	-3.1602	35.5877	Blumenschine (1986a)
Parc National des Virunga	Western Rift	Savanna ecology and natural bone deposition: Implications for early hominin site formation	DR Congo	-0.9842	29.4546	Tappen (1992, 1995)
Masai Mara National Reserve	Masai Mara	Testing meat-eating in early hominins	Kenya	-1.4061	35.1426	Domínguez-Rodrigo (1997)
Kibale National Park	Kibale forest	Taphonomy of colobus bones partially digested by chimpanzees in the Kibale Forest	Uganda	0.4851	30.3965	Tappen & Wrangham (2000)

Serengeti National Park	Serengeti ecosystem	Serengeti micromammals and their implications for Olduvai and Laetoli palaeoenvironments	Tanzania	-2.3328	34.8336	Reed (2011; 2005, 2007)
Kibale National Park	Kibale forest	Taphonomic analysis of skeletal remains from chimpanzee hunts	Uganda	0.4851	30.3965	Pobiner et al. (2007)
Ngamo Pan	Hwange National Park	Neotaphonomic measures of carnivore serial predation for interpreting open-air faunal assemblages	Zimbabwe	-19.1241	26.5926	Hutson (2012, 2016)
Tarangire National Park	Tarangire National Park	Ecological and taphonomy of carcass consumption by lions and relevance for human evolution	Tanzania	-3.9830	36.1465	Gidna et al. (2014)
Gorongosa National Park	Gorongosa ecosystem	Diversity, relative abundance and distribution of mammal bones across Gorongosa habitats	Mozambique	-18.9752	34.3553	Mathe and Bobe (2018)
Ghanzi District	Kalahari Desert	Barn owl assemblages as indicators of local environmental conditions	Botswana	-21.6349	21.8183	Linchamps et al. (2021)
Ngamiland Delta	Okavango Delta	Barn owl assemblages as indicators of local environmental conditions	Botswana	-19.9836	23.4167	Linchamps et al. (2021)
Ol Pejeta Conservancy	Ol Pejeta Conservancy	Bones of Ol Pejeta: Clues to the Past	Kenya	0.0462	36.9329	Pobiner and Kovarovic (2011)

Chapter Two. The Bones of Gorongosa: Establishing Live-Dead Fidelity in a Complex African Ecosystem

Modern African animal bone assemblages can reveal ecosystem structures and may reflect species interactions and population dynamics. Gaining a detailed understanding of how well current bone assemblages capture existing ecosystem properties can enhance our ability to reconstruct palaeoecology from fossilised bone assemblages. This is particularly pertinent for studying the evolution of fauna in ancient landscapes, for which most of our current understanding is derived from fragmentary fossil assemblages. Studying bone composition and distribution in diverse contemporary landscapes provides insights into factors influencing fossil density and distribution in palaeontological and archaeological sites. Here, we present a novel approach to assess how the living community is reflected in the dead assemblages (i.e., live-dead fidelity), by combining data obtained by three independent techniques/methods commonly used to carry out faunal censuses (i.e., camera trap; aerial surveys, walking transects). The study was conducted in the highly heterogeneous Rift Valley ecosystem of Gorongosa National Park, Mozambique, where we investigated how well modern bone assemblages mirrored the living mammal community recorded in four-biennial aerial surveys and camera traps across five different landscapes. Systematic surveys of bones were conducted across 38 transects (2 km) in 2017, 23 transects (5 km) in 2019, and 96 plots (100 m^2) in 2021 and 2022. Counts and rank order bone data were compared with the living mammal species' diversity, composition, and abundance, recorded by four aerial biennial counts and from a 300 km^2 grid of 60 camera traps. We found that species diversity in the dead community reflects that of living mammals across the five landscapes; the three survey methods have a high level of similarity and complementarity in documenting vertebrate species composition; the dead mammal community reflects the living mammal community as shown in rank order data. The species captured by

camera traps were more closely captured by osteological survey than by aerial surveys. The rank order of species identified from bones explained live-dead fidelity better than species counts. The taxonomic relative abundances of the living community based on aerial counts closely reflected those derived from the bone assemblages. However, almost half of the species recorded by camera traps were not recorded in bone assemblages and aerial surveys, suggesting that the use of a single survey method is insufficient to capture the abundance and richness of living mammals. These findings imply that relying on only one survey method (e.g., bone *or* aerial surveys) leads to an incomplete or biased understanding of mammalian diversity and abundance.

2.1. Introduction

Palaeoecological reconstructions of mammal evolutionary history depend on the information retained in fossil collections about the original living communities (Lyman 2017; Western and Behrensmeyer 2009) . If fossil assemblages closely mirror the original ancient communities, then the reconstruction of palaeocommunities from fossil assemblages are accurate. This improves our understanding of those ancient ecosystems and our own evolutionary context (Behrensmeyer and Miller 2012; Western and Behrensmeyer 2009).

Documenting diversity, distribution, and relative abundance of species is a primary target in palaeoecological reconstructions. Variables such as habitat preferences, rates and locations of death, movements, and rates of preservation of organic remains are key aspects to consider when we are trying to do palaeoecological reconstructions as well as understanding the environments in which hominin evolution occurred (Tappen 1995). Bones and teeth are the hardest and best-preserved tissues of vertebrate species and have been relied upon to understand various evolutionary contexts, such as where and under which circumstances early hominin scavenging occurred (Blumenschine 1986b; Blumenschine et al. 1987). For example, bones have provided insights into new perspectives on vertebrate palaeoecology from recent

assemblages (Behrensmeyer et al. 1979) and shed light on early hominin site formation, hunting, and scavenging behaviours (Tappen 1995). Bones and teeth constitute most specimens of archaeological and palaeontological sites and serve as a bridge between the present and the past. Moreover, studying bones can improve our understanding of the transition processes from the biosphere (living) to the lithosphere (Behrensmeyer et al. 2000; Behrensmeyer and Miller 2012), which in turn can enable the identification of potential biases associated with preserved specimens.

The factors that control the deposition and distribution of bones in modern sedimentary landscapes are crucial for understanding these same factors in fossil specimens. Studies like those conducted by Behrensmeyer (1979) at Amboseli National Park (ANP) with modern landscape bone assemblages are essential for better understanding the distribution and significance of fossil records of eastern Africa. Some researchers have established the relationship between the living and dead mammal communities (live-dead fidelity) and generally argued that the modern bone assemblages reflect the living communities (Behrensmeyer & Miller, 2012; Western & Behrensmeyer, 2009). However, past studies generally lacked and have not incorporated various methods of documenting the living fauna (e.g., via the use of camera traps). Most studies have also typically been limited to homogeneous habitats such as savannas and plains in VNP, and swamps, woodlands, bushes and hills in ANP (Tappen 1995; Western and Behrensmeyer 2009).

To try to fill some of the past gaps, our study adopted a novel approach in the field of neo-taphonomy, which included the comparisons of various methods commonly used in present faunal census. This included carrying out transect walks to record bones, alongside of obtaining live communities' data from aerial surveys and a camera trap grid established in the study area. We tested if 1) the species abundance calculated from both absolute counting and rank order data of the living mammal community is reflected in that of the dead community, 2) the rank

order estimates accurately the living community from the dead, and 3) species composition and diversity indices in the living community are reflected in that of the dead community. Furthermore, we test the similarity of the vertebrate species captured by the three survey methods. We predicted that (i) species richness, Shannon and Simpson diversity indexes in the dead reflect that of the living across five landscapes; (ii) the three survey methods have a high level of similarity in documenting vertebrate species composition; (iii) the relative abundance of the dead reflects that of the living mammal community; (v) this reflection is more accurate when using rank order data transformation than when using absolute count data; and (v) osteological survey complement aerial and camera traps in documenting the mammal species in GNP, and the species documented by osteological surveys accurately represent those captured by camera trap than aerial survey.

2.2. Methodology

2.2.1. Area of Study

Gorongosa National Park (GNP) is in central Mozambique, at the southern end of the Africa's Great Rift System (Figure 2-1, latitude: -18.82 and longitude: 34.50) with an area of ~3,674 km^2. Located between the Pùngué and Zambezi rivers, GNP is characterized by a mosaic of landscapes and currently sustains a thriving population of vertebrates. With its mosaic habitats and an extensive karstic system, GNP has been proposed to be an especially valuable analogue for studying the environments in which Pliocene and Pleistocene African mammals, including early hominins, evolved (Bobe et al. 2023; Bobe, Martínez, and Carvalho 2020; Bobe and Carvalho 2019; Hammond et al. 2025).

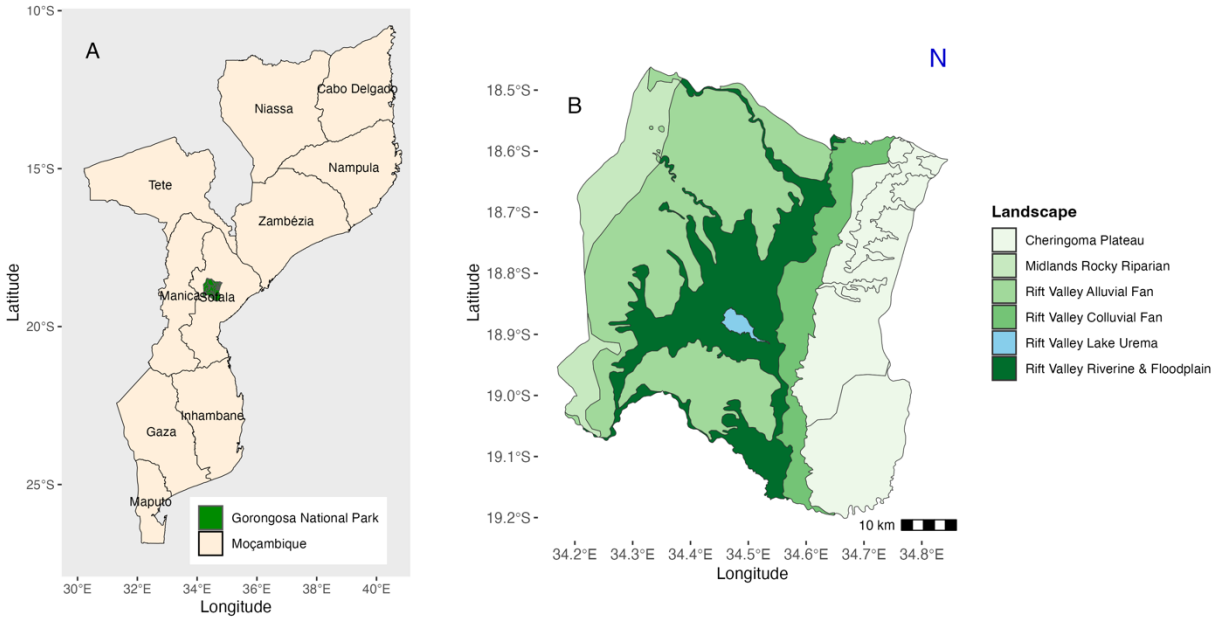


Figure 2-1. The location and lanscapes of GNP. (A) shows the location of GNP in the centre of Mozambique, and (B) shows the six landscapes found in GNP, with the bone surveys being conducted in five (excluding the Rifty Valley Lake Urema).

GNP is bounded by the Gorongosa Mountain to the west and the Cheringoma Plateau to the east. The climate is predominantly tropical, with annual rainfall of 700-900 mm on the Rift Valley floor but reaching over 2000 mm in Mount Gorongosa (Müller et al. 2012, McWethy et al. 2016). During the rainy season nearly 40% of the park experiences flooding (Tinley 1977).

GNP has been extensively mapped and classified into different landscapes based on vegetation, topography, and hydrology (Stalmans and Beilfuss 2008). These landscapes are: Rift Valley Riverine and Floodplain, Rift Valley Colluvial Fan, Midlands Rocky Riparian, Rift Valley Alluvial Fan, Rift Valley Lake Urema and Cheringoma Plateau (Figure 2-1).

Gorongosa Wildlife

Before the Mozambican Civil War (1977-1992), GNP was a refuge for various medium and large mammal (>5Kg) species, including buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), impala (*Aepyceros melampus*), and hippopotamus (*Hippopotamus amphibius*), primarily concentrated in the area of the Rift Valley floor in the floodplain region (Muala 2016; Tinley 1977). Other herbivores, namely, the kudu (*Tragelaphus strepsiceros)*, nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus scriptus*), sable antelope (*Hippotragus niger*), Lichtenstein's hartebeest (*Alcelaphus buselaphus*), common reedbuck (*Redunca arundinum*), oribi (*Ourebia ourebi*), warthog (*Phacochoerus africanus*), roan antelope (*Hippotragus equinus*), tsessebe (*Damaliscus lunatus*), and both species of rhinos (*Ceratotherium simum* and *Diceros bicornis*) were present but less abundant in 1960 (Stalmans et al. 2019). GNP also supported top predators such as crocodiles (*Crocodylus niloticus*), lions (*Panthera leo*), leopards (*Panthera pardus)*, hyenas (*Crocuta crocuta*), wild dogs (*Lycaon pictus*), and jackals (*Canis aureus*) (Stalmans et al. 2019) (Table S 2-1).

During the Mozambican Civil War, GNP was severely affected by massive animal culling to feed soldiers and by ivory trading for weapons, driving many species to near extinction: by some estimates only 5% of the fauna was left (Huntley 2023; Stalmans et al. 2019). The park's recovery only began in 2008 when a US-based non-profit organisation initiated the Gorongosa Restoration Project, signing a 20-year co-management agreement with the Mozambican government (Bouley et al. 2018; Pringle 2017). The project focused on conservation, science, education, and human development and was extended in 2018 for another 25 years (Stalmans et al. 2019).

GNP is known as one of the most biodiverse places on Earth (Wilson and Naskrecki 2014). By 2024, about 8,000 wildlife species had been documented, including 991 vertebrates

(177 mammals, 95 reptiles, 55 amphibians, 82 fishes, and 582 birds) (Gorongosa Biodiversity Database).

2.2.2. Data collection

Aerial Survey

The Park's wildlife has been regularly monitored since 1969, with biennial aerial counts conducted to assess mammal species populations. In the most recent biennial aerial survey, conducted in 2024, over 107,765 large mammals were counted across 60% of GNP's total area (see Table S 2-1). The last four biennial counts (2016, 2018, 2020 and 2022 used in this chapter) were conducted via helicopter by flying systematically over parallel strips 500 m wide. These flights covered 197,000 hectares (49.9% of GNP) - known as the 'central core count block'. The helicopters were flown at speeds of 96 km/h at an altitude of 50-55 m, allowing the observers to count animals within 250 m wide strips (Figure 2-2). The counts also covered the western, eastern, and northern sides of the central core count block, which added a further 22,500 hectares and increased the total coverage to ~ 60% of the area of the park (Stalmans and Peel 2020, 2022) (see Table S 2-1).

These surveys offer key information to assess the ongoing recovery of the Park's modern communities and associated dynamics across landscapes (Stalmans and Peel 2016, 2020, 2022, 2024; Stalmans, Peel, and Gonçalves 2018). The last four biennial surveys' data highlighted growing and declining species populations (see Table S 2-1), suggesting that predation and competition play significant roles in shaping these dynamics. In conjunction with other surveys, this biennial survey assesses the ecosystem's overall health and evaluates the impact of the effort applied to biodiversity conservation (Stalmans et al. 2019).

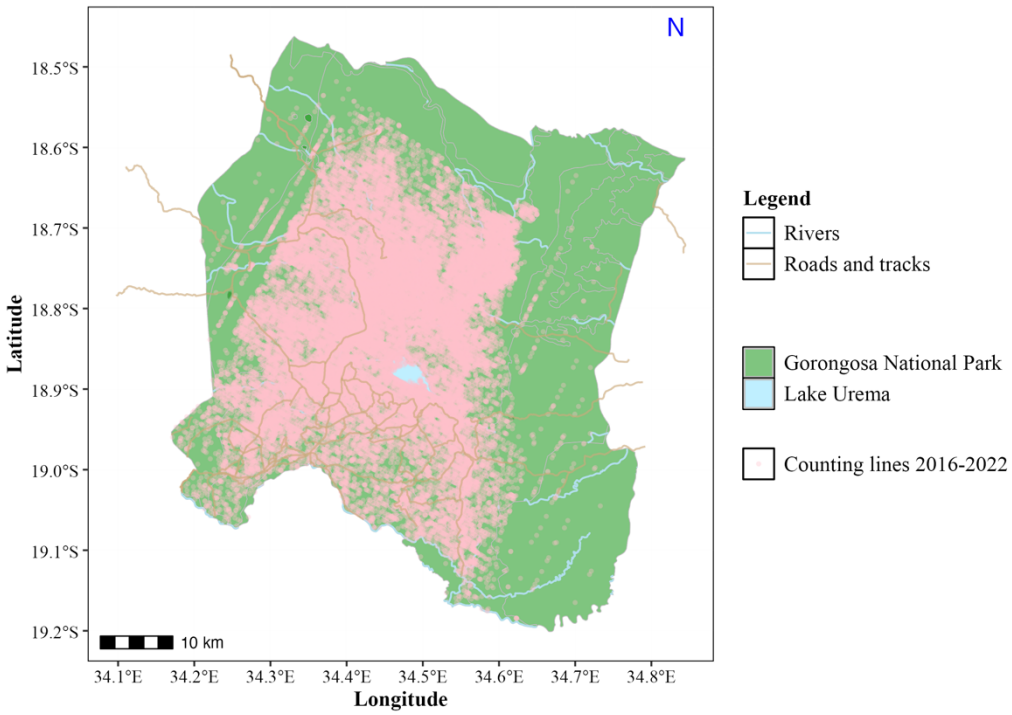


Figure 2-2. Count lines covered by the four-year aerial wildlife surveys in Gorongosa National Park.

Camera traps

Data has been collected between 2016 and 2019 from a camera trap grid implemented in 2016 by Gaynor et al. (2021). The grid consists, on average, of 52 camera traps (60 in 2016, 57 in 2017, 46 in 2018 and 2019) across a 300 km^2 woodland and floodplain areas. Its primary aim was to assess spatio-temporal mammal activity patterns within GNP (see Figure 2-3). The selection of this specific area was based on its high mammal density and accessibility through the Park's Road network. The camera trap grid configuration adhered to the recommended sampling effort for studies on species occupancy and richness, as outlined by Kays et al. (2020).

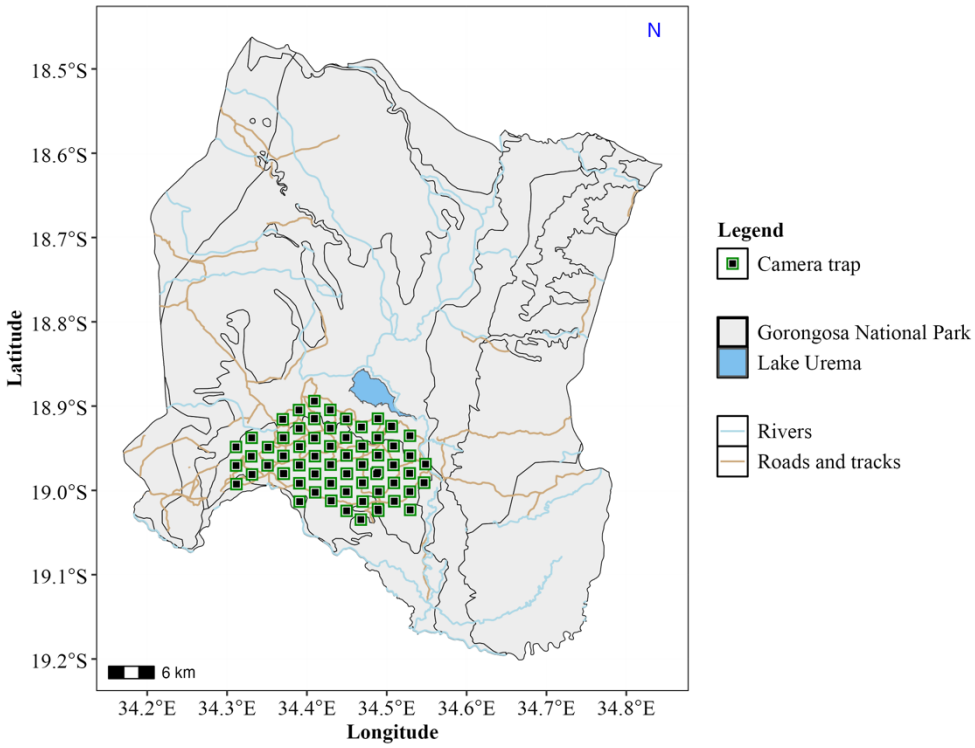


Figure 2-3. Camera trap grid set-up by the long-term research project led by Kaitlyn Gaynor (e.g., Gaynor et al. 2021). The grid originally had 60 camera traps covering 300 km^2.

Each camera trap was spaced approximately 2.4 km from its six nearest neighbours (Swanson et al. 2015), was affixed to a suitable tree within 100 m of the centre point and was positioned at a height of 1 m from the ground, angled slightly downward. In cases where a suitable tree was not within 100 m, cameras were placed on the nearest tree, within a 275 m radius. To optimise animal detections and reduce false triggers, cameras were directed towards open areas or small game trails exhibiting signs of recent animal activity. While each camera was located within 2 km of a road, none were positioned directly alongside or facing roads. Only five cameras were within 100 m of a road (Gaynor et al. 2021).

The cameras were programmed to capture two photographs per trigger event (a specific action that activates the camera to take a photograph or start recording video), with a 30-second interval between triggers. For data analysis, records of the same species captured within a 15-minute of each other at the same site were consolidated into a single detection. Animal

identification to the species level was carried out for each photograph at the trigger event level, and a record of detections was generated using the *camtrapR* package in R (Niedballa et al. 2016). Volunteers and Kaitlyn Gaynor classified images on WildCam Gorongosa (https://wildcamgorongosa.org/) between 2016 and 2018, and an online citizen science platform hosted by the Zooniverse (https://zooniverse.org/) between 2018 and 2019.

Osteological surveys

Bone collection was conducted using three different methods: walking transects, plots, and opportunistically. Transects surveys were conducted in 2017 and 2019, and plots were surveyed in 2021 and 2022. Bones were documented and collected opportunistically from 2016 to 2022. Henceforth, for the purpose of this study, the osteological survey data or bone assemblages refer to the combination of data collected through transects and plots. Data from opportunistic surveys were combined with data from transects and plots (used as osteological surveys) to analyse species composition. The aim was to assess the complementarity and redundancy of three survey methods—osteological surveys, camera traps, and aerial surveys—in documenting species presence. In other words, the analysis sought to determine whether the same species are recorded across all three methods or whether each method detects different species, and how the species recorded by one method compare to those recorded by the others.

Opportunistic sampling: this sample is a result of bones documented by various researchers conducting different projects in the park who came across bones or bone patches and then provided this information to members of our team. These specimens served to expand the osteological reference collection housed in the Palaeontology Laboratory in Chitengo, the park headquarters.

Walking transects line sampling: In 2017, we walked 38 line transects of 2 km in length each and 100-200 m in width. In 2019, we walked 23 line transects of 5 km each and

100-200 m in width. The total number of transects varied with accessibility to different parts of the park. A pilot study using the 2017 data revealed that osteological surveys are feasible in five primary landscapes (Stalmans and Beilfuss 2008), osteological surveys are feasible in only five: 1- Rift Valley Alluvial Fan, 2- Rift Valley Riverine & Floodplain, 3- Rift Valley Colluvial Fan, 4- Midlands Rocky Riparian, and 5- Cheringoma Plateau (Mathe and Bobe 2018). Two to three individuals assisted JM in each transect walk during the pilot study (Figure 2-4).

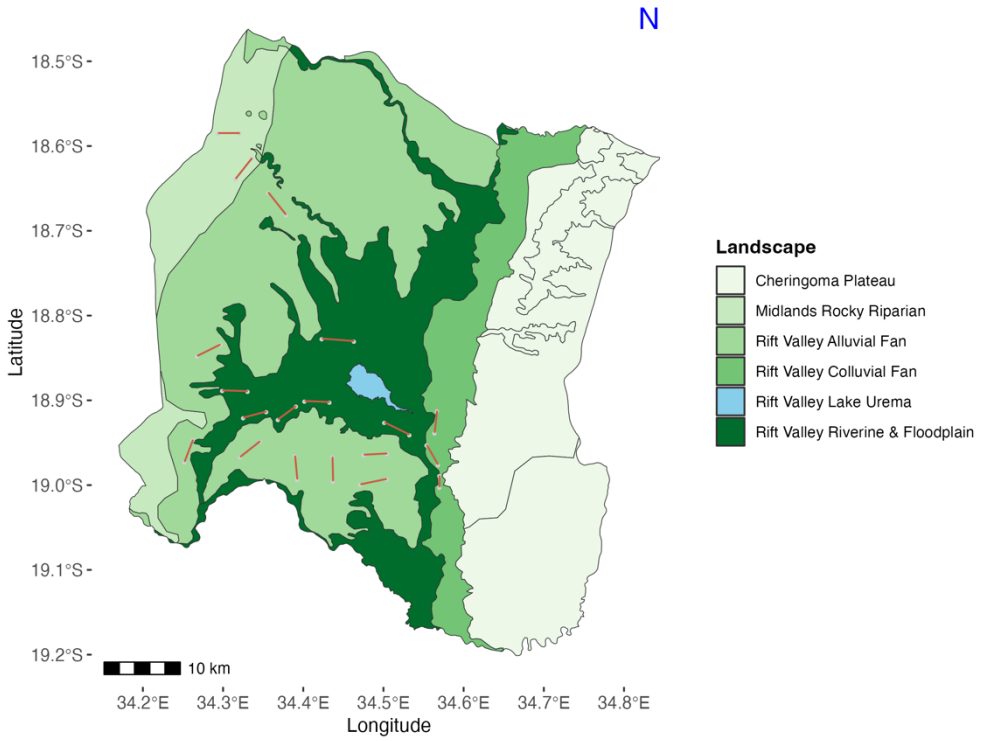


Figure 2-4. Representation of transects distributed across the primary landscapes of GNP during the 2017 and 2019 surveys. The white dots and coral lines indicate the transects in which the data were collected.

Plot sampling: in 2021, we conducted osteological surveys in 96 structured plots, distributed across six grids with 16 plots each. Two grids were established in each of three landscapes (1- Rift Valley Alluvial Fan, 2- Rift Valley Riverine & Floodplain, 3- Rift Valley Colluvial Fan). Each grid had an area of 16 km^2 and the distance from plot to another was one km and the area of each plot was 10000 m^2 (100 x100 m) (Figure 2-5).

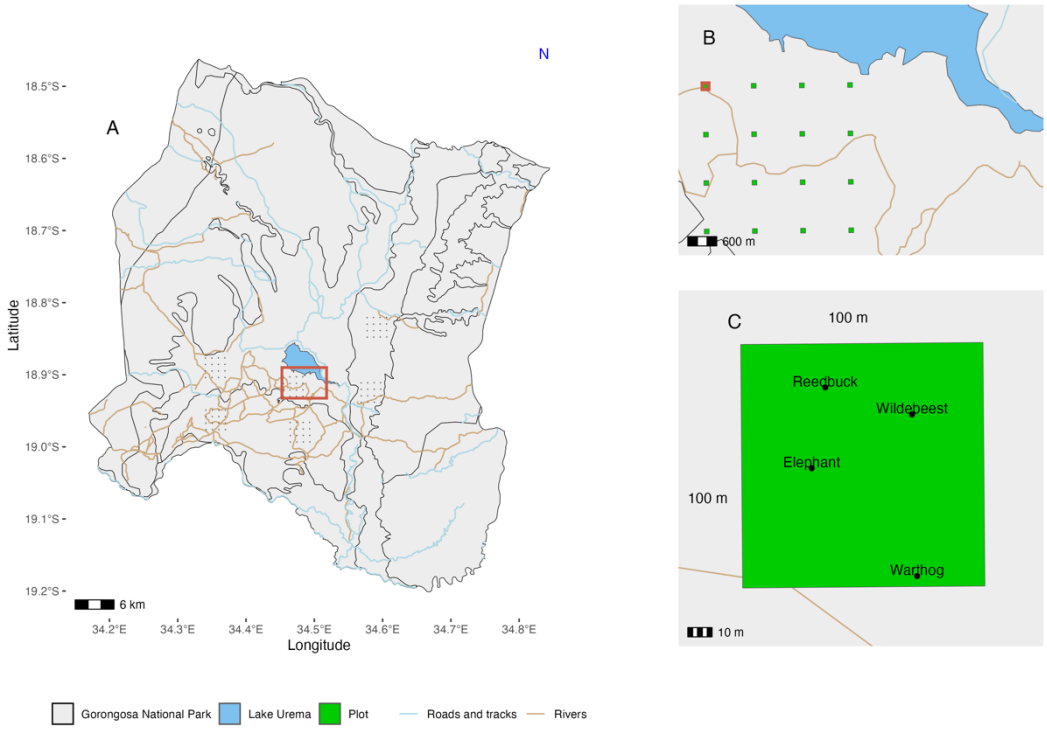


Figure 2-5. The plots used in the osteological survey. (A) Representation of the plot and grid distribution in GNP, (B) distribution of plots within the grids, and (C) the dimensions of the plots used for the osteological survey across different landscapes of GNP.

Surveying plots in addition to the transect lines had the aim to expand on the original sampling technique and adapt the osteological surveys to Gorongosa's irregular, dense and difficult terrain in terms of accessibility.

The bone collection in the plots started either from left to right or from south to north, with two observers going in one direction and another one going in the opposite direction. Each one-hectare area (10,000 m^2) was done in three rounds, with each round covering one-third of the area. All bones were documented until the entire plot area was covered. To ensure data consistency, the three observers were assigned separate tasks. One was responsible for taking GPS coordinates and photographs of the documented specimens. The second counted the specimens found, patch diameter, sex, and age whenever possible for better assessing the Minimum Number of Individuals (MNI). The third observer recorded information digitally

using the ODK Collect application (Anokwa et al. 2009; Bokonda, Ouazzani-Touhami, and Souissi 2019). Classifications such as the weathering stage were made by the same observer to avoid bias, applying methods developed by Behrensmeyer (1978).

2.2.3. Collected variables

Each bone was documented regarding intrinsic and extrinsic variables. Intrinsic variables are species, skeletal element, degree of fragmentation, age categories (neonate, juvenile, adult, and old adult), weathering stage (0-5), and sex (if applicable for sexually dimorphic species or fresh carcasses). These variables were collected to improve the assessment of minimum number of elements (MNE), minimum number of species, minimum number of individuals (MNI), and patch diameter (Behrensmeyer 1993; Tappen 1995). Extrinsic are those related to the surrounding environment and encompassed GPS coordinates and type of the landscape.

All long bone fragments were placed into five main categories for detailed analysis: proximal epiphyses (PE), proximal near epiphyses (NPNE), shaft or diaphysis (S), distal near epiphyses (DNE), and distal epiphyses (DE). This systematic categorisation (Braun, Pante, and Archer 2016), facilitates a comprehensive examination of bone fragments, ensuring accurate MNI documentation and a more nuanced assessment of each piece's anatomical location, progressing from proximal to distal regions.

2.2.4. Bone identification

JM conducted taxonomic identification for all documented skeletal remains, with the help of an osteological reference collection assembled by the Paleo-Primate Project Gorongosa, spanning 2016 to 2020, which served as foundational resources for accurate taxonomic assignments. These curated collections developed collaboratively, and encompass diverse skeletal elements, contributing to a comprehensive understanding of taxonomic diversity.

Furthermore, to enhance the precision of taxonomic classification, external resources such as field guides and the online platform ArchéoZoothéque (accessible here) were consulted.

2.2.5. Data analysis

The data were analysed using species similarity and diversity including species richness and composition**,** and generalised linear models (GLMs). From the aerial survey data, only species with absolute numbers were considered in the live-dead fidelity analysis and species diversity index. This meant that, for example, the number of troops of baboons and the number of birds' nests were excluded in live-dead fidelity analyses and were instead considered in species composition and richness comparison.

Species richness and diversity

We calculated the Shannon and Simpson indices - which consider evenness and the number of species (species richness) (Broms, Hooten, and Fitzpatrick 2015; Faith et al. 2020; Gaynor et al. 2021) of the dead and the living communities for each of the five landscapes. The indices of the dead were compared with the living communities to evaluate whether these indices from the living community could be estimated from the dead community.

Species composition and similarity

We calculated the species similarity using the Jaccard Index coefficient from the *vegan* package (Oksanen et al. 2013) to evaluate how much the three sampling methods (osteological surveys, camera traps, and aerial counts) capture similar species. Lastly, we represented the degree of overlap, redundancy, and complementarity among these methods in a Venn diagram using *VennDiagram* package (Yan 2023). This representation aimed to determine whether these methods capture identical or distinct, but complementary, species.

Generalised linear models (GLMs)

We used GLMs to perform six models (Figure S 2-1). In the first, we evaluated (i) whether the absolute abundance of the dead community accurately reflects that of the living from the aerial survey; (ii) for model two, the same was evaluated but using rank order data instead of absolute abundance; (iii) in model three, whether the absolute abundance of the dead community accurately reflects the RAI (relative abundance index) (Jenks et al. 2011) calculated from the number of detections and operating camera trap operating time to estimate the living community; (iv) for model four, the same but using rank order data instead of absolute abundance and RAI; (v) for model five, whether the RAI accurately reflects the absolute abundance of the living community from the aerial survey; and (vi) for model six, same but using rank order data of both variables. Rank order data transformation is a hierarchical classification system used to organise the species in order based on absolute abundance. It was used to make the abundance estimation resemble those applied in palaeocommunity reconstructions. We only used osteological data from transacts and plots for the dead community, excluding opportunistic bone collection data due to concerns regarding the study's reproducibility and repeatability.

To perform GLMs (Venables and Ripley 2002), we initially filtered species recorded in osteological surveys that were also documented in the aerial survey. A Poisson distribution was used with a log-link function in models one, two, four, and six. The data of these five models followed the Poisson distribution and thus we use this function to perform the GLM and create a regression equation. The data used in model five contains positive values that varied from 0 and 2 following the gamma distribution therefore we performed a GLM Gamma distribution (glmGamma) (Venables and Ripley 2002).

Model comparison

The six models (Figure S 2-1) were compared regarding their performance and fitness using the Akaike Information Criterion (AIC), Leave-One-Out Cross-Validation (LOOCV) from *boot* package (Canty and Ripley 2021) and goodness-of-fit test (R Core Team 2024), which uses cumulative distribution function (CDF) of the Chi-square distribution. Additionally, we compared the models based on residuals' distribution in scatterplots.

Coefficients (estimates, coefficients of correlation and determination, and residuals) from the final models were exponentiated (Robinson, Hayes, and Couch 2023) and interpreted to determine the direction and strength of relationships between living and dead communities in first four models and between living from camera trap and aerial survey in models five and six.

2.2.6. Statistical software

All statistical analyses were performed in R (v.4.3.3) (R. C. Team, 2024) and RStudio (v. 2023.09.1+494) 64 for MacOS (Posit Team 2024). The spatial data analyses and visualisation were conducted utilising Quantum Geographical Information System (v. 3.32.2) (Moyroud and Portet 2018) and R (v. 4.3.2) (Henry and Wickham 2022; Kassambara 2023; Neuwirth 2022; Pebesma and Bivand 2023).

2.3. Results

2.3.1. Species richness and diversity indices of the dead and living community across GNP landscapes

The five landscapes surveyed through the three osteological survey sampling methods show differences in species abundance. Rift Valley Riverine & Floodplain (RVRF) has the highest abundance with waterbuck and warthog as dominant species, and the lowest is Midland Rocky Riparian (MRR) mostly occupied by waterbucks. Waterbuck is the dominant species in almost all landscapes except in the Cheringoma plateau, where its abundance is relatively equal to that of baboon and warthog (Figure 2-6).

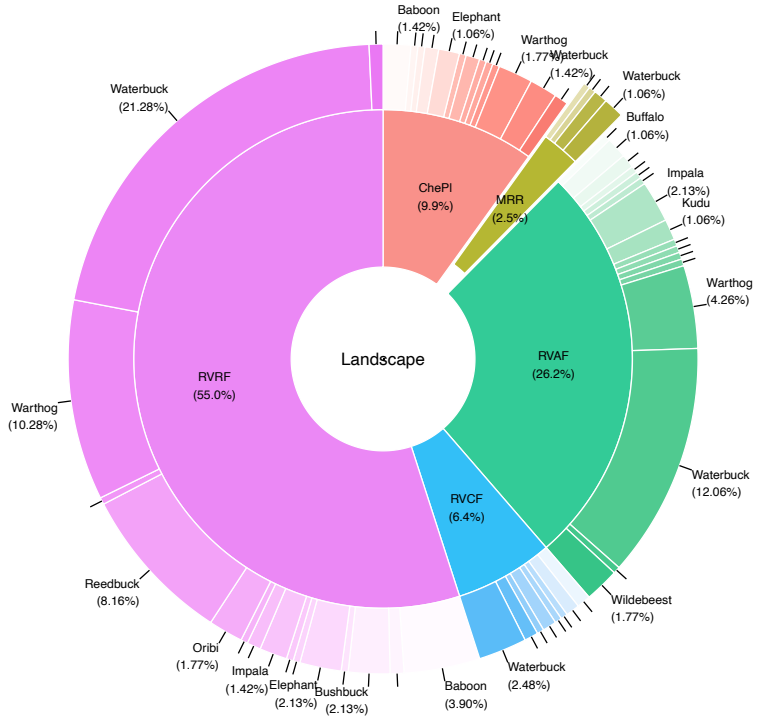


Figure 2-6. Relative abundance of the dead community per Gorongosa landscape. ChePl - Cheringoma Plateau, RVAF - Rift Valley Alluvial Fan; RVRF - Rift Valley Riverine & Floodplain; RVCF - Rift Valley Colluvial Fan; MRR - Midlands Rocky Riparian.

We documented 25 vertebrate species from five landscapes, among which 14 were medium- and large-sized mammals also recorded by the aerial counts and camera traps (Figure 2-7).

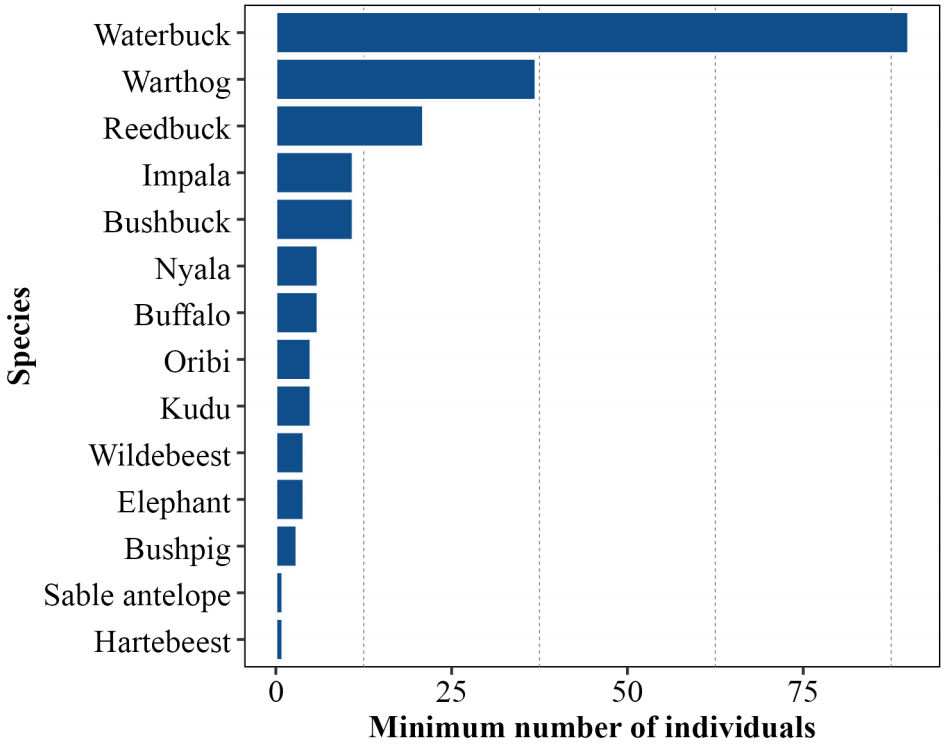


Figure 2-7. Minimum number of individuals recorded per species in the systematic osteological surveys (plots and transects) which overlap with aerial surveys and camera traps.

Relative abundance species richness

The relative abundance of species in the living community based on aerial surveys is relatively lower than in bone assemblages across the three landscapes of GNP (Cheringoma Plateau, Midlands Rocky Riparian, and Rift Valley Colluvial Fan; Figure 2-8a). Exceptions are observed in the Rift Valley Alluvial Fan and Rift Valley Riverine and Floodplain, where the living community show lower relative abundance than in bone assemblages (Figure 2-8a).

Regarding species richness, all five GNP landscapes exhibit a higher number of species in the living community than in the bone assemblages (Figure 2-8b, see also Table S 2-2).

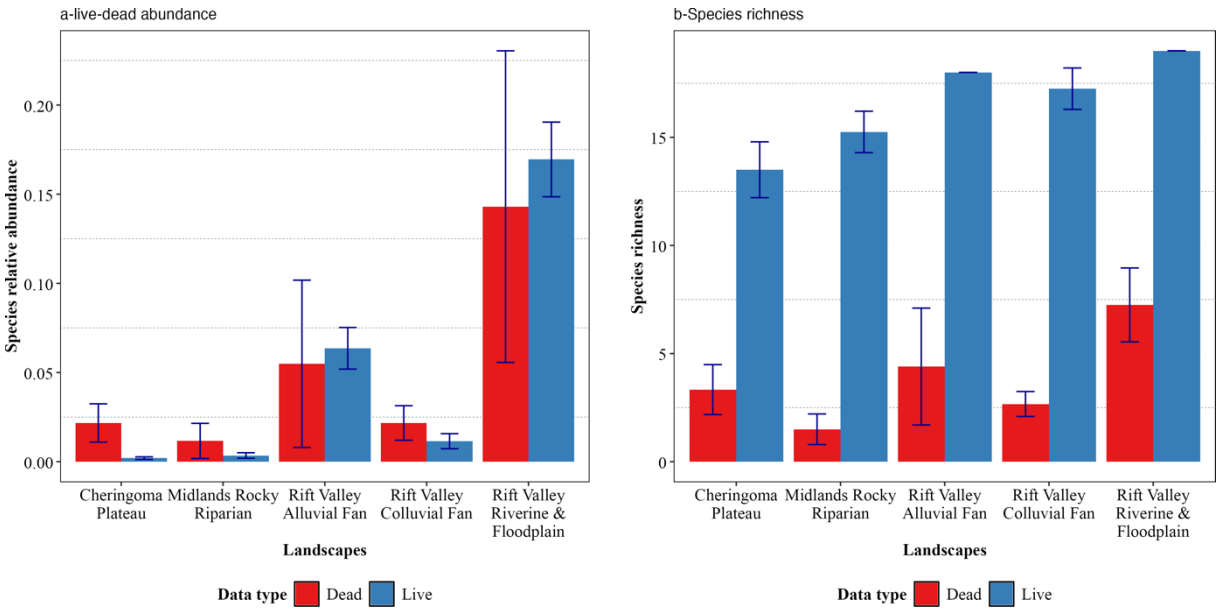


Figure 2-8. Relative abundance and species richness across five GNP landscapes, (a) the species abundance in the living (from aerial counts, n = 14 species, 89,862 individuals) and dead communities (n = 14 species, 205 individuals). (b) the species richness in the living (from aerial counts, n = 25 species) and dead communities (n = 30) (Table S 2-2).

Species diversity indices

In all five GNP landscapes, both Shannon and Simpson indices indicate higher diversity in the living community than in the dead. Both diversity indices are relatively higher in the living community than in bone assemblages across four GNP landscapes (Figure 2-9a for Shannon and Figure 2-9b for Simpson). Figure 2-9 also shows that landscapes with higher diversity values in the living community also indices higher in the dead community, the same pattern in the low values.

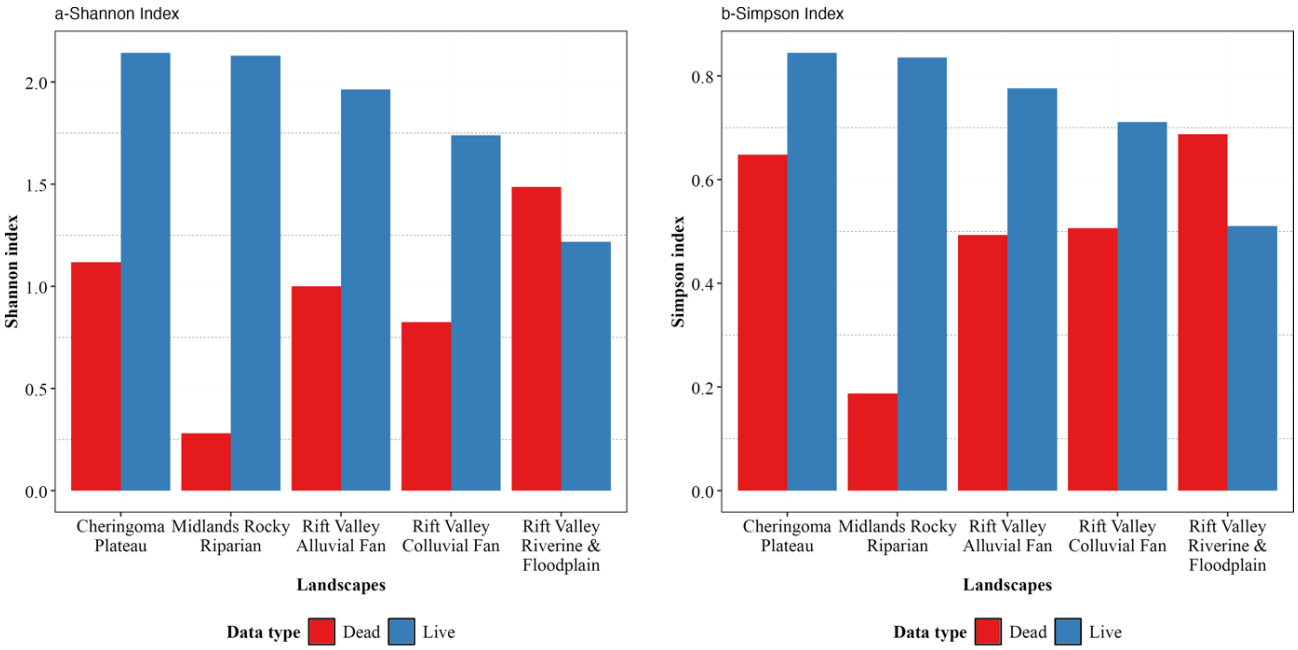


Figure 2-9. Figure a and Figure b showing the Shannon and Simpson diversity indices across five GNP landscapes in the dead (n = 25 species) and living communities (n = 30 species).

2.3.2. Species similarity of the three survey methods for documenting vertebrate species composition in GNP

The Jaccard Index for the vertebrate species compositions of the osteological survey and camera trap was 0.618, indicating that more than 60% of the species were common to both methods. The index was 0.672 for the species composition of the camera trap and aerial survey of almost, and the index of similarity between osteological and aerial surveys is 0.514. These indices reveal a higher similarity between camera traps and aerial surveys than osteological surveys.

The Venn diagram (Figure 2-10) shows that the three types of datasets (bone assemblages, living communities from aerial counts, and camera traps are complementary. For instance, bone assemblages captured about three species that none of the other two methods captured. Similarly, aerial counts also documented nine species not observed in either bone

assemblages or camera traps. Camera traps are the methods that documented more species (about 27 species) not recorded by bone assemblages and aerial counts (Figure 2-10).

However, there are many complementarities between aerial counts and bone assemblages because we have higher overlaps (18 species) and low uniqueness.

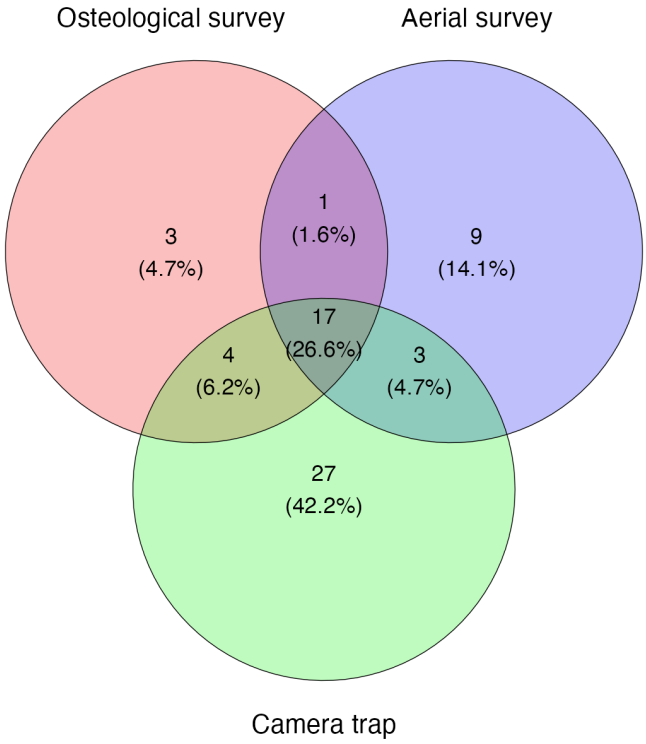


Figure 2-10. Venn diagram illustrating the species overlap and unique compositions captured by three distinct methods: osteological surveys, aerial surveys, and camera traps. Each circle represents the species found using the survey method, while the overlapping regions represent the number of shared species between methods. The numbers and percentages represent the species that overlap among the methods and those that are unique for each method. For more details, see Table S 2-2.

2.3.3. Representation of vertebrate communities in bone assemblages and camera trap data

Models one and two

Model one predicts the number of living mammals recorded by aerial surveys based on the number of dead, and model two predicts the rank order of the same outcome variable based on the rank order of the same predictor variable (number of living and dead mammals). The intercept indicates that when no carcass is recorded the living mammals in aerial surveys are

expected to be approximately 1699.45, and this number is expected to increase by one unit as an additional carcass is recorded (Table S 2-3). With rank order data (model two), for each additional carcass recorded, the number of living vertebrates only increased approximately by 1.13, but the intercept is low, and the confidence of the interval is narrower (Table S 2-3).

The coefficients of model one (1.04) and model two (1.19) were both statistically significant ($p < 0.05$) (Table S 2-3), suggesting a meaningful association between the dead and the living communities (r =0.85).

Models three and four

The prediction of the living community recorded by camera traps from the dead resulted in models three and four. Model three suggests that for each additional carcass recorded in the proportion of bone surveys, we expect the RAI of living mammals calculated from the camera trap data to increase approximately by 2.65 (Table S 2-3). With rank order data (model four), for each additional carcass, the number of living mammals increase approximately by 1.09 (Table S 2-3).

The predictor of model four (rank data) was found to be statistically significant ($p < 0.05$), while the predictor of model three was not (Table S 2-3). This means that the ranked proportions of the dead are meaningfully associated with the corresponding ranked data of the living community.

Models five and six

Model five predicts that for each additional unity in RAI, we expect the number of living mammals in aerial surveys to increase approximately by 2.92 (Table S 2-3). With rank order data (Model six), for each additional individual recorded in camera traps, the number of living vertebrates increased approximately by only 1.07 (Table S 2-3); this means that an increase of

mammals in camera traps is followed by the same increase in the mammal recorded in aerial survey.

2.3.4. Model comparison

Absolute abundance or RAI vs rank order

Generally, all absolute counting- and RAI-based models have wider confidence intervals than those based on rank order data. Similarly, AIC, LOOV errors and Goodness of the fit test indicate that models based on rank order data are the best-fit ones showing Low values in these best-fit measures (Table S 2-4) Among the rank order-based models considering the significance level of 0.05 for goodness of the fit test, models two and four are the best-fit models.

According to the distribution of the residuals in Figure S 2-4, all absolute counting-based models are not good-fitted models (Figure S 2-4a), while rank order-based ones are all best-fitted models with residuals normally distributed and exhibiting homoscedasticity (Figure S 2-4a). The scatterplot of residual distribution in absolute counting-based models suggests that the model assumptions are not met (Figure S 2-4a). In contrast, in rank order-based models, the model assumptions are all met (Figure S 2-4b).

2.4. Discussion

The relative abundance and diversity indices across the three landscapes reveal higher proportions of living communities than dead assemblages in the Cheringoma Plateau, Midlands Rocky Riparian and Rift Valley Colluvial Fan. The exception is the Rift Valley Alluvial Fan and Rift Valley Riverine and Floodplain (RVF), where the abundance is higher in bone assemblages than in the living. However, considering the standard deviation of these two landscapes, there is an indication that the abundance is proportionally equivalent between the two conditions (living and dead). This may be attributed to the methodological approaches employed, as both aerial and osteological surveys extensively documented the highest numbers of fauna. This equivalence could be related to two factors. First, visibility, a constraint in aerial counts, is overcome in this modern landscape because they are open, particularly the RVF where we have the highest number of dead mammals (Stalmans and Beilfuss 2008). Another is that these two landscape types are mostly accessible by road, which facilitates osteological surveys.

The results of the Shannon and Simpson diversity indicate that the landscapes with low values in the living community also show low values in the dead, except for the Midlands Rocky Riparian and Rift Valley Riverine and Floodplain, which present low values in the living and high values in the dead, respectively. The high values of both indices in bone assemblages in Rift Valley Riverine and Floodplain may be associated to higher ground visibility and accessibility by road for osteological survey. Moreover, this may also be explained by animal preferences for these habitats as they have main water bodies (rivers, Lake Urema and pans) nearby, enhancing higher animal congregation and species diversity. Whereas the low values in the Midlands Rocky Riparian may be attributed to vegetation coverage as this landscape is quite impenetrable on foot. Since most fossil sites are in low-energy aquatic or lacustrine environments, these findings may imply that open-ground landscapes with low-energy water conditions are favourable for bone preservation and fossilisation.

In this regard, these findings support our prediction that species richness and relative abundance, Shannon and Simpson diversity indexes of the dead community reflect that of the living across five landscapes (Rift Valley Alluvial Fan, Rift Valley Riverine & Floodplain, Rift Valley Colluvial Fan, Midlands Rocky Riparian, and Cheringoma Plateau).

The similarity index revealed that, in terms of species composition, camera traps are more like aerial surveys than to osteological surveys. This does not support our prediction where we expected higher similarity between osteological survey and camera traps as both approaches document species composition at the small-scale level meaning that both capture species in small areas with higher precision when compared with aerial surveys. On the contrary, the Venn diagram demonstrated that osteological surveys record species more like those recorded by camera traps than the ones documented by aerial surveys. This supports our prediction as we considered that with aerial surveys it would be difficult to cover some of the species detected by camera traps. For instance, species like bushpig and bushbuck could be unseen in aerial surveys and highly detected by camera traps and have higher chances of having their remains documented in osteological surveys. The similarity index between osteological surveys vs camera traps and camera traps vs aerial surveys, only shows about 5% (0.672-0.618) of difference, which means that may still consider the higher similarity (0.618) between camera traps and osteological surveys. Similarly, the Venn diagram does not show a considerable difference concerning species overlapping between osteological survey and camera trap when compared with camera traps and aerial survey.

Venn diagram and Jaccard indices show that the three survey methods are complementary; for instance, osteological surveys accurately recorded 25 species but not the full richness of the ecosystem, as this method missed 39 species, of which 9 were recorded by solely aerial counts and 27 by solely camera traps and 3 by both. Osteological surveys only captured 3 species that other methods failed to record. Despite camera traps' limitations, such

as recording only what is in their range, they captured 51 species corresponding to 80% of 64 species captured by all methods together, from which 42% are unique to camera traps. However, there is much complementarity among the three methods.

There are some significant overlaps among the three methods (27%), which reveal that from one method, we may cover about 27% of what others also cover. The considerable difference between camera trap and osteological surveys may be related to species size, turnover and sampling effort. However, despite the camera traps' limitations, such as being an open system with limited coverage, to estimate Relative Abundance Indices (RAIs), they can still be reasonably accurate and precise in inferring the relative abundance of fauna that can be compared to data from osteological surveys (Tanwar, Sadhu, and Jhala 2021). The explanation of the species differences among the three discussed methods here is given after reporting the differences among the tests used in the analyses.

Regarding the six performed GLMs, model two, which uses ranked data of the dead and living community, demonstrated the best fit. This model exhibited the lowest AIC value, a significant goodness-of-fit coefficient, and lower errors in Leave One Out Cross Validation (LOOCV) analyses (Vehtari et al. 2023). Although there are slight differences in AIC values among the models, model two stands out being the most fitted one. Models based on absolute counting data are not the best fitted ones due to higher AIC values, higher LOOCV errors, and did not fit the data well ($p < 0.05$). Among the rank order-based models, models four and six displayed low AIC values and low errors; however, they did not fit the data adequately. These discrepancies are associated with the type of data and limitations related to sampling effort, habitats, species detectability per survey method, ground visibility, ecological factors, assumptions made during GLM analysis, and potential preservation rates as discussed below. The best-fit model supports our predictions that the dead mammal community reflects the living mammal community more accurately when using rank order data transformation compared to

absolute numbers (untransformed data). Additionally, it supports the statement that osteological surveys more accurately document species captured by camera traps than by aerial surveys.

Some of the limitations that could explain the differences in the species documented by camera traps and osteological surveys are the height of the camera trap (Jacobs & Ausband, 2018; Meek et al., 2016) and species activity (Wearn & Glover-Kapfer, 2017). Species such as the African rock python, identified through osteological surveys, are not detected by camera trap. At night, camera traps use infrared sensors which only work for endotherm species. More active species have higher chances of being captured by camera traps (Palmer et al., 2018), while less active species may escape detection as they may pass by the camera trap's sensor less frequently compared to more active species. This aligns with the species' home range, especially for larger species, which naturally have larger home ranges. Their detectability via camera traps increases significantly as they tend to cover longer distances in open areas, enhancing the likelihood of being recorded (Wearn & Glover-Kapfer, 2017). Additionally, the differences in species richness and composition between camera trap and osteological surveys may be attributed to the shape, length, and size of bones, as well as the palatability of surrounding soft tissues on bones (Pickering & Carlson, 2002), which constitute opportunities for scavengers regardless of bone abundance (Faith et al., 2007). In other words, it indicates the amount of soft tissues available for scavengers to feed on. Some species have fragile bones that a predator would consume entirely or leave small remains that are less likely to be recorded by on-foot osteological surveys (Bildstein 2006). The species' longevity at certain extent may also influence the chance of finding remains in bone assemblages. Species living longer, such as an elephant, may be detected multiple times by camera traps, but not present in osteological surveys, particularly when these species are highly active. Similarly, sampling effort is required in osteological surveys to capture an equivalent number of species captured by camera traps. For instance, in just a week, we may find triple or more than that of what would be captured by

osteological surveys in a year (Silveira et al., 2003). However, animal detection is better for non-migratory species inhabiting open landscapes (Palmer et al., 2018).

The behaviour of predators like leopards and wild dogs might help explain why we observe fewer species in our surveys than those recorded in camera traps. For instance, leopards often hoist their prey into trees, creating bone accumulations beneath them (Tappen, 1995), whilst wild dogs, particularly females, may transport prey to dens for their young, thus removing bones from the examined landscape (Hutson, 2016). Yet, in Gorongosa, with only two documented leopards - one recently introduced and the other only detected once by camera traps - this behaviour likely does not skew our osteological sample. Similarly, the recent arrival of wild dogs suggests that carcass transport to dens hasn't had a major effect on our surveys. If it had, we would expect species detection numbers to have remained steady prior to their introduction.

Animal size does not explain the scarcity of carnivores like lions, leopards, and jackals in our records, as these are significantly larger than species like oribi found in our osteological surveys. This discrepancy is linked to conservation measures. Parts of these carnivores, such as skins, claws, and teeth, are sought after in the ivory trade. Consequently, for conservation reasons, these remains are intentionally incinerated by the conservation department if they are found in the field, leading to their scarcity in our bone assemblages (De Moçambique, 2017).

Considering all these discrepancies and limitations, taphonomy should shift towards probabilistic approaches instead of being regarded as an exact science where outcomes are always predictable. In reality, there is so much variation that needs to be considered when interpreting results from ours or other neotaphonomy studies. For example, take the case of species like elephants, which have vast home ranges (Palmer et al., 2018). Depending on the population size, the likelihood of an individual dying within the coverage area of our sampling methods - whether using plots or transects to record remains - is low. Similarly, for lions

estimated to be around 200 in an area of 3,674 km^2 in GNP, the density is approximately 5 lions per 100 km^2. The likelihood of one dying and having their remains recorded in the vicinity of our plots or transects is low. This small number is even more pronounced for solitary species.

Regarding the reflection of the living community in bone assemblages, Western and Behrensmeyer (2009) found a strong correlation between life and death in Kenya. In this study, we found similar results (particularly in model two), though the correlation coefficient is stronger than that found in Western and Behrensmeyer (2009)'s study. Similar findings were also revealed regarding the representation of the species according to their biomass, where the larger and mid-sized vertebrates had higher representativeness in bone assemblages compared to the small ones. Despite Amboseli National Park being geologically and ecologically different from Gorongosa National Park, we also observed similar higher live-dead fidelity.

The findings of this research align with Western and Behrensmeyer's (2009) results, with a highly significant correlation between relative species abundance in living and dead censuses. However, species richness and evenness from osteological surveys do not necessarily correlate with those from camera traps, as almost half of the species recorded by the three analysed methods are detected solely by camera traps. Even when comparing aerial and osteological surveys, the diversity indices calculated from these methods fail to accurately represent the living communities. Estimating the diversity index and evenness solely from osteological surveys would result in missing more than half of the recorded species. This may be related to methodological limitations discussed previously, particularly the sampling effort and the assumptions we make when comparing these data. Where we record a certain species is not necessarily where we are more likely to find its remains after death, and not all remains are recordable depending on the species' behaviour, ecological conditions, and predators (Behrensmeyer, 1993). The findings imply that much of what we know from the fossil record may only represent a fraction of what inhabited ancient ecosystems.

We also reported that a very large proportion of species detected by camera traps are not recorded in other methods (aerial and osteological surveys). These differences may be related to the sampling effort, which is higher in camera traps as they record data every day, including in the evenings. This is supported by the fact that many of the species recorded by camera traps but not in other methods are small-sized and nocturnal (e.g., mongooses, civets, and genets). Contrary to aerial counts, which involve helicopters flying above 50 m from the ground to count fauna (Stalmans & Peel, 2022), resulting in low visibility for recording many small-sized species, camera traps can record all the species in their operating range. Osteological surveys are also limited by less visibility, as some recorded landscapes had dense vegetation, leading to poor visibility (Blumenschine, 1986; Mathe & Bobe, 2018; Tappen, 1992). Additionally, sampling effort and the size of the species limit osteological surveys. For instance, these surveys were conducted once a year, and the skeletons of many small-sized species may be completely consumed by predators and scavengers, contributing to absence from bone assemblages.

According to Tappen (1995), six dominant species in bone patches vary across various zones, reflecting their abundance in the living community of Virunga National Park (VNP). Despite GNP being geologically and ecologically different from VNP, we also found that species abundance in bone assemblages reflects the abundance of the living community across the five surveyed GNP landscapes. These similarities suggest that different African parks may contribute to understand the ancient landscapes where our ancestors evolved.

After the intensive osteological survey, we also observed that the landscapes of GNP are similar to VNP in terms of the scarcity of animals with low population densities in the sample. Apart from baboons, other primates are absent, including vervets, Samango monkeys, and two species of galago (nocturnal primates), found in the living community. Even for baboons, we only have recorded about 16 carcasses, a number not correspondent to the living population as from the 220 troops counted via an aerial survey, we may estimate about 17,600

individuals, considering a rough troop mean of 85 individuals. According to Tappen and Wrangham (2000)'s findings in recognising "Hominoid-Modified Bones", we also observed the complete absence of carnivores, such as leopards, in our dataset. This absence and lower representation could be linked to hyena activities. However, up until the end of 2022, there were no hyenas in the park, indicating that they had not played a role in removing bones from the landscape. The underrepresentation of baboons and other primates in bone assemblages could be linked to various ecological factors, including predation, behaviour, proximity to water boundaries, roads, camping sites other features. These factors might favour the accumulation of bones from certain species while potentially hindering the preservation of non-human primate remains. This may be further investigated by evaluating how ecological variables influence non-human primate bone assemblage vs. other species in different GNP landscapes (See Chapter Four).

The research findings indicate that the fossil record from various locations in Africa, particularly those ecologically and geologically similar to Gorongosa, might exhibit omissions of certain taxa. This omission is particularly notable among species characterised by fragile skeletal structures, solitary behaviour, and low population densities like eland in GNP. However, most fossil assemblages were recorded from excavations where remains are most densely concentrated. Some of these may represent long-term accumulation by biological agents such as scavengers like hyenas, as well as by physical processes like erosion. For instance, Behrensmeyer's surface "squares" method (Behrensmeyer and Hill 1980; Orton 2000) at East Turkana and Tappen's surface square under tree lines in VNP (Tappen 1995), demonstrate a significant time-averaged (Behrensmeyer et al. 1992; Behrensmeyer and Chapman 1993) record compared to the bone landscape assemblages observed in GNP.

The main findings of this research suggest that 1) despite the small sample size, modern bone assemblages are reliable for estimating the presence/relative frequencies of living

mammals; and that 2) osteological, camera traps and aerial surveys are useful and complementary methods for documenting and estimating mammals' diversity and abundance. The research's findings also imply that the extinct faunal taxa recorded in Pliocene and Pleistocene epochs from places like Koobi Fora (Maglio, 1971), Shungura, and Nachukui sites, which are geologically and ecologically similar to landscapes of Gorongosa National Park (Bobe et al., 2023; Habermann et al., 2018), are probably under-represented by more than 50% in the fossil record. However, the sampling effort of this study is not equivalent to the sampling effort of the excavations and archaeological surveys conducted in many of these palaeontological sites. Nevertheless, this is still worth considering, as most of the missing faunal taxa from bone landscape surveys of this study were recorded by camera traps. Most missing taxa are nocturnal and small to middle-sized mammal species, which may not have the same chances for fossilisation as the large and medium-sized vertebrates.

2.5. Further directions

Due to time constraints, osteological surveys in the GNP caves and at their entrances were not conducted. Therefore, we strongly recommend further research to focus on covering this geological setting in the parks for better accuracy and interpretation of the faunal fossil record found in the cave settings like those of South Africa.

Additionally, we recommend future studies with increased sample sizes to investigate how ecological factors such as predation, prey behaviour, roads, and water boundaries affect bone deposition and carcass occurrences in GNP's five primary landscapes. Further, expanding carcass monitoring using camera traps in diverse locations to document predator and scavenger activities around the clock is advised. This would contribute to a better understanding of bone dispersion and the representation of species in bone assemblages, particularly those less represented in the data of this study.

Lastly, we propose further research leveraging ecometrics derived from modern bone collections to assess their reliability in estimating landscape and habitat structures. This method seeks to refine the interpretation of fossil record proxies, thus deepening our grasp of palaeolandscape dynamics. In essence, we advocate for employing bone assemblages to reconstruct their originating landscapes using proxies, subsequently validating these reconstructions against the collection sites.

2.6. Conclusion

Despite the differences between the Jaccard index and Venn diagram, species richness, Shannon, and Simpson diversity indexes, the diversity in the dead community generally reflects that of the living across five landscapes of GNP. The three survey methods (aerial surveys, camera traps, and osteological surveys) show high similarity and complementarity in documenting vertebrate species composition. We also concluded that the relative abundance of the dead mammal community mirrors that of the living mammal community, with greater accuracy achieved using rank order data transformation rather than absolute numbers. Additionally, osteological surveys more accurately document species captured by camera traps compared to aerial surveys.

These findings suggest that bone assemblages are not only useful for estimating the relative abundances of species recorded by aerial counts and camera traps but also for highlighting some gaps in the palaeontological records, which include species that are rarely documented in the fossil record.

The findings also hold significant implications for both ecology and palaeontology. In ecology, these implications include the evaluation of conservation measures through temporal faunal monitoring in areas that are ecologically and geologically like GNP. Furthermore, the use of bone assemblages is suggested as a complementary method for estimating the relative abundance of living species. In palaeontology, the findings imply that the relative abundance of middle- to large-sized mammals derived from the fossil record accurately reflects the relative abundance of the ancient mammal community. This is particularly relevant for palaeontological sites such as Koobi Fora, Shungura, and Nachukui, where the fossil data can reliably indicate the rank order of the ancient fauna.

2.7. Supplementary materials

Table S 2-1. Number of animals counted in the last nine years (2016, 2018, 2020, 2022, 2024) in GNP.

Common name	2016	2018	2020	2022	2024	Species
Buffalo	696	1,021	1,221	1,465	1,958	*Syncerus caffer*
Bushbuck	2,062	1,787	1,719	1,777	1,676	*Tragelaphus scriptus*
Bushpig	115	203	231	381	274	*Potamochoerus larvatus*
Duiker grey	61	66	60	61	29	*Sylvicapra grimmia*
Duiker red	22	28	31	24	24	*Cephalophus natalensis*
Eland	118	142	71	139	136	*Taurotragus oryx*
Elephant	563	544	781	620	873	*Loxodonta africana*
Hartebeest	569	647	473	464	497	*Alcelaphus buselaphus*
Hippo	440	546	766	964	1,106	*Hippopotamus amphibius*
Impala	4,721	6,274	6,491	9,907	16,291	*Aepyceros melampus*
Kudu	1,491	2,105	2,023	2,711	2,721	*Tragelaphus strepsiceros*
Nyala	1,320	2,269	2,656	3,481	4,188	*Tragelaphus angasii*
Oribi	3,896	4,027	1,946	1,451	2,000	*Ourebia ourebi*
Reedbuck	10,609	10,821	5,838	4,752	4,019	*Redunca arundinum*
Sable antelope	863	968	553	464	331	*Hippotragus niger*
Warthog	5,400	11,274	8,509	5,685	4,663	*Phacochoerus africanus*
Waterbuck	45,280	57,016	52,313	63,561	65,332	*Kobus ellipsiprymnus*
Wildebeest	363	627	815	1,525	1,519	*Connochaetes taurinus*
Zebra	34	44	44	41	68	*Equus quagga*
Baboon*	19,125	18,615	19,210	19,635	19,465	*Papio ursinus*

*Number estimated based on the mean of troop size (Hammond et al. 2022; King 2024).

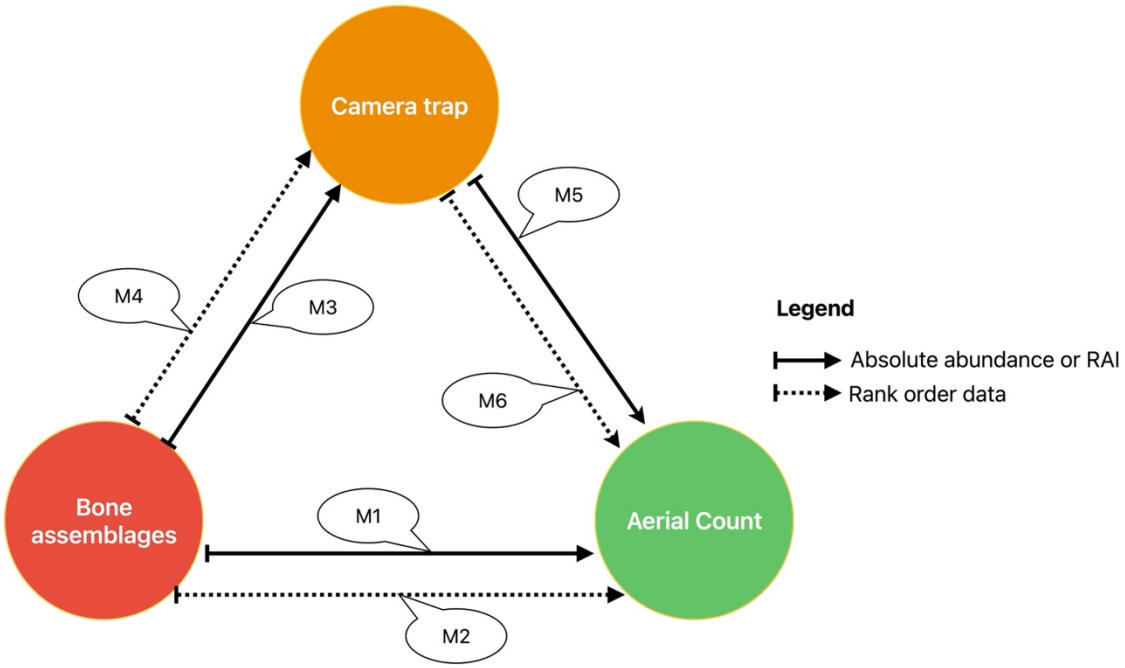


Figure S 2-1. Representation of the models applied for the analyses of relationship among the survey methods. Where, M1-model one, M2-Model two, M3-Model three, M4-Model four, M5-Model five, M6-Model six.

Table S 2-2. List the species recorded by each of the three survey methods.

Common name	Species	Aerial survey	Camera trap	Osteological survey
Aardvark	*Orycteropus afer*		X	
Baboon	*Papio ursinus*	X	X	X
Bat	*Chiroptera spp.*		X	
Bird of prey	*Accipitriformes* or *Falconiformes*		X	
Blue wildebeest	*Connochaetes taurinus*	X		
Buffalo	*Syncerus caffer*	X	X	X
Bushbaby	*Otolemur crassicaudatus*		X	
Bushbuck	*Tragelaphus scriptus*	X	X	X
Bushpig	*Potamochoerus larvatus*	X	X	X
Caracal	*Caracal caracal*		X	
Cat fish	*Clarias spp.*			X

Civet	*Civettictis civetta*		X	
Crane	*Balearica spp.* or *Grus spp.*		X	
Crocodile	*Crocodylus niloticus*	X		
Crowned Cranes	*Balearica regulorum*	X		
Duiker common	*Sylvicapra grimmia*		X	
Duiker grey	*Sylvicapra grimmia*	X		
Duiker red	*Cephalophus natalensis*	X	X	X
Eland	*Taurotragus oryx*	X	X	
Elephant	*Loxodonta africana*	X	X	X
Genet	*Genetta tigrina*		X	
Ground hornbill	*Bucorvus leadbeateri*	X	X	
Guinea fowl	*Numida meleagris*		X	
Guineafowl crested	*Guttera pucherani*		X	
Guineafowl helmeted	*Numida meleagris*		X	
Hare	*Lepus spp.*		X	
Hartebeest	*Alcelaphus buselaphus*	X	X	X
Hippo	*Hippopotamus amphibius*	X	X	X
Honey badger	*Mellivora capensis*		X	X
Hooded vulture	*Necrosyrtes monachus*	X		
Impala	*Aepyceros melampus*	X	X	X
Jackal	*Canis mesomelas* or *Canis adustus*		X	
Kudu	*Tragelaphus strepsiceros*	X	X	X
Lappet-faced	*Torgos tracheliotos*	X		
Leopard	*Panthera pardus*		X	
Lion	*Panthera leo*		X	X
Marabou stork	*Leptoptilos crumenifer*	X		
Mongoose banded	*Mungos mungo*		X	
Mongoose bushy tailed	*Bdeogale crassicauda*		X	
Mongoose dwarf	*Helogale parvula*		X	
Mongoose large grey	*Herpestes ichneumon*		X	

Mongoose marsh	*Atilax paludinosus*		X	
Mongoose slender	*Galerella sanguinea*		X	
Mongoose white tailed	*Ichneumia albicauda*		X	
Nyala	*Tragelaphus angasii*	X	X	X
Oribi	*Ourebia ourebi*	X	X	X
Pangolin	*Manis temminckii*		X	
Porcupine	*Hystrix africaeaustralis*		X	X
Reedbuck	*Redunca arundinum*	X	X	X
Rodent	*Rodentia spp.*		X	
Sable antelope	*Hippotragus niger*	X	X	X
Saddle-bill storks	*Ephippiorhynchus senegalensis*	X		
Samango monkey	*Cercopithecus mitis*	X	X	
Serval	*Leptailurus serval*		X	
Suni	*Nesotragus moschatus*		X	
Tortoise	*Testudinidae spp.*			X
Turtle	*Cheloniidae* or *Dermochelyidae*			X
Vervet monkey	*Chlorocebus pygerythrus*		X	
Warthog	*Phacochoerus africanus*	X	X	X
Waterbuck	*Kobus ellipsiprymnus*	X	X	X
White-headed vulture	*Trigonoceps occipitalis*	X		
Wild dog	*Lycaon pictus*		X	X
Wildebeest	*Connochaetes taurinus*	X	X	X
Zebra	*Equus quagga*	X		X

Table S 2-3. Outputs of Generalised Linear Models.

Model	term	estimate	std.error	statistic	p.value	conf.low	conf.high
Model1	(Intercept)	1699.45	0.01	1171.02	<0.05	1678.38	1720.7
Model1	dead	1.04	0	439.34	<0.05	1.04	1.04

Model2	(Intercept)	2.76	0.26	3.89	<0.05	1.61	4.49
Model2	dead_rank	1.13	0.03	4.58	<0.05	1.07	1.19
Model3	(Intercept)	0.22	0.42	-3.56	<0.05	0.09	0.6
Model3	dead_prop	886.98	3.57	1.9	0.08	0.97	2561187187
Model4	(Intercept)	3.73	0.22	6.02	<0.05	2.39	5.63
Model4	dead_prop_rank	1.09	0.02	4.49	<0.05	1.05	1.13
Model5	(Intercept)	2137.27	0.01	1335.2	<0.05	2113.3	2161.41
Model5	scale(RAI)	2.92	0	437.32	<0.05	2.9	2.93
Model6	(Intercept)	4.43	0.2	7.44	<0.05	2.95	6.46
Model6	RAI_rank	1.07	0.02	4.21	<0.05	1.04	1.11

Table S 2-4. Model comparison in terms of best fit.

Model	AIC	LOOCV min error	LOOCV max error	Goodness of fit test
Model 1	16932.63	1327326395.197	1429118969.522	0
Model 2	65.35	4.641	4.688	0.626
Model 3	86.2	119026.051	126961.095	0.077
Model 4	3.41	12.206	12.306	0.088
Model 5	28618.38	48359616.198	51002264.454	0
Model 6	102.05	16.068	16.15	0.005

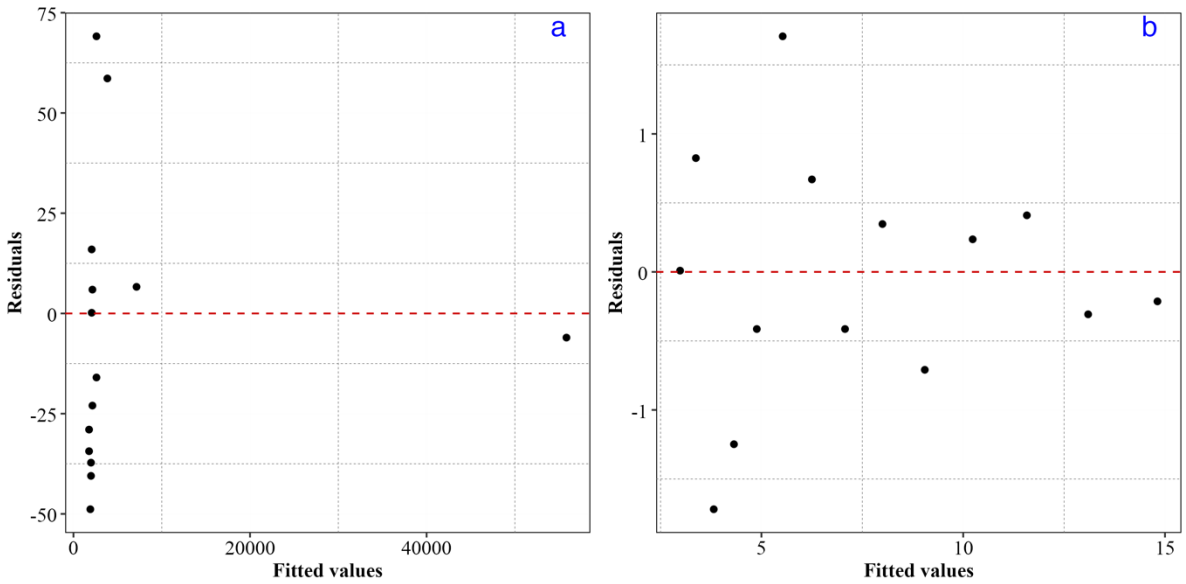


Figure S 2-2. Diagnostic Plot of Residuals vs. Fitted Values in the GLM: Assessing the model's performance by examining the relationship between residuals and predicted values of absolute abundance (a) and rank order (b) of the dead and living communities from aerial survey.

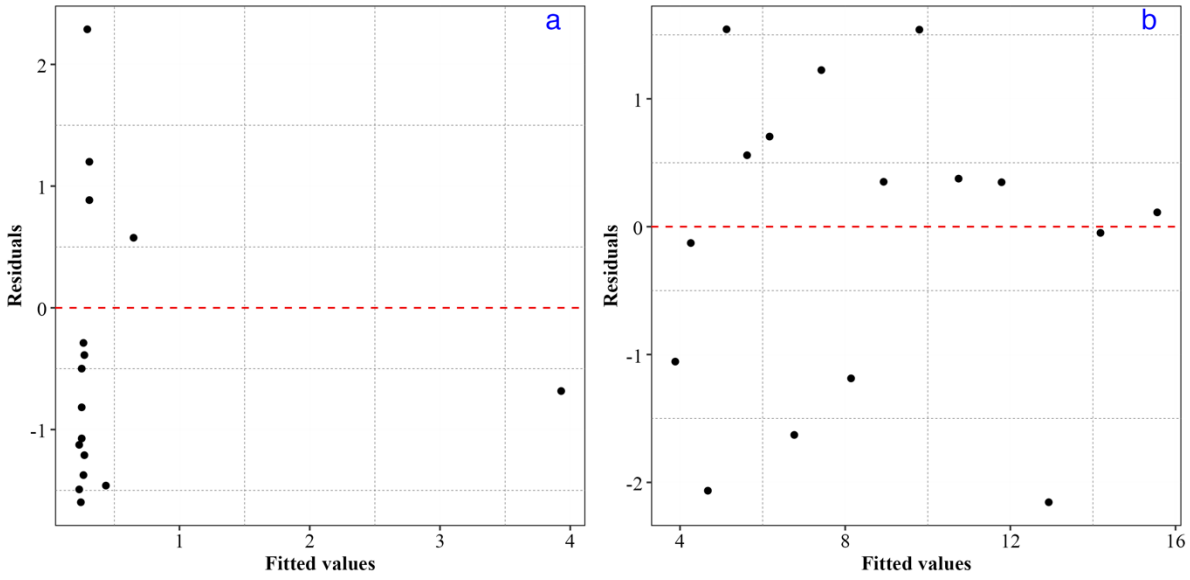


Figure S 2-3. Diagnostic Plot of Residuals vs. Fitted Values in the GLM: Assessing the model's performance by examining the relationship between residuals and predicted values of absolute abundance (a) and rank order (b) of the dead and living communities from camera traps.

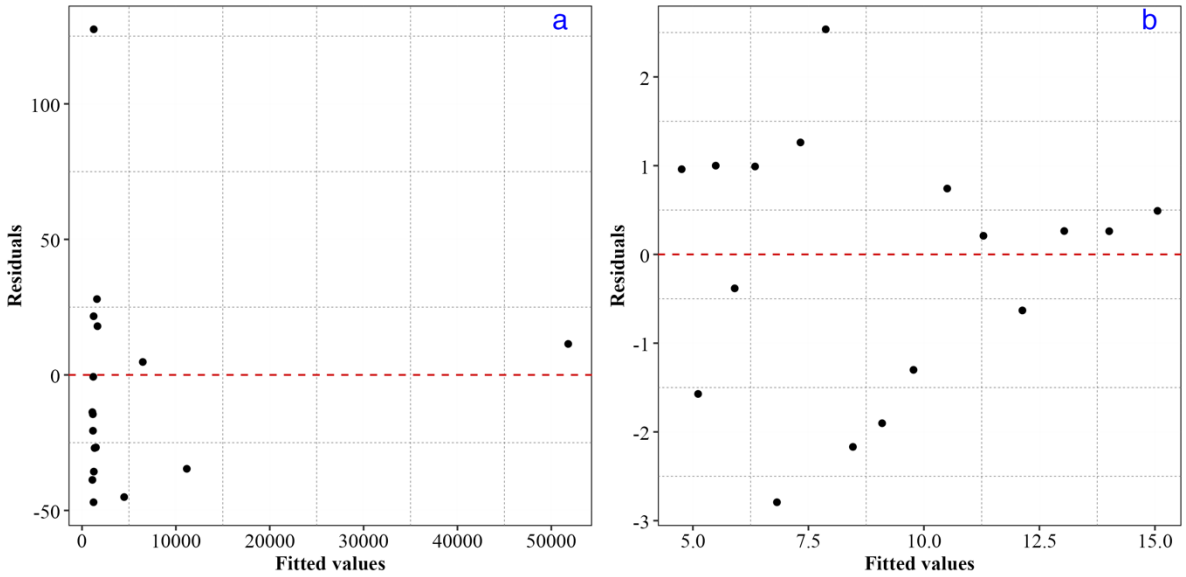


Figure S 2-4. Diagnostic Plot of Residuals vs. Fitted Values in the GLM: Assessing the model's performance by examining the relationship between residuals and predicted values of RAI calculated from camera trap data and absolute abundance of the living communities from aerial survey (a) and the rank order of the same data (b).

Chapter Three. Ecological Influences on Bone Deposition in the Rift Valley Landscapes of Gorongosa National Park, Mozambique

Palaeoecological reconstructions indicate that many Plio-Pleistocene African palaeontological and archaeological open-air sites are found in water-deposited sediments, which promoted sedimentation of bone remains and enhanced fossil site formation. This suggests that both permanent and ephemeral water bodies played a crucial role in fossil site formation. Studies using modern bone assemblages have revealed that bone deposition is also influenced by other factors such as tree distribution and suggested that various ecological variables, including water bodies and predator activity, are also drivers of differential bone deposition. Despite significant progress in understanding the role of water bodies and trees in bone deposition, the extent to which these factors predict bone abundance across diverse habitats remains unclear. In this research, we examined whether lakes, rivers, pans, roads and habitat types influenced the deposition of 2,313 bones from 270 carcasses of 19 species of mammals in Gorongosa National Park (GNP) in Mozambique. Negative Binomial Model outputs suggest that bone deposition is higher near roads and lower further away from these features. Conversely, bone deposition increases with greater distances from Lake Urema, the major lake in the park, and other water bodies like pans, and decreases closer to these water sources. Pans and roads significantly influence bone deposition only in woodlands, while roads in both habitats (grassland and woodland) with a stronger effect in woodlands ($p < 0.05$). Habitat type and distance to rivers show no significant effect ($p > 0.05$). These findings suggest that most faunal fossil assemblages found in the places ecologically and geologically similar to GNP were formed in the low energy water sources, rather than at the margins of these water sources.

3.1. Introduction

Palaeoecological reconstructions indicate that most of African palaeontological and archaeological sites from the Plio-Pleistocene occur in water-deposited strata. These places promoted rapid sedimentation of bone remains, enhancing fossil site formation (Behrensmeyer 1983). On the contrary, in places where bone remains are exposed for long periods, bone sedimentation is low, and bone decay is high (Tappen 1992). The role of sedimentation processes suggests that both permanent and ephemeral water bodies play an important role in fossil site formation (Behrensmeyer 1982). It has also been predicted that a higher abundance of mammalian fossils would be found in water-deposited strata due to the high levels of animal activity at water holes (Hutson 2012). Ancient water bodies, like the water bodies of today, likely attracted carnivores, enhancing high rates of predation and bone accumulation. Binford's "water hole hypothesis" further suggests that early Stone Age sites represent a complex record of carnivore hunting alongside hominin stone tool-making and scavenging activities near water holes in semi-arid landscapes (Binford 1983; Blumenschine and Madrigal 1993).

From taphonomic studies conducted in Africa, we also know that bone accumulations may be also caused by carnivores dragging their kills toward the trees to benefit from shade to eat, and by animals seeking shade to recover from illness that may lead to death (Brain 1967). This phenomenon was observed by Behrensmeyer (1993) and Tappen (1995) where carnivores use areas with trees or shade as ambush sites, and where bones may accumulate (see also Haynes (1988)). Glynn Isaac (1983, 1984) also suggested that shade would have attracted hominins and bone-accumulating carnivores.

Additionally, we know that rivers, lakes, trees, different species of predators and scavengers influence bone deposition (Miller et al. 2014). This knowledge comes from studies of open-air sites such as Serengeti, Virunga and Amboseli National Parks. However, when evaluating the hypothesis that across the landscape of an ecosystem, bone deposition rates are

higher in the water holes than inland, found no evidence of increased bone deposition near both permanent and ephemeral water holes in Virunga National Park (VNP) in the Democratic Republic of Congo. Instead, the study found that tree-line rather than water bodies were the only habitat (out of eight: Plateau, Southern plateau, lake, Riverine, Tree-line, Cross-tree line, Hills, Valley) of VNP where higher bone abundance and a higher ratio of isolated remains were found (Tappen 1992).

From observations and experience, we know that carnivores, such as lions, wild dogs, hyenas (Lansing et al. 2009) and particularly leopards, accumulate bones in hunting spots or near trees (Tappen 1995). However, we are thus far only aware of a few ecological variables, which influence the middle- and large- sized living mammals and their distribution in national parks and buffer zone – an area surrounding the park that serves as a transitional zone between the strictly protected core area of the park and surrounding human-dominated landscapes (Easter, Bouley, and Carter 2019; Gaynor et al. 2021). These ecological variables, which include active roads, vegetation, and settlements, are also more likely to influence dead communities recorded in bone assemblages (Chapter Two).

Although Tappen (1995) explored the influence of ecological variables such as tree density and proximity to water bodies (e.g., rivers, lake holes, and shores) on bone distribution, there remains a very limited understanding of how these factors operate in ecosystems beyond the Virunga National Park (VNP). Specifically, we do not know the extent to which ecological variables can predict bone distribution density across diverse habitat types, particularly in regions where faunal fossils were formed. Addressing this gap is critical for advancing our understanding of bone deposition processes in both modern and palaeontological contexts. Additionally, filling this gap will contribute to more accurate reconstructions of past community structures, while helping to determine whether faunal fossil formation was influenced by ecological factors such as rivers, habitat type, lakes and anthropogenic activities, and how these

factors may have biased fossil site the locations and composition formation of fossil sites (Tappen 1995).

Therefore, in this research, we examine whether ecological variables, including both permanent and ephemeral water bodies (i.e., lakes and pans), roads, and habitat types (i.e., grassland and woodland) influence bone accumulation in Gorongosa National Park (GNP) in Mozambique. We hypothesize that both permanent water bodies, such as Lake Urema, rivers (e.g., Urema, Pùngué, Mussicadzi, Sungue) and ephemeral water bodies like pans, will have an increased bone abundance (Figure 3-1). We base this on the assumption that water sources consistently attract more wildlife, leading to higher rates of predation, scavenging and natural deaths, especially during the dry season when water is scarce.

We finally predict that proximity to roads will correlate with lower density of bone distribution density, as roads may diminish faunal abundance (for both prey and predators) due to human activity, leading to fewer natural deaths and predation events near these areas.

Understanding the influence of these ecological variables will lead to a better comprehension of which aspects of fossil assemblages are the result of geological processes (e.g., sedimentation) associated with diagenesis, and which aspects are likely to be influenced by ecology and fluvial deposition (e.g., rivers, lakes, vegetation and habitat type) that determined the original bone deposition. Additionally, this research will enhance our understanding of how both anthropogenic (roads) and ecological factors influence bone deposition in GNP habitats and shape prey-predator interactions.

3.2. Methodology

3.2.1. Study site

Data were collected in Gorongosa National Park (GNP), located in the centre of Mozambique in Africa. The central GNP is a protected area of 3,674 km^2 as a whole and with approximately 10,000 km^2 when including the buffer zone (Figure 3-1). GNP is delimited by the Pùngué and Zambezi rivers at the southern end of the East African Rift System, with diverse landscapes that sustain almost 8,000 species of fauna and flora (Gorongosa Biodiversity database and Piotr Naskrecki, personal communication) (Gorongosa National Park 2024). With its mosaic modern landscapes and extensive cave system, Gorongosa is a valuable analogue for studying environmental and ecological variables that have determined fossil site formation (Bobe et al. 2023, 2020; Bobe and Carvalho 2019).

GNP is known as an example of wildlife rebounding from almost 90% of loss due to the Civil War (1977-1992). During this period, fauna was hunted for sustenance and for exchange of ivory and military equipment (Daskin et al. 2016). The Civil War devastated a place previously known as a sanctuary for a variety of large mammals, including buffalo, blue wildebeest, zebra, waterbuck, impala, and hippopotamus (Stalmans et al. 2019).

The park's revival commenced in 2008 with the launch of the Gorongosa Restoration Project by a US-based non-profit organisation. This initiative, which signed a 20-year co-management agreement with the Mozambican Government, concentrated on conservation, science, and human development. The project was extended for an additional 25 years in 2018 (Stalmans et al. 2019).

Geographically, the GNP is between -19.44799 and -18.01795 of latitude and within 33.91316 and 34.89479 of longitude. To the west, GNP is bounded by Gorongosa Mountain and to the east by the Cheringoma Plateau. Gorongosa Mountain was proclaimed part of the GNP in 2010 and is home to many endemic species (Ministério da Terra 2016). It is also where

many rivers begin and flow to the GNP landscapes. The climate is predominantly tropical, with a dry season spanning from May to November and a rainy season from December to April (Tinley 1977). Annual rainfall ranges from 700-900 mm, reaching higher levels of over 2000 mm in Gorongosa Mountain (Stalmans and Beilfuss 2008). Every year, GNP floods in the rainy season, leaving about 40% of the park inundated (Tinley 1977).

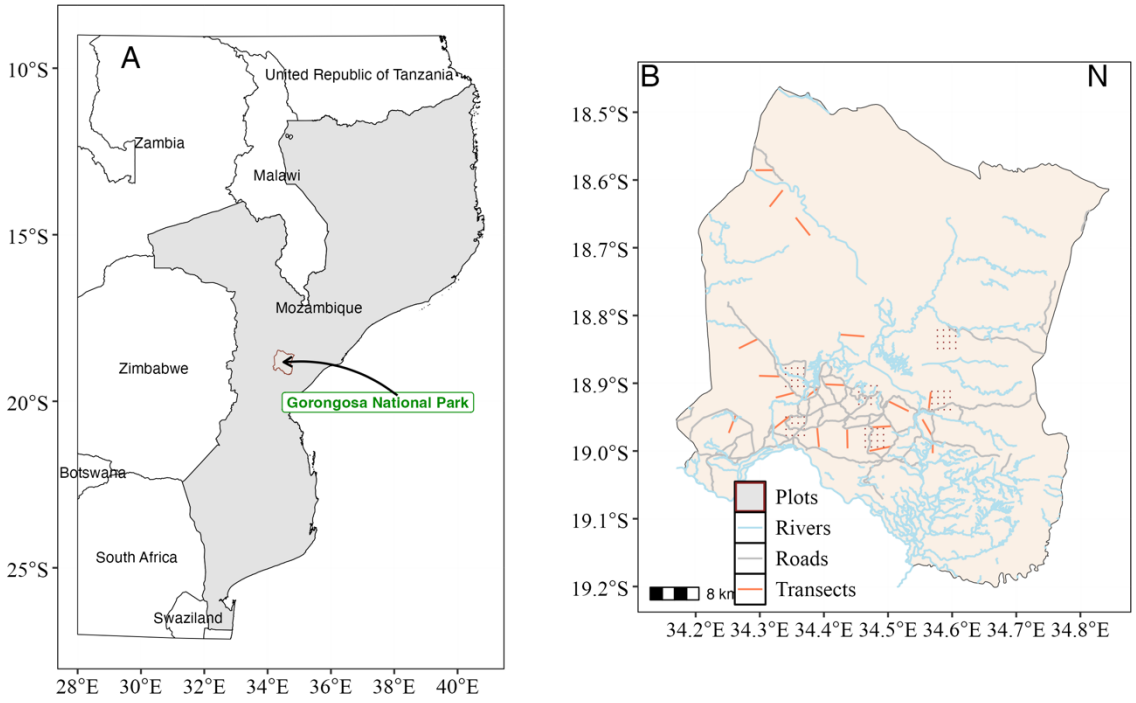


Figure 3-1. Map showing the location of Gorongosa National Park in Mozambique (a) with transects, plots, rivers, and roads highlighted within the park (b).

Geologically, GNP is in the end of the Great Rift Valley setting, which is generally characterised by alluvial deposits with colluvial material deposited at the bottom of the Cheringoma plateau with grey soils. The Cheringoma Plateau consists of grauwackes and limestone with impermeable horizons and soils with low pH and high phosphorus content. Between Rift Valley and Gorongosa Mountain, there are Midlands, mostly underlain by gneiss and pegmatites with many dolerite dykes and sandy and fersiallitic soils. The mountain consists of granites and has high annual rainfall (Stalmans and Beilfuss 2008).

The hydrology of the park and its buffer zone consists of a multitude of rivers and streams. These water sources start from Gorongosa mountain, Midlands and Cheringoma plateau and end in the Rift Valley with Lake Urema as the epicentre of water accumulation and draining its water to the Indian Ocean through the Pùngué River. GNP has currently about 15 rivers, most of them rising from Gorongosa Mountain and draining the water into the Urema Lake. During the dry season, some pans, or small water ponds, retain the water until the next rainy season, while others are seasonal. All permanent and some seasonal pans are well-mapped and described and are about 2,671 evenly distributed across the GNP landscapes (Stalmans and Beilfuss 2008).

For patrolling and tourism purposes, unpaved roads were established in the park. Most activity in GNP, including research, is conducted around the road network, which covers around 20% of the park. Most of these roads are in the south near the main camp (Chitengo) and the Community Education Centre.

Currently, GNP host about 177 mammalian species, 582 birds, 95 reptiles, 55 amphibians, and 82 fish (Gorongosa Biodiversity database and Piotr Naskrecki, personal communication).

GNP has been conducting fauna reintroduction since the beginning of the restoration project. Among many species, there are the predators: leopards, spotted hyenas, Wild dogs (see Bouley et al. 2021), and golden jackals. Wild dogs were first introduced in 2018, and then in 2019 from three sites, iSimangaliso Wetland Park, Magudu area in KwaZulu-Natal and Khamab Kalahari Game Reserve in South Africa (see Bouley et al. 2021). Only eight black-backed jackals were introduced in 2023. Six spotted hyenas were introduced from Karingani Game Reserve (southern Mozambique) in 2024.

During the Civil War, lions and other large carnivores experienced a dramatic decline due to steel-jaw traps and snares (Bouley et al. 2018; Daskin et al. 2016; Stalmans et al. 2019). This was remedied by a combination of measurements, such as community involvement, intensified patrolling work by rangers, systematic wildlife monitoring and some reintroductions by the carnivore team under the Gorongosa Restoration Project. These measurements contributed to, for instance, the recovery of the lion population from below 20 to about 104 in 2016 (Bouley et al. 2018) and more than 250 in 2025 (Gorongosa National Park 2024). Before the reintroduction of leopards, hyenas, golden jackals and wild dogs, lions were the main predators in the park and at the time of this research, along with wild dogs, they constituted the population ecological controllers (Bouley et al. 2021).

3.2.2. Data collection

Bone surveys were carried out from 2016 to 2022 using three main approaches: opportunistic observation, transects and plots. During six years, bone surveys through opportunistic observation were conducted continuously, where researchers conducting different projects opportunistically recorded carcasses around places of their data collection. Transects were carried out in 2017 and 2019, and they constituted established lines of 5km in length and 50 to 100 m in width recorded using Garmin GPS devices. Survey plots were added and surveyed in 2021 and 2022 to enable better comparison with data from other methodological approaches, including the Normalized Difference Vegetation Index (NDVI), which is presented in pixels and can be directly applied to grid cells.

Two to three individuals assisted JM in conducting the bone survey along the transects, maintaining 10 to 20 m between them, depending on visibility (for similar approaches see Western & Behrensmeyer (2009)). In grasslands, the maximum spacing was used, while in woodlands, the minimum distance was applied. This approach aimed to minimise bias and improve the likelihood of detecting bones.

Bone surveys in plots were performed starting from one site to another in zigzag movements from left to right or south to north. Each one-hectare plot was walked in three rounds, with each round covering one-third of the plot area.

For data consistency, we assigned each observer a specific role. For instance, one observer recorded GPS coordinates and photographed the specimens. A second one other counted the collected specimens, while the third observer took key measurements, including patch diameter, and entered data into a digital form using the ODK Collect application (Anokwa et al. 2009; Bokonda et al. 2019) (Figure 3-2). To minimise bias, classifications like weathering stage were conducted by the same observer, following the methods established by Behrensmeyer (1978).

As referred in Chapter Two, for logistical efficiency, transects and plots were located near accessible roads, allowing transportation by car for systematic sampling on foot.

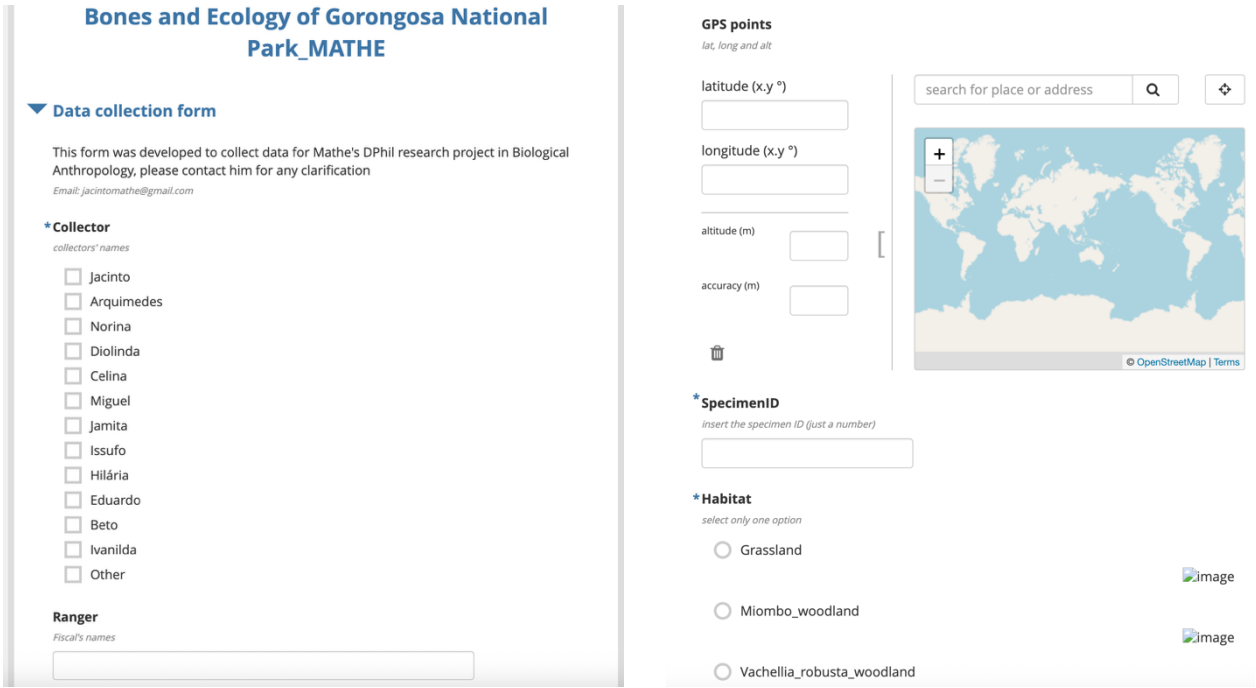


Figure 3-2. Screenshot of the digital form used for data collection in the ODK Collect application.

3.2.3. Collected variables

Each bone underwent meticulous documentation, with the recording of GPS coordinates, species ID and skeletal element ID. In cases of multiple bones within patches, documentation also included the minimum number of elements (MNE), minimum number of species, minimum number of individuals (MNI), and patch diameter (Behrensmeyer 1993; Tappen 1995).

For determining the minimum number of elements, various sections of long bones were segmented into five main categories: proximal epiphyses (PE), proximal near epiphyses (NPNE), shaft or diaphysis (S), distal near epiphyses (DNE), and distal epiphyses (DE). This systematic categorisation (Braun et al. 2016) also facilitates a comprehensive examination of bone fragments, ensuring accurate counting and a more nuanced assessment of each piece's anatomical location, progressing from proximal to distal regions (see Figure 3-3).

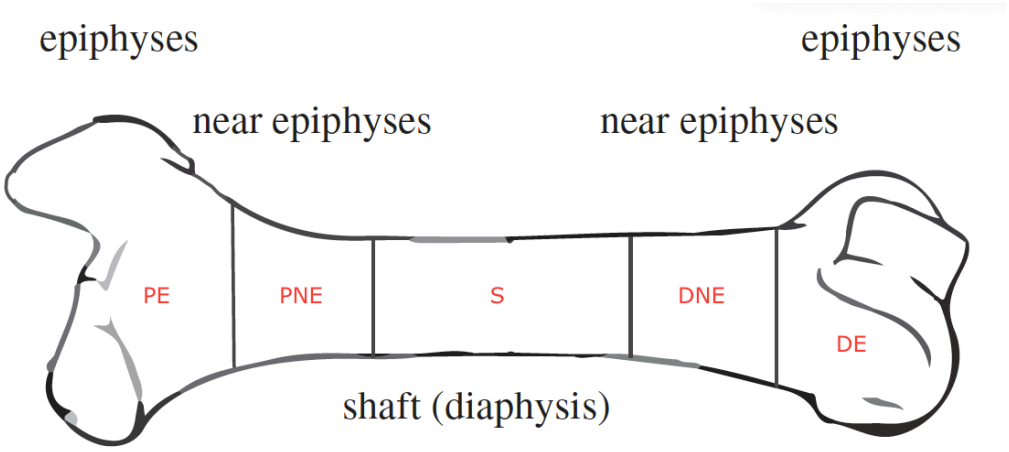


Figure 3-3. Representation of different portions of the long bones, in particular of femur and the codes used to document MNE (minimum number of elements). Adapted from Braun et al. (2016).

3.2.4. Bone identification

JM documented and identified all skeletal elements, with the assistance of a modern osteological reference collection assembled by the Paleo-Primate Project Gorongosa, spanning 2016 to 2022. Furthermore, to enhance the precision of taxonomic classification, external

resources such as field guides (Walker 1985) and the online platform ArchéoZoothéque (accessible at https://www.archeozoo.org/archeozootheque/index/category/132-mammiferes_langen_mammals_lang_langes_mamiferos_lang_/start-15#content) were consulted.

3.2.5. Data analyses

All analyses were performed in R (v. 4.3.3) (R Core Team 2024) using RStudio (v. 2023.09.1+494) 64 for MacOS (Team 2024). The spatial analyses and visualisation were conducted utilising Quantum Geographical Information System (v. 3.32.2) (Moyroud and Portet 2018) and R (v.4.3.2) (Henry and Wickham 2022; Kassambara 2023; Neuwirth 2022; Pebesma and Bivand 2023; Pebesma, Mailund, and Hiebert 2016; Team 2024; Yan 2023). All the data set and R scripts used for the analyses presented below are available in the repository: https://github.com/jacintomathe/Mathe_paper_three.git.

Grid cell creation for GNP

The study utilised geospatial data and environmental metrics to analyse carcass distribution and ecological factors within Gorongosa National Park. Carcass locations were represented as a convex hull, forming the spatial boundary for analysis using the *sf* package (Pebesma and Bivand 2023). A 100m x 100m grid was generated across this area, with grid cells intersecting the convex hull to refine the focus on relevant regions. ESRI shapefiles of roads, rivers, Lake Urema, and pans, were integrated in the data for the analyses. All special data used the same coordinate reference system (CRS = 4127) with the *sf* package (Pebesma and Bivand 2023).

The cells so created were overlaid with transect, plots and locations where opportunistic observations were conducted. From this grid cells, were filtered only cells that overlapped with survey locations. Cells that overlapped with at least one of the three survey locations were

retained for further analysis and a unique identifier was then assigned to each grid cell. After the selection, almost 80% of grid cells had zero bone occurrence. To ensure statistical robustness and accurate model interpretation, we balanced the dataset by randomly resampling an equivalent number of grid cells containing at least one bone element.

Geographic and ecological variables

Vegetation - Vegetation classification was performed using the Normalised Difference Vegetation Index (NDVI), calculated from Landsat 9 Level 2 Surface Reflectance images B4 and B5, acquired on November 30 2024 from the United States Geological Survey (USGS) EarthExplorer (earthexplorer.usgs.gov). The NDVI was derived from the red and near-infrared bands of Landsat imagery, using the formula: NDVI=NIR−RedNIR+RedNDVI=NIR+RedNIR−Red, where NIR: Near-Infrared and Red **-** Red band**.**

NDVI values were extracted for all pixels within each grid cell, and the mean of these values was used to classify GNP habitats into grassland (NDVI below 0.194) and woodland (NDVI above this value). The threshold value was derived from the median and box plot calculated from 85 randomly sampled grid cells, with 43 from grassland and 42 from woodland (Figure 3-4). Although there was some slight overlap between the two habitats, they were sufficiently distinct for classification, considering that most woodlands are mixed and may contain decayed plants that reflect less light, thereby lowering the NDVI value.

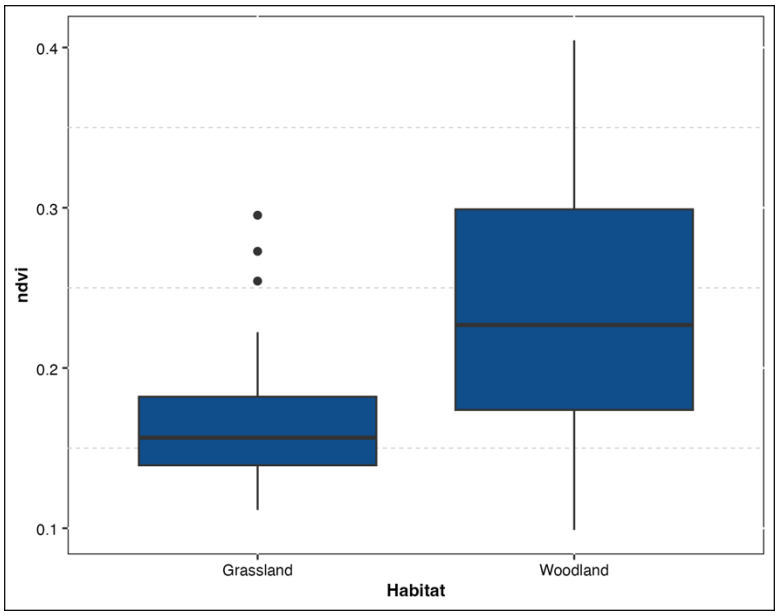


Figure 3-4. Boxplot of NDVI values of Grassland and Woodland habitats of GNP.

For distance measurements, we first calculated the centroid of each grid cell, which served as the reference point for measuring the distance to each of the spatial variables listed below (see the R script in the repository: https://github.com/jacintomathe/Mathe_paper_three).

Distance to Roads –The road network was clipped to the GNP boundary, and the minimum distance from each carcass grid centroid point to the nearest road was calculated using the *sf* package and stored in the dataset.

Distance to Rivers—The main rivers within GNP were also analysed for proximity to carcass grid centroid points. After importing and processing the river shapefile, the minimum distance from each grid point to the nearest river was calculated and added to the data.

Distance to Lake Urema—Lake Urema's boundaries were represented as a multiline feature, and the distance from each carcass grid centroid point to the nearest section of the lake was computed and integrated into the dataset.

Distance to Pans —The shortest distance from grid centroid points to pans was measured and integrated into the dataset, also using the *sf* package.

Generalised linear model

A Negative Binomial (NB) model was used to assess the factors influencing the number of bone elements (MNE). MNE, the dependent variable, represents the count of bones observed across the three survey methods. The predictor variables were habitat type (grassland and woodland), minimum distance to roads, Lake Urema, rivers, and to pans.

The Variance Inflation Factor (VIF) was calculated to evaluate multicollinearity among the predictors, aiding in the identification of potential collinearity issues that could affect the accuracy of the model's parameter estimates.

Statistical significance was determined at a 95% confidence level ($p < 0.05$) for the Generalised Linear Model. A *p*-value below 0.05 indicates that the observed results are statistically significant and unlikely to have occurred by chance, providing evidence to reject the null hypothesis in favour of the alternative hypothesis.

3.3. Results

3.3.1. Minimum number of individuals and species representation

In seven years (2016 to 2022, inclusive), we recorded 270 carcasses and 2,313 bones of 19 species in 38 transects and 96 plots. These bones were in 246 grid cells of 100 x 100m, 159 in grassland and 87 in woodland.

The analysis of carcasses illustrated in Figure 3-5 reveals that most species exhibit relatively low abundance levels. The waterbuck (*Kobus ellipsiprymnus*) has the highest number of bones, followed by the blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), reedbuck (*Redunca arundinum*) and warthog (*Phacochoerus africanus*). Most other species, such as, bushbuck (*Tragelaphus scriptus*), baboon (*Papio ursinus griseipes*), and bushpig (*Potamochoerus larvatus*), had a similar bone abundance, while species like honey badger (*Mellivora capensis*), hippo (*Hippopotamus amphibius*), and zebra (*Equus quagga*) had very low bone abundance.

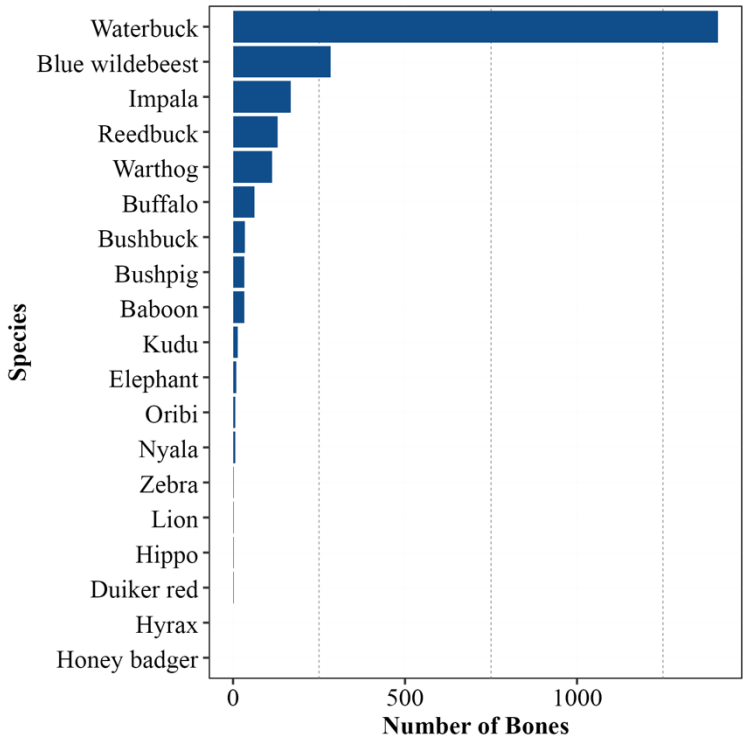


Figure 3-5. The abundance of vertebrate species recorded through osteological collection across the ecosystem of Gorongosa National Park.

The total number of recorded bones varies across habitats, with certain environments exhibiting higher concentrations than others. Grasslands yielded a slightly greater number of bones (n = 1248) compared to woodland habitats (n = 1065), indicating potential habitat-related differences in bone deposition or preservation.

3.3.2. Ecological effect on bone deposition

Table 3-1. Results from NB using ecological variables as predictors for bone deposition in Gorongosa National Park ecosystem.

GLM	estimate	std.error	statistic	p.value
(Intercept)	2.303	0.376	2.219	0.027*
VegClassWoodland	0.35	0.567	-1.852	0.064
mDist_to_road	0.928	0.039	-1.911	0.056
mDist_to_river	0.788	0.166	-1.433	0.152
mDist_to_UREMA	1.155	0.03	4.806	<0.01**
mDist_to_gnp_pans	0.671	0.241	-1.659	0.097
VegClassWoodland:mDist_to_road	0.869	0.054	-2.628	<0.01**
VegClassWoodland:mDist_to_river	1.233	0.226	0.926	0.354
VegClassWoodland:mDist_to_UREMA	1.052	0.043	1.191	0.234
VegClassWoodland:mDist_to_gnp_pans	2.028	0.324	2.183	0.029*

Note: Asterisks indicate statistical significance of p-values (* = $p < 0.05$, ** = $p < 0.01$).

The results from negative binomial regression model in Table 1-1, provide strong evidence that minimal distance to roads ($p = 0.056$) and Lake Urema ($p < 0.01$) statistically and significantly affect the bone deposition across GNP landscapes. Pans have significant effect only in bone deposited in woodlands ($p = 0.029$) while roads significantly affect in both, but the effect is significantly higher in woodlands. It is important to note that no roadkill animal deaths were observed that could have affected the sample.

Additionally, the model reveals that habitat type, as well as distance to rivers and pans in grasslands, do not have a statistically significant effect on bone deposition ($p > 0.05$). The lack of a significant effect of rivers on bone deposition persists across both habitats, while the significant effect of Lake Urema observed overall is not evident in woodlands ($p > 0.05$).

3.4. Discussion

The negative binomial regression model reveals that vegetation type and proximity to roads and Lake Urema are the key landscape features that influence bone deposition across Gorongosa National Park ecosystem. Key ecological features, such as roads and Urema Lake emerged as important predictors of bone deposition.

Proximity to roads was positively associated with carcass deposition, suggesting that as the distance from these features increases, bone deposition decline; in other words, close to roads there is higher bone deposition, and it is lower further away. This trend may at certain extent reflect methodological bias, as most of the transects and plots used to survey bones were established close to roads for accessibility of the location and make the survey plausible. Only 20% of the park is accessible by roads. Evidence for this is shown by the interaction of roads and habitat type, where the effect of roads on bone deposition is greater in woodland than in the grasslands as in this habitat is only accessed by roads and some woodlands are impenetrable by car and the visibility is low. On the other hand, most of the grasslands are penetrable by car making the bone survey straightforward and the visibility is higher than in woodlands.

Additionally, these trends may also be related on one hand to prey behaviour and on the other to the predators such as lions. Grazing herbivores like waterbuck constitute the majority of the park's prey (Stalmans et al. 2019; Stalmans and Peel 2016, 2020, 2022, 2024) which are water dependent and during the dry season water sources become scarce and the only spots that hot some are pans and rivers, which may also be used by predators as hunting spots (Hutson 2012, 2016). For instance, ephemeral pans in woodlands may dry quickly but the permanent hold water longer and may attract both predators and grazers, but grazers may reduce the risk of being preyed by setting different time to access the water or drinking water from water sources in grasslands considering that most of these herbivores as grazers range mostly in

grasslands and grassy woodlands. This may contribute to reduce accumulation of bones close to pans and higher accumulation further away in woodlands than in grasslands.

Predators like lions and wild dogs may have prey preferences that contribute to the bone accumulation of certain species in specific locations over others. For instance, lions in Gorongosa National Park prefer warthogs over other large and medium-sized mammal species, whereas wild dogs show a higher preference for waterbuck over other species (Bouley et al. 2021). Hyenas may consume and remove bones from the landscapes (Blumenschine 1986a; Egeland, Egeland, and Bunn 2008; Faith, Marean, and Behrensmeyer 2007). However, during the data collection period, hyenas had not yet been introduced in the park, wild dogs had but still in low population and in the habituation stage and may not have significant influence period. Therefore, these species were not part of the analyses. Lions also had recovered from almost 90% of loss, but the population was still low, less than 150 individuals, from which less than 20% was collared.

Roads may also influence bone deposition by attracting prey due to the palatable grass that grows near water channels created by cars used for tourism and/or research (Forman 2000). The water channels hold water longer after the rain and provide moisture that favour grass regeneration for the prey. This scenario was observed in the living mammals' occupancy detected by camera traps, where, living mammals' occupancy was strongly associated with roads, with strong effect on herbivores such as impala (Gaynor et al. 2021). The increased proximity to roads may have contributed to greater bone accumulation, as predators could use these areas strategically to enhance prey catchability and reduce energy expenditure during predation (Balme, Hunter, and Slotow 2007).

In contrast, distance from Lake Urema and pans (this only in woodlands) was positively associated with bone deposition, suggesting that areas closer to Lake Urema and pans have

fewer bone accumulations compared to those farther away. This suggests that these water-associated features are less likely to serve as focal points for animal activity and have low bone accumulation in their margins. This trend reflects findings from Camera trap (Gaynor et al. 2021) and aerial surveys data, where grazers which form most data analysed in this research are found in low density close to Lake Urema. Before civil war, more grazer pastured near Lake Urema's margins (Stalmans et al. 2019). These findings may be explained by the fact that the main predators at the time of data collection were lions (Bouley et al. 2018) are more abundant close to Lake Urema and due to risk avoidance, grazers shifted their occupancy to more wooded areas such as *Vachellia xanthophloea* and palm tree woodlands (Stalmans and Beilfuss 2008; Stalmans and Peel 2016, 2020, 2022). Woodlands are habitats where most predation events occur, involving both lions and wild dogs, with lion predations being more frequent than those of wild dogs (Bouley et al. 2021).

When comparing the two permanent water sources — rivers and Lake Urema, where more than 2,748 Nile crocodiles occur (Stalmans and Peel 2024) and where some carcasses have recently been reported moving from the landscape into the water (Erin Phillips, personal communication) — differences in bone accumulation relative to distance suggest multiple contributing factors, including the role of Nile crocodiles in carcass movement and possibly in bone deposition. One would expect to find more bones accumulated by crocodiles closer to rivers and lakes, but this was not supported by the findings of this research. This is due to, on one hand, higher energy of the water in rivers that contribute to moving bones at the margins to the riverbed particularly when rivers overflow during the rain seasons. On the other hand, crocodiles may accumulate bones at the lakebed, making detection challenging using the methods employed in this study. Even the bones brought by crocodiles may remain submerged. Future investigations may consider adapting methodologies to account for different water sources, including pans, to improve the detection of submerged bones. For pans, separate

analyses for the ephemeral and permanent ones would help to better interpret effect of this water source on bone deposition. Even with methods targeting only water source margins would greatly contribute to the understanding of predation and bone deposition near these features.

Additionally, GPS tracking devices, such as those developed for marine research, could be attached to carcasses and crocodile to provide valuable insights into their role in carcass transport. This approach would also help us to understand other predator's role in bone deposition at the river and lake shores and in aquatic environments in general.

Understanding the relationship between bone deposition and ecological features is essential for interpreting modern bone deposition patterns and their implications for the formation of faunal fossil assemblages in African environments. This relationship is also critical for assessing mortality rates and the factors influencing them, which can inform conservation strategies and the development of management plans in protected areas such as Gorongosa National Park.

This study has certain limitations, including the exclusion of potential unmeasured variables that could influence carcass and bone distribution, such as seasonal variations and predator contributions (e.g., lions, wild dogs, hyenas—recently reintroduced into the park, and crocodiles). Furthermore, the reliance on spatial proximity measures may not fully capture the complex interactions between predators, prey, and their environment. However, this approach was the most feasible given the available data. For example, less than 10% of lions were collared. Other predators—such as wild dogs, hyenas, and jackals—were only reintroduced two years, one year, and a few months before the end of data collection, respectively. At the time of this study, detailed data on their distribution were not yet available.

Apart from attaching GPS tracking devices on crocodiles and fresh carcasses for movement monitoring, seasonal carcass monitoring and bone walks in open landscapes are

recommended. Furthermore, future studies should also include other ecological factors, such as pH, salinity, human activity-preferred locations for tourism and patrolling. Involving these variables in future studies would provide a more comprehensive understanding of the factors influencing carcass and bone distribution in different seasons and periods of the days.

Based on the findings, this study did not support the hypothesis that areas closer to water sources — such as Lake Urema, rivers, and pans — exhibit higher bone density and distribution compared to areas farther away. Moreover, it is more likely that water sources consistently attract more wildlife, but most of predation events happens further away these features enhancing lower bone accumulation near these water sources.

Despite higher human activity near roads, the research findings also failed to support the prediction of higher bone deposition close to roads than further. However, this may be related to human and methodological bias than other factors stated in this discussion.

Overall, while the results suggest significant effect of low energy water sources (Lake Urema and pans in woodlands) and no significant of habitat type on bone deposition, they also highlight the need for further investigation into other ecological and taphonomic factors that might influence bone deposition across GNP habitats.

3.5. Conclusion and further directions

In this research, we revealed that higher bone deposition occurs closer to roads and farther from low energy water sources like Lake Urema and pans. These findings suggest that both water bodies influenced faunal fossil deposition in palaeontological and archaeological sites that are geologically and ecologically similar to Gorongosa National Park. The results also indicate that faunal fossils may have accumulated further from water sources. However, water margins may have served as high-risk zones, particularly for grazers, due to increased predator activity. This research expands our understanding of the complex interactions driving the highlighted carcass and patterns of bone distribution density, and fossil site formation in ecosystems resembling Gorongosa National Park. Further research with an increased sample size covering other ecological factors, such as, soil pH, salinity and predator, and carcass movement tracking is recommended.

Chapter Four. The ecology of primate carcass distribution in an East African Rift ecosystem

Primates constitute an integral part of many African ecosystems. In some areas, primate species can be locally very abundant, while in others they are rare or absent. Our central question is: does the abundance of primate bones (or carcasses) reflect the abundance of local living populations? Bone surveys in Amboseli National Park (ANP), Kenya, and Virunga National Park (VNP), Democratic Republic of the Congo, revealed a positive correlation between carcass abundance and living mammal communities, with a notable exception: a low abundance or absence of primate carcasses when compared to other medium-sized and large mammals. Recent research conducted at Gorongosa National Park (GNP), Mozambique, revealed a similar disparity between the abundance of primate carcasses and mammalian live census data. This study aims to understand this mismatch between live and dead by examining the influence of ecological factors on primate carcass occurrence and bone deposition in the modern rift valley ecosystem of Gorongosa National Park. To address these issues, we investigated whether (1) landscape type, proximity to roads, and water sources (pans, rivers, and lakes) predict primate carcass occurrence relative to other mammal taxa, and (2) the accumulation of primate bones significantly differs from that of other mammals in annually flooding and non-annually flooding landscapes (broadly speaking, in the floodplain vs. higher areas). We analysed 26 bones from 18 chacma baboon individuals (*Papio ursinus*) and 255 bones from 20 other mammal species. Generalised Linear Model (GLM) outputs suggest that permanent water sources such as rivers and lakes are key drivers for primate bone accumulation ($p < 0.05$). A Fisher's Exact Test indicates that primate bones are deposited more in Rift Valley Riverine & Floodplain landscapes (in the floodplain) ($p < 0.05$). These findings may have implications for our understanding of primate bone accumulations in the African fossil record, where some palaeontological sites have abundant primate fossils, but others have few or none.

4.1. Introduction

Primates constitute an integral part of many African ecosystems, both modern and ancient. In some areas, primate species can be locally very abundant, while in others they are rare or absent. Our central question is: does the abundance of primate bones (or carcasses) in the landscape reflect the abundance of local living populations? For example, live census data from places such as Gorongosa National Park (GNP), Mozambique, indicate that cercopithecoid primates such as *Papio* are among the most numerous mammals in the region, surpassed only by a couple of species of highly abundant antelopes (Stalmans and Peel 2024). Nevertheless, osteological surveys at Gorongosa suggest that the abundance of primates is lower than expected based on the living population numbers. Bone surveys from other parts of Africa have similarly yielded relatively low numbers of primates compared to other mammalian taxa. For instance, Behrensmeyer's long-term taphonomic study at Amboseli National Park (ANP), Kenya, recovered only a few baboon bones over a 50-year period (Behrensmeyer 1993, 2007; Behrensmeyer et al. 1979; Western and Behrensmeyer 2009), even though baboon are abundant in the park. Baboon abundance at Amboseli declined markedly from around 2,500 individuals in 1963–1964 to just 125 individuals by 1979 (Altmann, Hausfater, and Altmann 1985). In more recent years, the main baboon study group at Amboseli has consisted of approximately 350 individuals, representing a minimum estimate for the park's population (Alberts et al. 2012). Thus, the scarcity of baboon bones in Behrensmeyer's study is puzzling. A similar pattern was observed in a surface bone study at Virunga National Park (VNP) in the Democratic Republic of the Congo, which did not yield a single primate bone among roughly 4,500 osteological specimens, even though baboons were common in the study area (Tappen 1995). What factors account for the abundance or scarcity of primate bones in regions where the animals are clearly present? Answering this question may help clarify patterns in the primate fossil record.

Beyond the many variables that are likely to affect differential distribution in bone assemblages (e.g., life history, demographics, body mass, bone abundance and surrounding tissue) ecological factors are thought to influence and partially explain aspects of bone preservation and deposition (Lam and Pearson 2005; Pickering and Carlson 2002; Tappen 1995). Previous studies focusing on neotaphonomy and modern bone assemblages in the East African Rift System (EARS) are limited and focused on a few ecological variables, i.e., presence of water and trees (Tappen 1992, 1995). For example, Tappen's research in VNP found that more bones accumulated in the plateau grasslands and riverine habitats than in other habitat types such as hills and valleys. In Tappen's habitat categories, plateau is an open grassland with abundant ungulates, particularly dense herds of kob and reedbuck; the riverine zone has higher tree and bush density than the plateau but does not form a dense gallery forest; hills are mainly covered in grassland, with ridges of trees and bushes; between the hills there are valleys, which are also characterized by trees and bushes. Tappen (1995) found no evidence of increased bone deposition near permanent water bodies or ephemeral water holes (Tappen 1995). In Gorongosa, the abundance of primate carcasses did not match the abundance of living primates estimated from the recorded number of troops (Mathe, Bobe and Carvalho, in review; Mathe et al., in review). Data captured by camera traps and biennial aerial surveys places baboons as the second most abundant medium-sized mammal species in the park. However, in osteological surveys baboons were the fourth most abundant species, suggesting lower bone recovery or preservation for this primate species in relation to the living population. Despite their abundance and wide distribution in the Gorongosa ecosystem, vervet monkeys were not counted in aerial surveys (Beardmore-Herd et al. 2025; Stalmans and Peel 2016, 2020, 2022; Stalmans et al. 2018), and they are captured at low frequencies by a camera trap grid that has been ongoing

since 2016 (Gaynor et al. 2019). No skeletal remains were found in osteological surveys in GNP (Mathe et al., in review). Moreover, the biennial aerial survey data show that baboon troops recorded in aerial surveys between 2016 – 2022 are widely distributed across the surveyed block area (Figure 4-1A). A smaller number of troops was found in areas that flood annually, while larger numbers were found areas that do not flood annually (Stalmans and Peel 2016, 2020, 2022; Stalmans et al. 2018) (Figure 4-1B). Baboon data from four aerial counts sampled years 2016, 2018, 2020, and 2022, which overlap the period of osteological surveys (2016 to 2022).

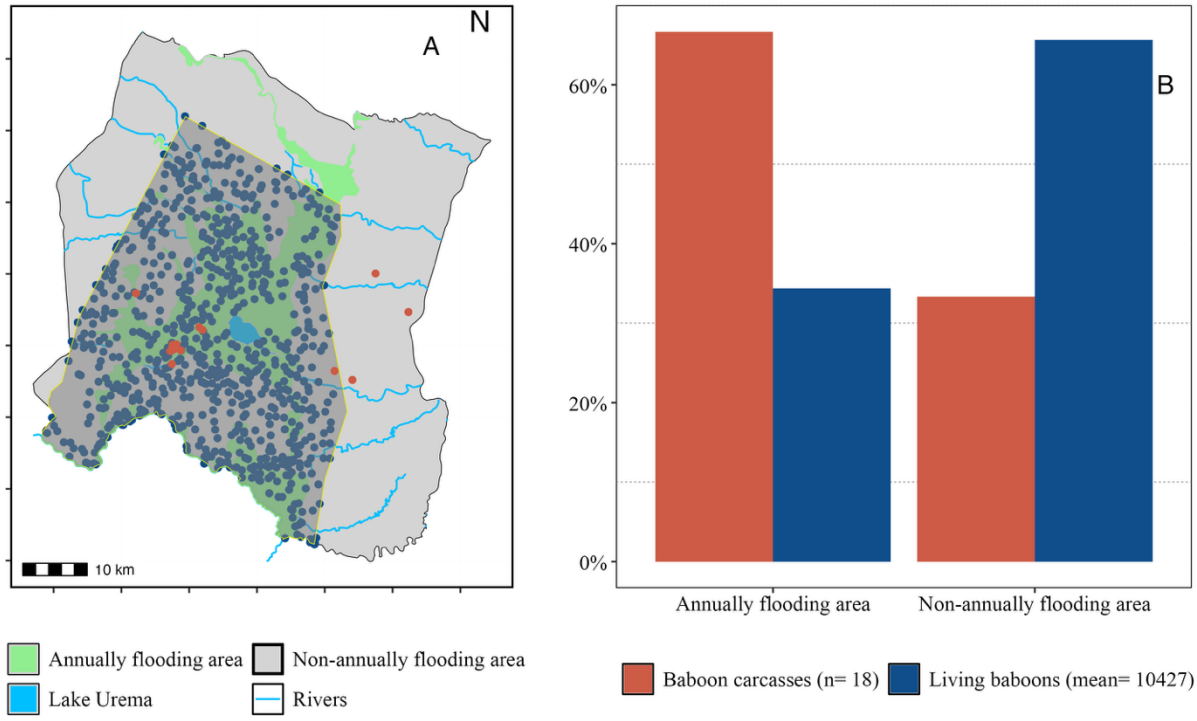


Figure 4-1. Map showing the distribution of baboon troops (blue) and carcasses (red) in annually and non-annually flooding areas in Gorongosa National Park; shaded area with blue dots is a count block area in aerial surveys (A). Accompanying bar charts illustrate the living baboon and carcass abundance in annually flooded and non-annually flodded areas (B) (data from Chapter Two).

4.1.1. Behaviour and ecology of chacma baboons (*Papio ursinus*)

Baboons prioritize safe habitats over food-rich areas, foraging near refuges like trees and cliffs to minimize predation risk, which may also affect where skeletal remains accumulate. As omnivores, their diet includes animals, fruits and pods (including seeds), flowers, leaves and

subterranean items (e.g. roots and corms) (Hill and Cowlishaw 2002; Kingdon 2013a). While they prefer daily drinking, they can survive extended periods without water, increasing mortality risks during droughts (Hamilton 1985). Seasonal dietary shifts, particularly during food shortages, influence survival, especially for juveniles learning from adults (Kingdon 2013a). The home range expansion due to baboon movement across the year varies according to seasonality, weather, and food resource availability (Johnson et al. 2015). These factors influence where the baboons live and die, and thus where their bones may occur.

Chacma baboons (*Papio ursinus*) live in stable troops of 22–79 individuals with female-biased sex ratios (Henzi 1999; Kingdon 2013a). In Gorongosa NP there are more than 200 baboon troops, two of which are being intensively studied. The 'woodland troop' has 88 individuals while the 'floodplain troop' has 37 individuals (Hammond et al. 2022; Lewis-Bevan et al. 2025). At ANP, the troop size ranges from 35 to 65 individuals (Bulger and Hamilton 1987). Males disperse at adulthood, while females are philopatric. Males may commit infanticide upon joining a group to induce oestrus in females, who counter this by mating with multiple males and forming protective friendships (Palombit, Cheney, and Seyfarth 2001).

Social dynamics involve dominance hierarchies; dominant males monopolise fertile females, while dominant females access better resources and experience higher infant survival rates (Palombit et al. 2001). Grooming maintains social bonds and is exchanged for tolerance or access to resources (Silk, Seyfarth, and Cheney 1999). However, grooming time limits in larger groups lead to social fragmentation and eventual fission. Vocalisations, such as soft grunts and contact calls, help manage social cohesion and response to predation risk (Silk et al. 1999). Groups are not territorial, and no physical altercation characterises usual encounters with other troops, though males may compete for mates (Kingdon 2013a).

The main cause of mortality in baboons is predation, mostly by leopards, occasionally by lions, hyenas, crocodiles, jackals, eagles, cheetah, domestic dogs, pythons, and wild dogs

(Cheney et al. 2004). Adult males often defend groups, taking on high-risk roles during travel (Cheney et al. 2004). Baboons also suffers from parasites, including ticks, and diseases such as bacterial yersiniosis. The most common diseases reported in captivity are haemorrhage and colitis, and these vary across sex and age (Dick et al. 2014). In the wild, mortality is highest among infants, mainly due to infanticide and predation, and can vary with group size and rank (Dick et al. 2014). Starvation has been documented in extreme cases, disproportionately affecting females, juveniles, and infants (Hamilton 1985). Seasonal dispersion and predictable travel routes increase predation and mortality risks (Cheney et al. 2004).

4.1.2. Baboons as models for early hominin ecology and behaviour

Palaeoanthropological research helps us to understand the ecology and behaviour of early hominins (Clarke et al. 2021). However, there are limitations regarding the preserved physical remains used for palaeoanthropological interpretations (King 2024). The use of baboons as models for studying early hominin ecology and behaviour is rooted in three main functional similarities: cosmopolitan distribution, flexibility in adaptation to different environments, and body mass. Both hominins and baboons inhabit wide and diverse habitats, from woodlands to grasslands and cold highlands, and are adapted to drastic cycles of climate change with great flexibility in their physiology and behaviour (Arráiz et al. 2017; Bobe et al. 2023, 2020; Magill et al. 2016). The flexibility and adaptability to diverse environmental conditions is a shared characteristic between hominins and baboons (King 2024). This adaptation allows them to navigate a variety of habitats in search of food, climb trees, and tolerate different levels of stress. Body mass is slightly different between the two taxa, as early hominins weigh between 25 and 75 kg, and baboons range from 15 to 35 kg, with significant overlap, making this factor one of their shared traits (Fischer et al. 2019; Simpson et al. 2019). Both are considered medium-sized when compared to large mammals like elephants or hippopotamus and considered large-sized in comparison to most primates, except for

chimpanzees, bonobos, and gorillas (King 2024). Despite aspects of body mass and canine teeth regarding sexual dimorphism, which varies across baboon species but is relatively large in all of them and not as evident in early hominins, baboons continue to be considered as models for understanding the ecology and behaviour of early hominins, helping to shed light on hominin evolution and fossil deposition in different ecosystems (King 2024).

In this study, we examine whether 1) the landscape type, proximity to water bodies (pans, lakes and rivers) and roads predict baboon (hereafter primate) carcass occurrence compared to other mammal taxa, and 2) the abundance of primate bones is significantly different from other mammal taxa in annually flooding and non-annually flooding landscapes. We predict that 1) the likelihood of primate carcass occurrence will be lower than that of non-primate carcasses in both, annually flooding and non-annually flooding landscapes, 2) primate carcass occurrence will be lower close to water sources and roads than further away and 3) primate bone abundance differs significantly from that of non-primate carcasses across the two GNP landscapes, with the annually flooding landscape harbouring a higher bone abundance than non-annually flooding landscapes. This pattern is driven by behavioural and ecological factors unique to primates, such as reduced water dependency (Pontzer et al. 2021) and higher risk perception (Hammond et al. 2022), which lower the bone abundance of primates relative to other mammal taxa in these environments. These factors may affect bone preservation and deposition rates and carcass accumulation in inaccessible and low-elevation locations. These predictions aim to provide a comprehensive understanding of the factors influencing primate carcass occurrence and bone distribution in GNP. An understanding of the variables that influence the occurrence and distribution of primate bones in modern landscapes can help us understand the variability of primate fossils in palaeontological contexts (Bobe 2011).

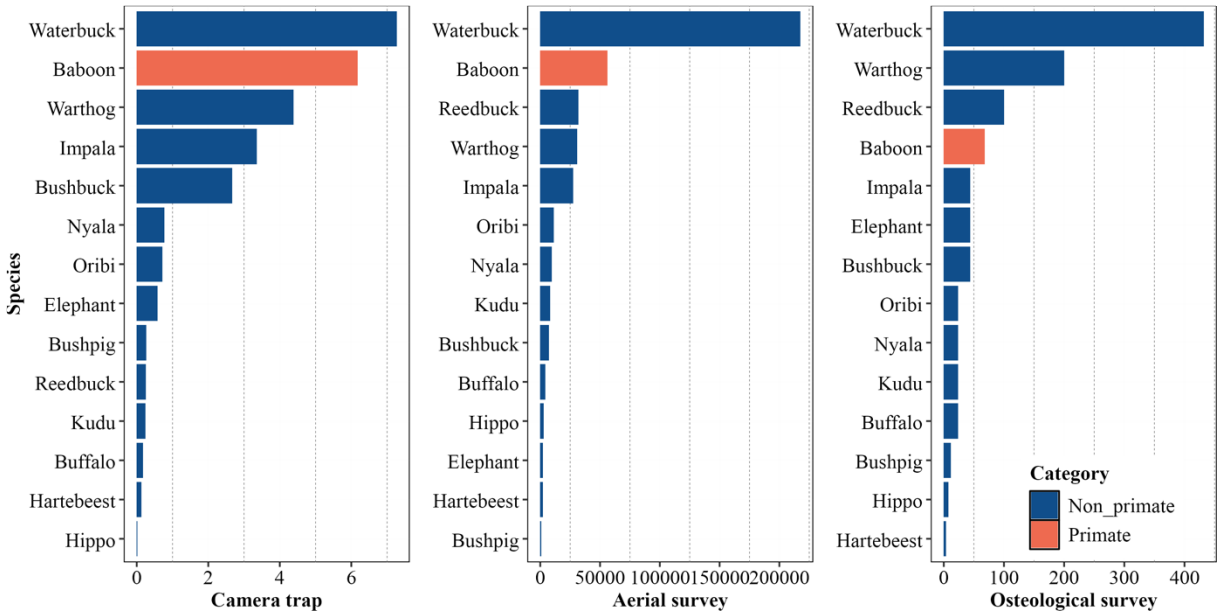


Figure 4-2. Abundance of living and dead medium-sized and large mammal species recorded by camera traps, aerial surveys, and osteological surveys in Gorongosa National Park, with baboon abundance highlighted across three methods (data from Chapters Two and Three, above).

4.2. Methodology

4.2.1. Study site

This research was conducted in Gorongosa National Park in central Mozambique. GNP is a protected area of approximately 4000 km^2 bounded by the Pùngué River in the south and Zambezi River in the north (Figure 4-3), at the southern end of the East African Rift System (EARS) (Stalmans et al. 2019; Tinley 1977). GNP has diverse landscapes (Stalmans and Beilfuss 2008) that sustain almost 8000 identified species of flora and fauna (Gorongosa Biodiversity Database) (Gorongosa National Park 2024). Containing the last portion of the EARS dated to 3MA (+/-1MA) (Habermann et al. 2019; Macgregor 2015) and extensive cave system, Gorongosa is a valuable analogue for studying environmental and ecological variables that have determined fossil site formation in eastern Africa (Bobe et al. 2023, 2020; Bobe and Carvalho 2019).

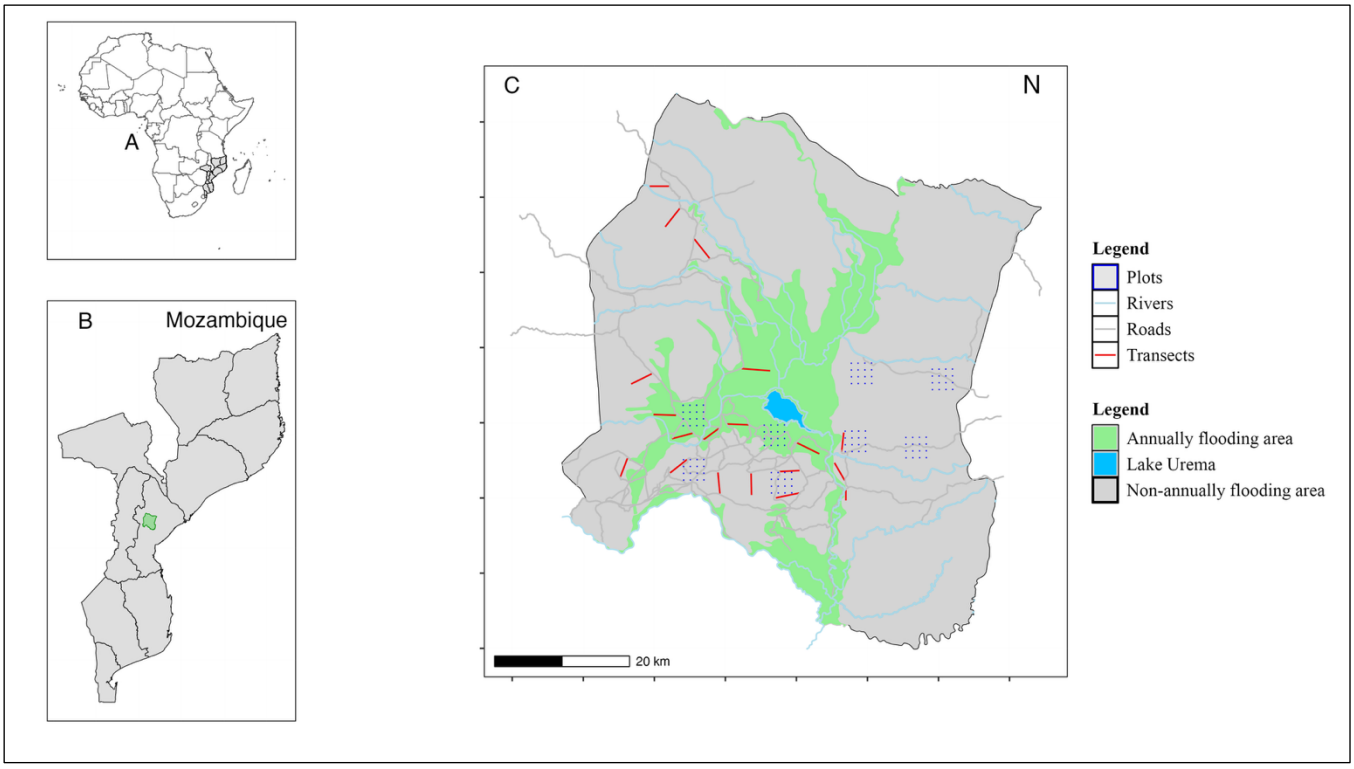


Figure 4-3. Map of Gorongosa National Park, Mozambique, showing the locations of plots and transects used for bone surveys (C). Insets show the location of Gorongosa National Park within Mozambique (B) and Mozambique within Africa (A).



Annually flooding landscape Non-annually flooding landscape

Figure 4-4. Examples of annually and non-annually flooding lansdscapes of Gorongosa National Park, Mozambique

Historically, GNP is known as an example of wildlife rebounding after losing almost 90% of its wild animal population due to the Mozambican Civil War (1977-1992), during which

fauna was hunted for sustenance and military equipment/ivory exchange (Daskin et al. 2016). This war devastated a place that was known as a sanctuary for a variety of large mammals, including buffalo, blue wildebeest, zebra, waterbuck, impala, and hippopotamus (Stalmans et al. 2019). The park's revival commenced in 2008 with the establishment of the Gorongosa Restoration Project by a non-profit organisation. This initiative, which signed a 20-year co-management agreement with the Mozambican Government, concentrated on conservation, science, and human development. The project was extended for an additional 25 years in 2018 (Stalmans et al. 2019).

Geographically, GNP is between -19.44799 and -18.01795 of latitude and within 33.91316 and 34.89479 of longitude. On the west GNP is bounded by Gorongosa Mountain and on the east by the Cheringoma Plateau. Gorongosa Mountain was proclaimed part of GNP in 2010 and is home to many endemic species. It is also where many rivers start and flow to Lake Urema, the largest body of permanent water within the park, as well as the many water courses within GNP landscapes. The climate is predominantly tropical, with a dry season spanning from May to November and a rainy season from December to April (Tinley 1977). Annual rainfall ranges from 700-900 mm in the Rift Valley floor, reaching higher levels of over 2000 mm on Gorongosa Mountain (McWethy et al. 2016; Müller et al. 2012). Every year, GNP floods in the rainy season and about 40% of the park is underwater (Tinley 1977).

Geologically, GNP hosts the southern end portion of the East African Rift System which is generally characterised by alluvial deposits with colluvial material deposited at the bottom of the Cheringoma Plateau. The Cheringoma Plateau consists of grauwackes and limestone with impermeable horizons and soils with low pH and high phosphorus content, which contribute to the fast bone weathering. Between the Rift Valley and Gorongosa Mountain, there are the Midlands, mostly underlain by gneisses and pegmatites with many dolerite dykes and sandy

and fersiallitic soils, which also contribute to quick bone weathering due to dissolving hydroxyapatite, the main bone component (Stalmans and Beilfuss 2008).

The hydrology of the park consists of a multitude of rivers and streams. These water sources start from Gorongosa Mountain, Midlands and Cheringoma Plateau and end in the Rift Valley with Lake Urema as the centre of water accumulation, and draining its water to the Indian Ocean through the Pùngué River (Stalmans and Beilfuss 2008). During the dry season, some pans (wetlands with waterlogged soils and/or aquatic vegetation) maintain water until the next rainy season while others are seasonal. Permanent pans are well-mapped and described in the park.

Unpaved roads, locally called 'picadas', are used in the park for patrolling and tourism purposes. Only 20% of GNP is covered by the road network, most of which is in the south of the park close to the main camp, Chitengo, and the Community Centre of Education (Figure 4-3, where roads are depicted).

Currently, GNP has over 8000 species of fauna and flora identified, among which 825 are vertebrates (Gorongosa Biodiversity Database). Among these are five primate species: grey-footed chama baboons (*Papio ursinus griseipes*), vervet monkeys (*Chlorocebus pygerythrus*), Samango monkeys (*Cercopithecus mitis erythrarchus*) and two species of galago (*Otolemur crassicaudatus* and *Paragalago granti*). Of the approximately 230 troops of baboons recorded in the park, six individuals of the two troops (three individuals per troop) were collared and are being monitored since 2018.

The reintroduction of fauna in Gorongosa National Park has been part of a restoration agreement signed in 2008 between the Carr Foundation and the Mozambican government. Among the many species reintroduced, notable predators include leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), African wild dogs (also known as painted wolves, *Lycaon*

pictus), and golden jackals (*Canis aureus*). These carnivores were firstly introduced in 2018, 2022, 2018, and 2022, respectively. Currently, seven leopards, 19 hyenas, seven golden jackals, and more than 200 wild dogs are present in the park (data from Gorongosa annual reports). Wild dogs were first introduced in 2018 and then again in 2019 from South Africa. The Park started with the introduction of these carnivores after the period of this study. According to the data from camera traps and direct observation, some hyenas have already started repopulating the park.

By 2016, the carnivore team, under the Restoration Project recovered the lion population from below 20 to about 104 (Bouley et al. 2018) and more than 200 in 2025 (Carnivore Team, personal communication, 2025). Before the Civil War, lions and wild dogs were the main ecological controllers of the herbivores (Bouley et al. 2021).

4.2.2. Data collection

Bone surveys

Bone collections were carried out from 2016 to 2023 using transects, plots and opportunistic methods. The opportunistic method consists of surveys by researchers conducting different projects and opportunistically recorded carcasses around places of their data collection. Nineteen transects (six in annually and 13 in non-annually flooding landscapes) were carried out in 2017 and 2019. The transects consisted of lines of 5 km in length and 50 to 100 m in width. Ninety-six (96; 32 in annually and 64 in non-annually flooding landscapes) plots were designed and surveyed in 2021 and 2023 to better compare the data with other sources of data such as camera traps and biennial aerial surveys. For each specimen, species, sex, age, weathering stage, GPS points, minimum number of individuals (MNI), and minimum number of elements (MNE) were recorded.

Spatial data extraction and integration

Spatial data for roads, rivers, lakes, and pans were obtained from Gorongosa scientific reports and other publications (Stalmans et al. 2019; Stalmans and Beilfuss 2008). To accurately measure distances and extract environmental data for our analysis, we utilised spatial data from landscape type, roads, rivers, pans, and Lake Urema in GNP. We calculated the minimum distances from each carcass to the nearest road, pan, river, Lake Urema boundary. Relevant shapefiles were imported and transformed using the *sf* package (Pebesma and Bivand 2023), ensuring that all coordinate reference systems matched (CRS = 4127). This approach allowed us to quantify environmental variables critical for understanding the factors influencing primate and non-primate carcass distribution in GNP.

4.2.3. Data analyses

Using a binary response variable (primate vs. non-primate taxa), we applied Generalized Linear Models (GLMs) to identify key predictors. The best-fit model was selected based on the lowest Akaike Information Criterion (AIC) and VIF (Variance Inflation Factor) using the *car* package (Fox and Weisberg 2019), for removing multicollinear variables. Additionally, we used Fisher's Exact Tests to investigate whether the bone abundance of primates significantly differs from that of other mammal taxa across annually and non-annually flooding landscapes in GNP. This integrated approach highlights the crucial role of environmental variables in shaping both primate carcass distribution and bone abundance patterns.

All statistical analyses were conducted in R v. 4.4.1 (R Core Team 2024) , and RStudio v. 2024.12.0+467, 64 for MacOS (Posit Team 2024) with α set at 0.05. The original code can be found in the repository available in the link: https://github.com/jacintomathe/Mathe_paper_four.git. The spatial data analyses and visualisation were conducted using Quantum Geographical Information System (v. 3.32.2; (Moyroud and Portet 2018) and v. 4.4.1 (R Core Team 2024).

4.3. Results

For the analyses, we used 266 specimens representing 18 different mammal species: 17 carcasses of chacma baboons and 249 for the other mammalian taxa documented over a seven-year period in GNP (2016-2023). The complete list of analysed mammalian species and their relative abundance across landscapes of GNP is provided in Figure 4-5.

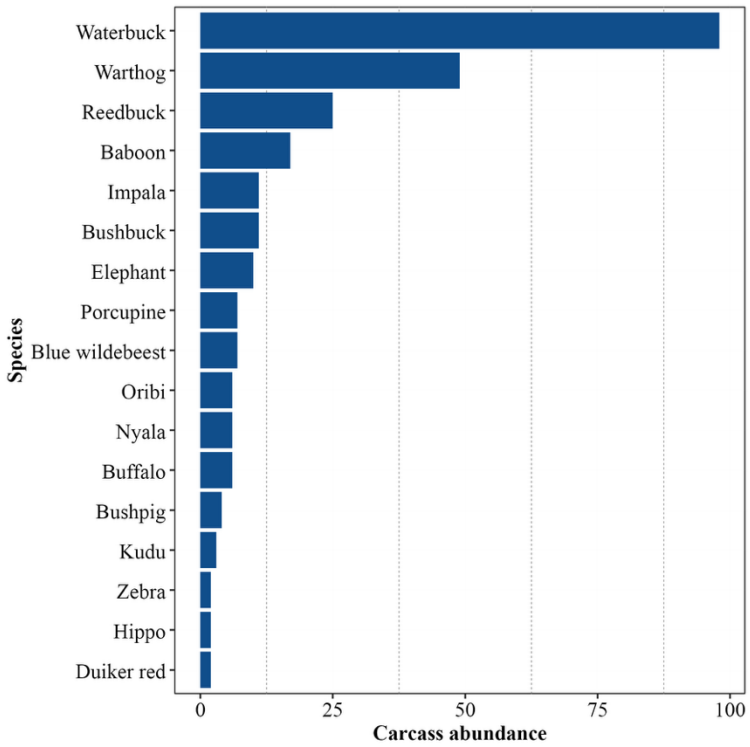


Figure 4-5. Abundance of mammalian carcasses recorded across GNP.

The proportion of primates vs non-primates, displayed in Figure 4-6, highlights that there are more non-primates than primates recorded overall (Figure 4-6A) in bone surveys in the ecosystems of GNP (Figure 4-6B). Primate carcasses in the annually flooding areas are twice as abundant as in the areas that rarely flood (Figure 4-6A and B).

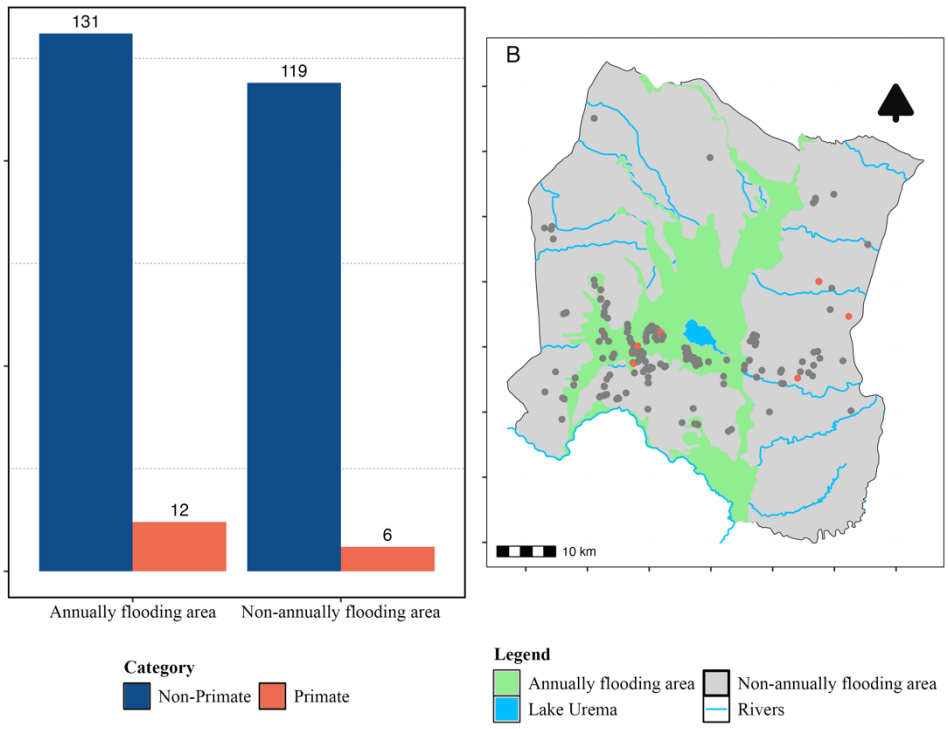


Figure 4-6. Number of carcasses in annually flooding and non-annually flooding areas (A). Map of the distribution of primate and non-primate carcasses in the landscapes of Gorongosa National Park (B).

4.3.1. Ecological influence on the likelihood of recording primate carcass

In the Generalized Linear Models (GLMs), although we found that proximity to rivers wasn't significant (p = 0.072 see Table S 4-1), there was a general trend such that close to the rivers there is a slightly higher number of primate bones than further away. Distance to roads and estimated proximity to Lake Urema and pans did not significantly impact primate bone occurrence (p > 0.05 see Table S 4-1). Similarly, flooding does not affect primate bone occurrence as bone numbers deposited in flooding landscapes are not significantly different from non-flooding areas (p > 0.05). The results further revealed that despite not being significant, proximity to rivers positively affect primate bone occurrence (estimate = 0.12, p = 0.072). However, in annually flooded areas, the opposite pattern prevails: proximity to rivers shows negative impact on primate bone occurrence (estimate = 0.135, p < 0.05 in Table S 4-1).

4.3.2. Bone abundance in annually and non-annually flooding landscapes in GNP

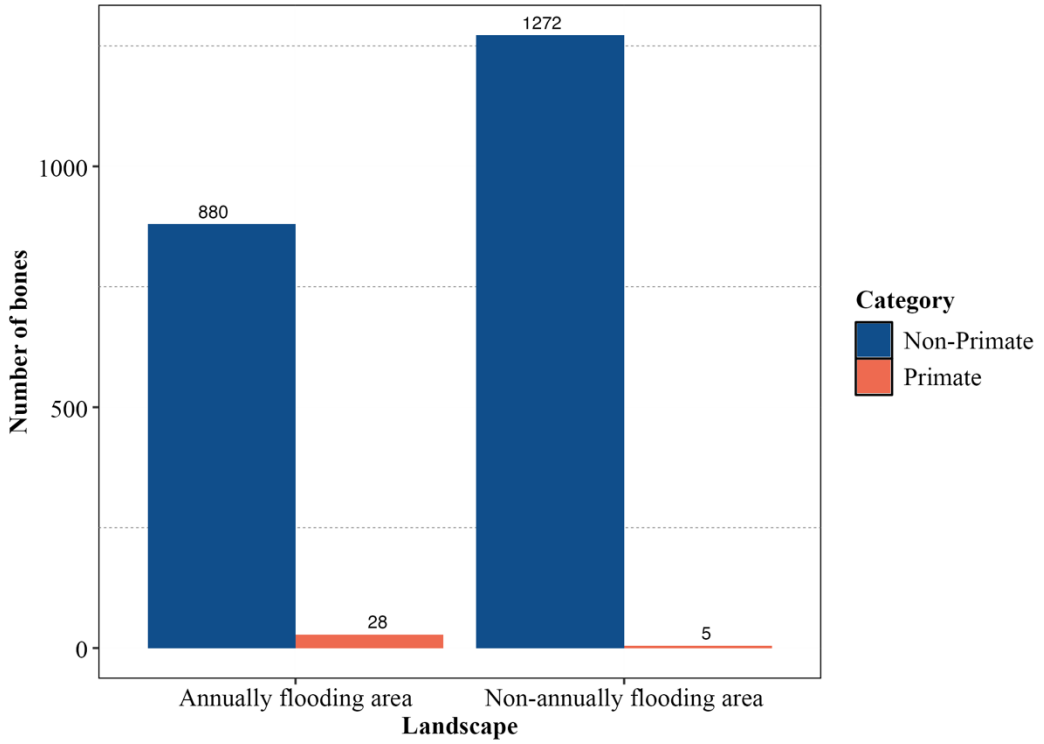


Figure 4-7. Number of bones of primate and non-primates across the annually and non-annually flooding landscapes in GNP.

The results from the Fisher's Exact Test indicate that the landscape type (annually and non-annually flooding) significantly influence the bone deposition of primate nor non-primates ($p < 0.05$), with annually flooding landscapes harbouring slightly higher proportion of primate bones and lower proportion of non-primate bones. In contrast, non-annually flooding landscapes harbour a greater proportion of bones of non-primates than of primates.

4.4. Discussion

The high representation of larger herbivore carcasses such as waterbuck and warthog in the osteological surveys of GNP, as shown in Figure 4-5, may indicate high mortality rates in open landscapes or differential carcass preservation due to body size and predator preferences. The lower representation of primates could be attributed to the resilience of primate species during periods of food scarcity in the long dry seasons. Primates often have access to alternative food sources (Conklin-Brittain, Wrangham, and Hunt 1998; Wrangham, Conklin-Brittain, and Hunt 1998) such as fruits and plant bulbs from succulent species, making them less susceptible to starvation, and thus primate death rates may be lower, resulting in fewer bone remains. In contrast, herbivores, which rely heavily on grass and shrubs, face fewer alternatives when these food sources dry out, leading to higher mortality rates. Other factors that may affect primate carcass abundance include ecological influences, which are explored and discussed in further detail below. In addition, the life history of primates may play a significant role. Baboons can live up to 45 years in captivity and 30 years in the wild (Rhine, Norton, and Wasser 2000), while vervet monkeys have a maximum lifespan of around 30 years (Kingdon 2013a). In the absence or scarcity of their primary predators, baboons and vervets likely have reduced mortality rates. Currently, in GNP, there is a repopulation of leopards due to reintroductions and new births from reintroduced individuals. Despite this repopulation, the leopard population remains low. Consequently, vervet monkeys and baboons are less abundant in bone assemblages compared to species of similar body mass, such as bushbuck, impala, and oribi, whose remains are almost comparable to their living populations (Chapter Two). This discrepancy can be explained by two factors: predation and lifespan. These herbivore species live two to three times shorter lives than vervet monkeys and baboons, making their remains more prevalent in bone collections. Additionally, the primary predators of impala, oribi, and bushbuck are in higher abundance,

with an estimated 200 lions in the park according to the latest carnivore team count and aerial survey (Bouley et al. 2018; Stalmans and Peel 2022).

Furthermore, the birth rates and lower death rates of these primates contribute to their population growth and stability in the ecosystem. For instance, vervet monkeys typically have a birth rate of around one offspring every 1-2 years (gestation length of 163 days) per female and a death rate of about 2% per year, while baboons have a slightly slower reproduction rate, with females giving birth approximately every three years (20-28 months of inter-birth interval) (Hill 2000; Kingdon 2013a) and only 3-4% of the population die per year (Rhine et al. 2000). On the other hand, impala, oribi, and bushbuck have potentially rapid population growth indicated by shorter gestation periods (less than eight months) and inter-birth intervals below 18 months (Kingdon 2013b) and higher death rate of at least 20% and shorter longevity, 12, 14, and 18 years for bushbuck, oribi, and warthog, respectively (Kingdon 2015). This implies that these herbivores will contribute greater numbers of carcasses to the ecosystem.

The Generalized Linear Models (GLMs) for predicting the likelihood of finding primates over other taxa based on the ecological variables revealed that water bodies, particularly rivers, have a significant influence. However, other factors do not have any significant influence in this analysis. Our analysis indicates that in contrast to other taxa, primate remains are preferentially accumulated closer to water bodies. Water bodies may be avoided by primates as a strategic adaptation to minimise predation risk. Rivers, pans and lakes are known to be ambush sites for predators such as lions and wild dogs, especially during the dry season when these water sources become critical for survival (Hutson 2016). Furthermore, despite primates being less water-dependent compared to other species, particularly grazing species like oribi, waterbuck and impala, a fact that would contribute to a low abundance of primate carcasses close to water bodies known as high-risk areas for predation (Hill 2000, Kingdon 2013), they cross rivers, especially when water levels are lower during the dry season

(Lewis-Bevan et al. 2025). During the river crossing, they are more likely to be caught by crocodiles, which camouflage themselves under mud and plants (unpublished camera trap videos). These observations of individuals crossing rivers, which contribute to the higher risk to be caught by predators such as crocodiles underscores the importance of seasonal mobility and expanded home ranges in shaping mortality risk. This pattern—where floodplain river crossings increase vulnerability to predation—offers a valuable framework for interpreting the relationship between seasonality, ecology, and the occurrence of hominin remains, particularly regarding the extent of carnivore damage and predation signatures observed in the palaeoanthropological record of Eastern and Southern Africa.

A higher abundance of primate carcasses near rivers than in areas further away is supported by the higher number of carcasses found in flooding regions of GNP, which is twice as many as those recorded in areas that do not experience annual flooding. These observations may be linked to the behaviour of primates during the change of the season, particularly from dry to rainy seasons. Primates living in the floodplain tend to have larger home ranges compared to those in woodland areas (Hammond et al. 2022). Expanding their home range requires considerable effort, as flooding forces them to cross rivers such as the Mussicadzi, Sungue, and Urema in search of safer areas. Previous studies have shown that during the rainy season, baboons in floodplains move towards the southern part of the park, which is elevated and drier (Hammond et al. 2022). During this movement, a significant number of individuals, particularly the infected and weaker ones, may perish.



A-Baboon river-crossing



B - Pans (water marshes)



C-Annually flooding landscapes (rivers)



D-Annually flooding landscape



E-Bone patch



F-Roads (picadas)

Figure 4-8. A female baboon ventrally carrying a juvenile jumps to cross the shallow Mussicadzi River, Photo: Lee Bennett, 2018 (A). A pan during the rainy season with a baboon and a sable antelope (B). Pùngué river during the transition from dry to rainy season (C). Floodplain durig the peak of rainy season (D). Bone patch on sodic soil during dry season (E) and roads (picada 3) at the end of rainy season (F).

Baboons in the park face a range of natural threats, with leopards being their primary predators. However, the low abundance of leopards in the area suggests that other factors may

contribute more significantly to mortality. Notably, crocodiles, which have been observed to move up to 300 m from the water (field observation from camera traps videos), may play a key role in the distribution of primate carcasses. This suggests that although some baboons may die from injuries or infections away from water sources and subsequently carried to rivers or Lake Urema by crocodiles. The observed accumulation of primate carcasses near water could also be influenced by a variety of other factors. Changes in baboon home ranges during the rainy season could lead to higher mortality in flooding areas, where conditions are harsher and movement more difficult (Beardmore-Herd et al. 2025).

The findings of this research also provide a foundation to test whether ecological influences vary by species group. For example, some fossil sites, such as the Mursi Formation, contain few primate fossils. This scarcity may not only reflect the absence of predators that preferentially targeted primates but could also result from taphonomic factors—such as bone decomposition and preservation conditions—that were unfavourable for primate remains. Insights from Gorongosa, where baboons and vervets have been reported transporting their kills to yet not identified locations (Video available here), suggest that similar behaviours in the Mursi palaeoenvironment may have influenced bone distribution. If primates at Mursi dragged carcasses into habitats with higher soil pH or more acidic conditions (Behrensmeyer 1978), this could have accelerated bone decay and reduced the likelihood of fossil preservation.

Future research could focus on tracking fresh carcasses within the floodplain, using GPS devices attached to them and increasing the number of collared baboons in the floodplain. This approach would provide insights into baboon movement patterns across different seasons and allow for a more detailed understanding of how environmental factors influence mortality and carcass movement. Seasonal bone surveys in the same baboon home range could complement this data, shedding light on seasonal carcass accumulation over time. Moreover, long-term monitoring of the two baboon troops studied previously would help assess population turnover

and identify the primary causes of mortality under varying environmental conditions. This research could provide valuable information for conservation efforts, particularly in understanding how different species interact with their environment and the factors influencing their survival.

The insignificance of distance to roads, and proximity to predators (lions, wild dogs, and leopards), in impacting primate carcass occurrence contradicts the initial predictions and suggests that these factors are less critical in shaping primate bone distribution in GNP. The minimal impact of these variables highlights the unique role that water bodies play in the spatial patterns of primate carcasses. The insignificance may also be related to the fact that leopards are in low abundance in GNP having been detected only once via camera traps.

This insignificance is supported by the fact that in other African ecosystems, leopards (*Panthera pardus*) are well-documented as primary predators of baboons, highlighting a predatory relationship that can significantly influence primate populations. For example, in Moremi Game Reserve, Botswana, leopards frequently prey on chacma baboons (*Papio ursinus*), utilising ambush tactics that exploit the dense vegetation and open water sources where baboons gather, making them accessible despite their social vigilance (Busse 1980). Similarly, studies in the Ngorongoro Conservation Area, Tanzania, show that leopards opportunistically target baboons, particularly during periods of food scarcity, when they become a key dietary component (Bertram 1982).

In Phinda Private Game Reserve, South Africa, leopards are the main natural predators of baboons, with observed hunting strategies adapted to the savanna-woodland mosaic that characterises this region (Balme et al. 2007). Here, leopards rely on their stealth and climbing ability to capture baboons near their roosting sites. Additionally, Mahale Mountains National Park, Tanzania, provides another example of leopards preying on olive baboons (*Papio anubis*),

often targeted when moving on the ground or away from their sleeping trees (Nishida, Uehara, and Nyundo 1979).

These examples illustrate that, in areas like Moremi, Ngorongoro, Phinda, and Mahale, leopards occupy a crucial ecological niche as primary predators of baboons. The abundance of leopards in these areas correlates with notable impacts on baboon populations and carcass availability, particularly in habitats where baboons constitute the primary prey of leopards. In contrast, GNP lacks a sufficient predator population to influence primate carcass abundance, highlighting the distinct ecological dynamics in GNP relative to other African ecosystems.

Primates often live in social groups that provide several benefits, including enhanced vigilance and collective defence mechanisms. These social structures likely contribute to the lower predation rates for primates enhancing lower bones recorded in the landscape. However, other causes of death, such as infanticide and secondary infection of injured individuals, may maintain population stability (Kingdon 2013a).

This analysis underscores the importance of specific environmental features, particularly water bodies, in understanding primate and non-primate carcass occurrences in GNP. These findings provide valuable insights for conservation and management strategies, emphasizing the need to consider species-specific behaviours and ecological needs. By focusing on the unique role of water bodies and the adaptive strategies of primates, conservation efforts can be better tailored to protect these species and maintain the ecological balance in GNP.

Fisher's Exact Test indicates significant differences among landscapes of GNP concerning the bone abundance of primates with non-flooding landscapes showing slightly higher occurrence of non-primate and lower primate bones. Conversely, annually flooding landscapes harbour a higher density of primate bones and a lower density of non-primate bones.

This could be explained by the methodological approaches employed, as the osteological surveys are affected by visibility, accessibility by road and sampling effort. The flooding landscapes (Rift Valley Riverine & Floodplain) are more open and provide higher visibility for osteological surveys (Stalmans & Beilfuss, 2008), and higher numbers of primate carcasses were found in these landscapes. Flooding landscapes are also more accessible by road (Stalmans & Beilfuss, 2008), which facilitates osteological surveys. However, the sampling effort was higher in non-annually flooding landscapes (13 transects and 64 plots) than in annually flooding landscapes (6 transects and 32 plots).

In general, the low abundance of primates in the Gorongosa bone assemblages, despite their high abundance in aerial surveys, suggests that their scarcity or absence in the fossil record does not necessarily indicate a true absence or low population in past landscapes that may have been geologically and ecologically similar to Gorongosa National Park (Bobe 2011, Reynolds and Bobe 2022). Instead, it may reflect that primates were differently affected by taphonomic processes and ecological and demographic factors that influenced the preservation of other taxa. This underscores the importance of targeted sampling strategies to optimise the discovery of primate fossils.

From these insights, one could further this research by increasing the sampling effort targeting the analysed features (lakes, rivers, pans, and roads) and applying the modern technology to track carcasses in both type of landscapes to further understand other variables that may influence bone deposition in GNP. For instance, baboons have been reported to carry their infants after death, but there is not report of accumulating them in specific locations, but it could happen that the places they are left were not targeted in this study and or are not accessible, but with the application of for example GPS tracking devise, one would understand where they are mostly and perhaps be found, which would contribute to some adjustment to the methodology applied in this study. Apart from increasing the sampling effort, one could also

consider increasing the sample size and analysing the data using the same approaches to better understand the fossilization process under different terrain conditions and the ecology of GNP.

4.5. Conclusion

The bone assemblage in Gorongosa National Park reveals a disparity: the number of baboons in the assemblage does not reflect their abundance in the living community. Our results show that primate carcasses are more frequently found near rivers, while non-primate carcasses tend to accumulate further away from these water bodies. Furthermore, our findings indicate that the distribution of primate bones differs significantly from that of other mammals, with the higher number of primate bones observed in the annually flooding landscapes than in non-flooding landscapes. These findings challenge assumptions about the scarcity of primate fossils at sites like the Mursi Formation. Rather than signifying a low abundance of primates in these ancient ecosystems, such patterns may instead reflect ecological factors—particularly the role of water sources—influencing fossil preservation and accumulation. Further studies should also focus on automated detection methods (e.g., camera traps and GPS tracker devices) to examine crocodile and other predator interactions with primate carcasses, as well as primate involvement in carcass distribution and bone deposition. Additionally, further studies with increased sample size would shed light on the variables that contribute to primate carcass absence in some ecosystems and scarcity in others. These research outcomes have implications for our understanding of primate bone accumulations in the African fossil record.

4.6. Supplementary materials

Table S 4-1. GLM outputs of the Influence of ecological variables on the likelihood of recording primate carcasses. In blue are the significant GLM outputs.

term	estimate	std.error	statistic	p.value
term	**estimate**	**std.error**	**statistic**	**p.value**
(Intercept)	0.03	1.283	-2.72	0.006
landscapeNon-annually flooding area	1.073	1.474	0.048	0.962
mDist_to_UREMA	2.627	0.96	1.006	0.314
mDist_to_road	0.863	1.706	-0.087	0.931
mDist_to_gnp_pans	1.654	0.703	0.716	0.474
mDist_to_river	0.135	1.115	-1.798	0.072
landscapeNon-annually flooding area:mDist_to_UREMA	0.158	1.208	-1.529	0.126
landscapeNon-annually flooding area:mDist_to_road	1.032	1.766	0.018	0.986
landscapeNon-annually flooding area:mDist_to_gnp_pans	1.688	0.972	0.539	0.59
landscapeNon-annually flooding area:mDist_to_river	13.246	1.256	2.057	0.04

Chapter Five. Discussion: Exploring mammalian bone fossil deposition in the EARS during the Plio-Pleistocene

Palaeoecological reconstructions of human evolutionary history rely on the information preserved in fossil assemblages to infer the composition of past communities. However, some ancient environmental conditions may lack direct analogues in modern ecosystems. As a result, our interpretations may not always yield reliable insights for testing evolutionary hypotheses. Taphonomy therefore offers critical data on the characteristics of past communities based on inferences drawn from durable remains, such as bones and shells. As such, bone surveys are invaluable for evaluating the relationship between mammalian bone assemblages and their source communities. They provide insights into population dynamics, species diversity, community structure, and changes in modern mammalian populations.

In this chapter, I will review key Plio-Pleistocene fossil sites within the Eastern African Rift System (EARS), focusing on their significance for understanding hominin evolution and behavioural ecology. I explore how the palaeoenvironments of these sites compare to those of Gorongosa National Park (GNP), which represents a modern analogue to many terrestrial palaeontological contexts where mammalian relative abundance data have been recovered. I then summarise the main findings of the empirical chapters, highlighting their contributions to the existing literature including their implications for palaeoecological reconstruction of Plio-Pleistocene environments, their limitations in addressing the central research questions, and the future directions required to bridge the remaining gaps in our understanding.

5.1. Introduction

Most of the palaeontological and archaeological record of early human evolution in Africa comes from two distinct settings: depositional environments in the East African Rift Valley System (EARS) and caves in South Africa. In these settings, zooarchaeological records are used to understand the evolution of hominin dietary habits, language, and culture (Binford 1981, Domínguez-Rodrigo 1999) Importantly, associating zooarchaeological with hominin records is fundamental for better understanding the factors that drove our evolution. And yet it remains unclear why i) both records (zooarchaeological and hominin) are not randomly distributed across African landscapes in the EARS, but deposited in specific places, such as tree lines, hills and swamps (Tappen 1995), and ii) the bone elements of carcasses are not equally represented in the fossil records (Behrensmeyer and Hill 1980). These gaps cannot be filled without a knowledge of what was fossilised in different epochs and the local ecologies at the time in relation to what happens with carcases in modern environment (Western and Behrensmeyer 2009). For instance, recent analyses using modern bones to reconstruct the fossil record refined our inference about the environment in which ancient hominins lived (Callaway 2022; Tsutaya et al. 2025) and their locomotion (Karoui Canedo et al. 2024; Meyer et al. 2023).

In this thesis, I first reviewed neotaphonomic studies focused on assessing species abundance and diversity in living vertebrate communities, based on modern bone assemblages from open-ground landscapes (excluding caves) in Africa. This involved: i) Exploring the primary ecological factors influencing bone deposition across various African ecosystems; ii) Explaining key biases in mammalian bone assemblages compared to living communities; iii) Discussing methodological challenges and identifying knowledge gaps; and iv) Highlighting target locations for future neotaphonomic research in Africa.

After addressing these elements, I proposed tentative answers and outlined specific methodological steps for conducting innovative empirical studies to test the accuracy of modern faunal assemblages in reflecting the abundance and diversity of living vertebrate communities.

Of the six key research gaps identified in Chapter One and summarized in Table 1-1, in this thesis, I addressed three of them. First, I presented a novel multi-method approach (aerial surveys, bone surveys, and camera traps) to evaluate how closely mammalian bones in open-ground landscapes mirror the living mammalian communities they originate from ("live-dead fidelity") within the heterogeneous Rift Valley ecosystem of Gorongosa National Park (GNP). Second, I examined whether ecological variables—such as lakes, rivers, pans, roads, and habitat types—impact mammalian bone accumulation in open-ground landscapes of GNP. Lastly, I investigated the factors driving the scarcity of primates in modern bone surveys conducted in open ground landscapes of Africa such as Amboseli NP, Virunga NP and Gorongosa NP, and in fossil sites like Konso, Omo Shungura, Nakuchui, and Mursi formations (Reynolds and Bobe 2022). I approached these issues by empirically testing whether i) landscape type, proximity to roads, and water sources (pans, rivers, and lakes) are ecological variables that predict primate carcass occurrence relative to other mammal taxa, and ii) the density of primate bones significantly differs from that of other mammals in annually and non-annually flooding landscapes of GNP.

Given the answers to each of the outlined questions that formed the chapters of the thesis, in this discussion chapter, I review data from some Plio-Pleistocene fossil sites in the EARS in which there are palaeontological records regarding relative abundance of mammalian taxa. These taxa have been used to infer the ancient mammalian diversity and reconstruct the palaeoenvironments. Additionally, I integrate insights from empirical chapters of this thesis, employing a relative abundance of mammalian taxa, particularly bovids used to reconstruct the palaeolandscapes of the Plio-Pleistocene fossil sites in the EARS. This discussion aims to

enhance our understanding of fossil site formation and its implication for our understanding of human evolution.

The Pliocene and Pleistocene epochs are highlighted in this discussion as they represent pivotal transitional phases in mammalian evolution, characterized by global cooling and increased climatic and environmental variability (Bobe and Eck 2001). These epochs also coincide with the geological context of the southern extent of EARS in Mozambique (Bobe et al. 2023; Coelho, Anemone, and Carvalho 2021; Habermann et al. 2019).

GNP hosts the southernmost portion of the EARS and is the first national park in this setting where modern bone surveys have been conducted with the aim of understanding how the diversity and relative abundance of carcasses reflect the living mammalian community, which is the focus of this thesis. Several fossil sites across the EARS are geologically and ecologically like GNP.

5.2. Plio-Pleistocene fossils site formation in the EARS

The East African Rift System (EARS) is a prominent example of continental rifting, where the African continent is gradually splitting into separate landmasses. This extensive rift system extends approximately 6,400 km from the Afar region in northeastern Ethiopia southward through eastern Africa to Mozambique (Habermann et al. 2019). EARS has two branches, Eastern (Gregory Rift) and Western (Albertine Rift) (Reynolds and Bobe 2022). Eastern branch runs through Ethiopia, Kenya, and Tanzania. It is characterised by significant volcanic activity, leading to the formation of numerous volcanoes and highlands (Michon, Famin, and Quidelleur 2022). Western branch extends through Uganda, Rwanda, Burundi, and the Democratic Republic of Congo. This branch is marked by deep basins that have evolved into some of the world's largest and deepest freshwater lakes, such as Lake Tanganyika and Lake Malawi (Michon et al. 2022). EARS exemplifies the intricate processes of continental

rifting, influenced by both tectonic forces and magmatic activities, leading to the gradual separation of the African continent and the formation of new geological features.

Eastern Africa hosts one of the richest records of hominin evolution, largely preserved in a variety of tectonically and volcanically active basins. In Ethiopia, Plio-Pleistocene fossil sites include Middle Awash (encompassing Sagantole, Bouri, Maka, Bodo, Belohdelie, Matabaietu and Gamedah localities), Hadar, Dikika, Ledi-Geraru, Kesem-Kebena, Mille-Logya, Woranso-Mille, Buia (Dandiero Basin), Asbole, and Melka Kunture (Bobe and Reynolds 2022). These sites, mainly located within the Afar Triangle and the Ethiopian Highlands, have yielded some of the most important fossil assemblages for understanding early hominin morphology and environmental context.

In Kenya, critical stratigraphic formations and fossiliferous regions include the Koobi Fora and Nachukui Formations, Kanapoi and Ekora in the Turkana Basin. Other significant localities include Chesowanja (Chemoigut Formation), Kantis and the Homa Peninsula (Kanam, Homa, Rawi, and Kanjera Formations) (Bobe and Carvalho 2019; Bobe and Reynolds 2022).

In Tanzania, the fossiliferous regions of Laetoli (Lower and Upper Laetolil Beds, Ndolanya Beds), Olduvai Gorge (Beds I–IV and Masek Beds), Peninj, and the Manonga Valley (Ibole, Tinde, and Kiloleli Members) are fundamental to reconstructing Plio-Pleistocene hominin evolution and behavioural ecology (Bobe and Reynolds 2022; Leakey et al. 1976; Leakey and Hay 1979).

In Malawi, the Chiwondo Beds contribute key data from the southern Rift (O. Kullmer et al. 1999; Ottmar Kullmer et al. 1999; Kullmer 2008; Lüdecke, Schrenk, et al. 2016). In Mozambique, Gorongosa National Park is emerging as a new fossil-bearing region in the southernmost rift (Bobe et al. 2023; Habermann et al. 2019).

This extensive geographic and stratigraphic diversity reflects the complex tectonic history of the East African Rift System and provides the context where most of the evidence for early human evolution comes from. This evidence improves our perception environmental change, faunal turnover, and adaptive landscapes through the Neogene and Quaternary periods.

5.3. Environments of the Plio-Pleistocene fossil sites in the EARS

Some of the Plio-Pleistocene fossil sites have a record of relative abundance of mammalian fossils that has been systematically recorded, and these data that may be comparable with modern bone collection from Gorongosa National Park. Bovid tribes are often used in palaeoenvironmental inferences. Here I present data on tribes that are present in twelve Plio-Pleistocene fossil sites (Figure 5-1) but differ in terms of their relative abundance. Therefore, I discuss the main differences in terms of their reconstructed palaeoenvironments.

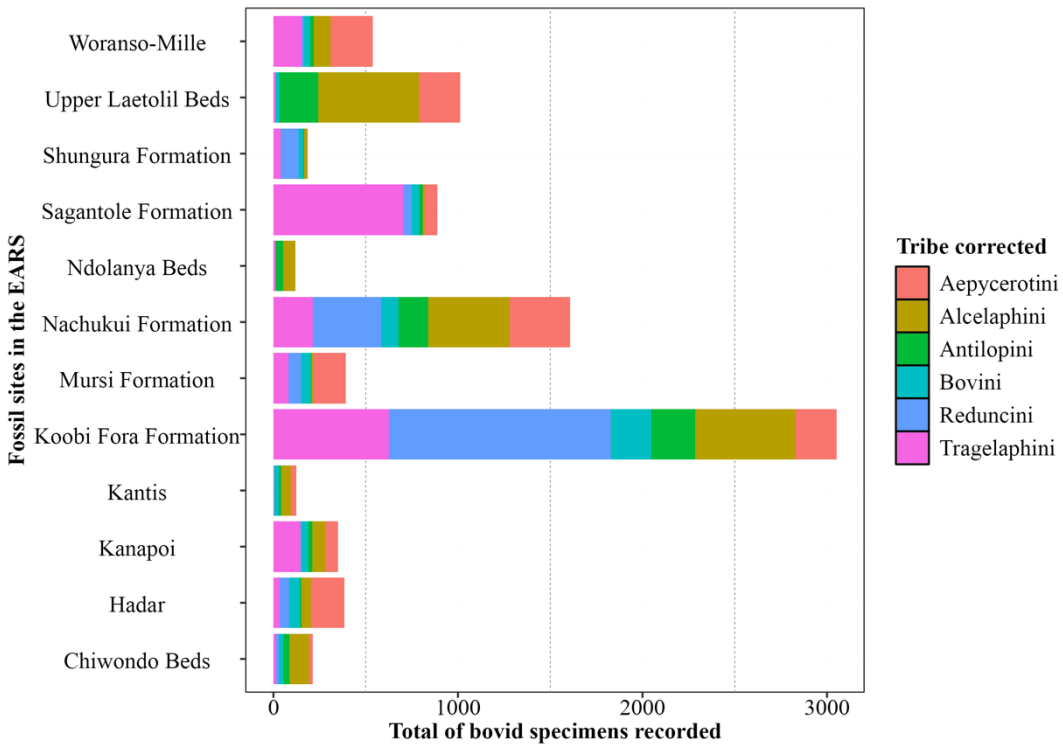


Figure 5-1. Plio-Pleistocene fossil sites in the EARS with relative abundance of bovid tribes. Data from the PaleoTurkana Database (Bobe and Carvalho 2019) and Reynolds and Bobe (2022).

The palaeoenvironments of Woranso-Mille, Laetoli, and the Shungura Formation reveal notable differences in habitat structure during the Plio-Pleistocene epochs (Reynolds and Bobe 2022). Woranso-Mille is characterised by extensive grasslands dominated by *Theropithecus oswaldi*, alongside well-developed riparian woodlands, indicating a mosaic landscape with strong aquatic influences, such as rivers and lakes (Curran and Haile-Selassie 2016), whereas Laetoli's Upper Laetolil Beds are more arid, with open habitats and limited woodland restricted to seasonal watercourses, and little aquatic influence (Andrews and Bamford 2008; Kingston and Harrison 2007; Musiba et al. 2008). On the other hand, the Shungura Formation presents a more complex setting, with grasslands embedded within diverse fluvial, lacustrine, and deltaic systems, and intermittent aquatic phases. Geological complexity also varies: Woranso-Mille's river-lake ecosystems show moderate geological development, Laetoli's landscape was heavily shaped by volcanic activity and tuff deposits, and the Shungura Formation offers an exceptional sedimentary record spanning over 2.6 million years, allowing detailed reconstructions of environmental change.

The Sagantole Formation at Gona, dating to the early Pliocene represents a heterogeneous palaeoenvironment characterised by a dynamic mosaic of habitats (Wynn, Dumouchel, and Drapeau 2023). Sedimentological and faunal evidence indicates a landscape comprising a mix of open grasslands, wooded areas, and permanent water bodies, shaped by fluvial and lacustrine processes with strong volcanic influence (Quade et al. 2008). The presence of both grazing and browsing fauna, including *Eurygnathohippus, Tragelaphus, Kuseracolobus*, and aquatic taxa such as crocodiles and hippopotamids, reflects a mix of C_3 and C_4 vegetation and varied ecological niches (Bernor et al. 2013). Overall, the formation suggests a patchy environment with woodland, forest, grassland, and wetland elements, offering a diverse habitat for early hominins such as *Ardipithecus ramidus* (Fredieu et al. 2007).

The Nachukui Formation, spanning from around 4.3 to 0.7 million years ago, reflects a long and complex palaeoenvironmental history in the western Lake Turkana Basin. Comprising alternating fluvial and lacustrine deposits, the formation reveals a dynamic landscape influenced by changing lake levels and sedimentation patterns. During the earlier phases (4–2.5 Ma) carbon isotope and faunal data indicate a dominance of woodlands and wooded grasslands, transitioning to more open C_4 grasslands after 2 Ma (Uno et al. 2016). Faunal assemblages, particularly bovid distributions, suggest significant environmental heterogeneity, with West Turkana generally more open than nearby regions like the Omo or East Turkana (Harris et al. 1988).

The Upper Ndolanya Beds at Laetoli, Tanzania, dating to 2.6 million years ago, represent a semi-arid bushland—considerably drier and more open than the earlier Laetolil Beds (Kovarovic, Andrews, and Aiello 2002; Su 2011). The vertebrate fossil assemblage from the Mursi Formation is notable for its high proportion of suids (44%) and relatively low proportion of bovids (14%), compared to other Pliocene African sites (Drapeau et al. 2014). Additionally, there is an unusually high frequency of deinotheres (7%). Stable carbon isotopic analyses of these mammals suggest diets predominantly based on C_3 plants, reinforcing the interpretation of a closed, forested environment (Andrews et al. 2011; Drapeau et al. 2014). The Mursi Formation represents a humid, forested ecosystem with adjacent low energy freshwater sources during the Early Pliocene (Drapeau et al. 2014). This environment contrasts with the more open, arid landscapes of nearby contemporaneous formations. The unique combination of dense vegetation and aquatic habitats likely influenced the distribution and evolution of the resident fauna (Drapeau et al. 2022; Reynolds and Bobe 2022).

Koobi Fora Formation records extensive environmental variability shaped by tectonics, volcanism, and fluctuating fluvial–lacustrine conditions (Feibel 1988, 2011). Fluvial and deltaic systems dominated during some intervals, when rivers such as the palaeo-Omo, palaeo-Kerio,

and palaeo-Turkwel meandered across the basin (Feibel 2011). In contrast, other periods supported expansive lakes of varying sizes, with sedimentation influenced by hydrological connectivity to distant highlands, and possibly to the Nile system in earlier phases. Among eight members (Lonyumun, Moiti, Lokochot, Tulu Bor, Burgi, KBS, Okote and Chari), the KBS Member in particular reveals a dynamic palaeoenvironment marked by alluvial, floodplain, and lacustrine deposits. Features such as varve-like laminations and paleosol slickensides indicate strong seasonal to interannual climatic variability (Feibel 1988). These lake-margin ecosystems likely presented both opportunities and constraints for early hominins, influencing patterns of resource use and mobility. Vegetation reconstructions and mammalian abundance data suggest a major ecological shift after 2 Ma, with a peak in faunal turnover around 1.8 Ma. This turnover aligns with increased environmental instability and is thought to have played a role in shaping hominin evolution. Faunal assemblages document changes in species composition across time, reinforcing the role of Koobi Fora as a key site for understanding Plio-Pleistocene hominin habitats (Reynolds and Bobe 2022).

The Kantis fossil site preserves evidence of a mixed but predominantly open palaeoenvironment in the highlands of central Kenya. Sedimentary deposits—volcanic mudflows (lahars), fluvial sands, and poorly sorted gravity flows—indicate a dynamic, water-influenced landscape, likely near a river or lake (Mbua et al. 2016). The faunal assemblage is dominated by hippopotamids, Alcelaphini, and other C_4-grazing taxa such as *Notochoerus* and *Eurygnathohippus*, suggesting expansive grassland habitats. However, the presence of giraffids, which are obligate C_3 browsers, points to patches of woodland or bushland. These interpretations are supported by isotopic analyses indicating that most herbivores had diets dominated by C_4 vegetation, consistent with open grasslands, while giraffids retained a C_3-based diet (Reynolds and Bobe 2022). Compared to Hadar and Dikika in Ethiopia, Kantis appears to have been more open and arid, likely due to its higher elevation. The site thus

represents a mosaic environment, with dominant grassland habitats interspersed with woodland and water sources, offering insight into habitat variability in early hominin landscapes during the mid-Pliocene.

The Kanapoi Formation consists of up to 60 metres of fluvial, deltaic, and lacustrine sediments, overlying Mio-Pliocene deposits. Palaeoenvironments were highly seasonal and heterogeneous, characterised by a mosaic of habitats that included woodlands, wooded grasslands, and aquatic environments. Freshwater availability was abundant, especially during the lacustrine phase, as evidenced by numerous fish, crocodilian, mollusc, and amphibian remains. Stable isotope data from soils and enamel indicate a mixed vegetation structure, with a significant presence of C_4 plants (grasses) in the diet of herbivores, but woodland vegetation predominating the landscape (Manthi and Winkler 2020; Quinn and Lepre 2020; Wynn 2000). The Kanapoi Formation is characterised by a diverse, seasonally variable environment, with wooded grasslands and riparian habitats that supported a wide range of fauna and provided favourable conditions for early hominins, particularly *Au. anamensis* (Wynn 2000).

The Hadar palaeoenvironments are characterised by dynamic landscapes of lacustrine conditions interspersed with fluvial–deltaic deposits, suggesting a water-rich environment with fluctuating water bodies (Quade et al. 2004). This pattern is consistent across the broader Awash region and supported by stable isotopic analyses of soil carbonates from at Gona, which indicate diverse vegetation types from forests to grasslands. This variability reflects a mosaic environment, likely shaped by rapid sedimentation rates of approximately 20 cm/kyr, which preserved short-term habitat changes and more localized environmental shifts (Campisano, Rowan, and Reed 2022). Stratigraphically, the Hadar Formation is composed of the Basal, Sidi Hakoma, Denen Dora, and Kada Hadar members. Additionally, palaeoenvironments were reconstructed with faunal evidence that reveals a rich vertebrate assemblage, including early hominins like *Australopithecus afarensis* (Campisano et al. 2022).

The Chiwondo Beds of the Karonga Basin in northern Malawi, dated to the Late Pliocene–Early Pleistocene, offer important insights into the palaeoenvironmental conditions associated with early hominin presence in the southern East African Rift System (Kullmer et al. 2022). Fossiliferous localities such as Mwenirondo, Malema, Mwimbi, and Uraha preserve a diverse vertebrate fauna dominated by bovids, followed by equids, suids, hippopotamids, giraffids, and primates. Bovids include both grazing and mixed-feeding taxa such as *Syncerus*, *Damaliscus*, Reduncini, and Tragelaphini, while equids are represented by *Eurygnathohippus*. Suids, especially diverse at Uraha, include *Notochoerus* and *Metridiochoerus* (Reynolds and Bobe 2022). Giraffids (*Giraffa pygmaea, Sivatherium*) and rare primates such as *Parapapio* and *Theropithecus* also occur (Kullmer et al. 2022). The palaeoecological reconstruction indicates a mosaic landscape that varied regionally across the basin. Mwimbi reflects scrubland–wetland conditions comparable to the Tulu Bor Member at Koobi Fora; Mwenirondo shows bushland–woodland and edaphic grassland; Malema suggests open scrubland–woodland akin to Hadar and Denen Dora; and Uraha, where arboreal/frugivorous taxa are least represented, indicates open woodland–shrubland. Despite modern vegetation being classified under the Zambezian phytochorion, the faunal composition shares affinities with the arid Somalia–Masai biome. Stable isotope analyses provide further evidence of palaeoenvironmental conditions. $\delta^{13}C$ values from pedogenic carbonates and suid enamel indicate a dominance of C_3 vegetation, suggesting woodland habitats rather than open grasslands. Most herbivores were mixed feeders; only *Connochaetes* displays a typical grazing signal. $\delta^{18}O$ data suggest seasonal rainfall but generally stable and humid conditions, contrasting with the more arid East African Rift contemporaries (Lüdecke, Mulch, et al. 2016; Lüdecke, Schrenk, et al. 2016). Together, the faunal and isotopic data point to high ecological diversity along the margins of palaeo-Lake Malawi. These habitats would have offered consistent resources and supported a variety of large mammals and early hominins, highlighting

the significance of the Chiwondo Beds in understanding southern Rift Valley palaeoenvironments (Reynolds and Bobe 2022).

5.4. Contributions to the literature

The current literature on African fossil site formation and live–death fidelity is largely based on the pioneering studies of Behrensmeyer and colleagues in Amboseli National Park, Kenya (Behrensmeyer 1978, 1993; Behrensmeyer et al. 1979; Western and Behrensmeyer 2009), and Tappen in Virunga National Park, Democratic Republic of the Congo (Tappen 1992, 1995). Since then, and up to 2020, very few related studies had been conducted. Notably, some research in Zimbabwe by Hutson explored aspects of fossil site formation, particularly the role of carnivores and seasonality in carcass accumulation in pans and marshes (Hutson 2012). However, these studies did not focus explicitly on live–death fidelity, and no recent research has addressed this topic within African ecosystems more broadly.

The three empirical chapters of this thesis therefore provide new insights into live–death fidelity, fossil site formation, and conservation palaeobiology. Over a decade has passed since the last neotaphonomic studies addressing these topics, highlighting a significant gap in the literature that this work aims to fill.

Moreover, no previous neotaphonomic studies in Southern Africa have focused specifically on estimating ecological diversity based on bone assemblages—despite this being a region rich in Plio-Pleistocene fossil sites. Much of the debate regarding whether fossil assemblages accurately represent past faunas stems from such areas. This thesis directly addresses this gap by providing updated, context-specific data relevant to the reconstruction of Plio-Pleistocene African palaeoenvironments, based on the diversity and relative abundance of middle- to large-sized mammal remains.

Previous live–death fidelity studies were conducted in relatively homogeneous or anthropogenically disturbed landscapes, such as Amboseli National Park, where bones from livestock (e.g., domestic dogs, goats, cattle, sheep, and donkeys) were found due to Maasai pastoralism within the park. In contrast, Gorongosa National Park (GNP)—where the three

empirical chapters were conducted—has experienced a significant reduction in human disturbance since the initiation of a major restoration programme in 2008. By the time this research was undertaken, human impact was minimal, with only occasional signs of snares, a few steel gin traps, and isolated fires associated with illegal hunting.

Importantly, GNP is characterised by high habitat heterogeneity, with over 15 distinct landscape types recorded. These form a mosaic of environments ranging from open grasslands to dense woodlands (e.g., miombo) and forest in the limestone gorges. This environmental diversity greatly enhances the relevance of the findings presented in this thesis.

Additionally, whereas earlier work—such as the 40-year tracking bones study in Amboseli—compared bone assemblages to aerial survey data, this thesis incorporates camera trap data from long-term faunal monitoring in GNP. The inclusion of this method adds significant value, revealing discrepancies in species diversity estimates between survey techniques. Only the species detected by all three methods (aerial counts, bone surveys, and camera traps) reliably reflected the abundance patterns seen in aerial surveys. Notably, more than 50% of species recorded via camera traps were absent from both aerial and bone survey data.

Finally, regarding species diversity and site formation, Tappen's study treated ecological variables such as proximity to rivers and habitat types as simple categorical factors (e.g., comparing bones near rivers to those further away). While this approach remains foundational for understanding fossil site formation, it overlooks potential interactions among variables—such as the influence of carnivores on carcass movement. As shown in Chapter Three of this thesis, the effect of water sources on bone accumulation varies by habitat; for example, pans influence bone distribution differently in woodlands compared to grasslands. This thesis thus offers a more nuanced analysis by incorporating multiple interacting variables that shape bone accumulation in GNP's ecosystems.

5.4.1. Connecting Gorongosa with Plio-Pleistocene fossil sites in the EARS based on bovid tribes

The palaeoenvironmental reconstructions of Plio-Pleistocene fossil sites across the East African Rift System (EARS) suggest that Gorongosa National Park (GNP) shares important similarities with many of these localities. While the degree of similarity varies across sites, GNP aligns with them in key aspects of geology, ecology, and vegetation. Geologically, GNP represents the southernmost extension of the Rift Valley, with its valley floor lying between 15 and 80 m above sea level. This floor is bounded by two elevated regions: the Cheringoma Plateau to the east, rising to 300 m, and the dissected Midlands to the west, reaching elevations of around 400 m. Dominating the western margin is Mount Gorongosa, a prominent inselberg that rises to 1,863 m above sea level. It exerts significant ecological and hydrological influence over the region. The geological substrates across GNP are highly varied. The Rift Valley floor is characterised by alluvial and colluvial deposits, supporting grey hydromorphic soils derived from detrital fans and sands. Mount Gorongosa is underlain by granite, which weathers under heavy rainfall into nutrient-poor ferralitic soils. However, richer soils occur on its talus slopes, where gabbro (an intrusive igneous rock that forms when magma cools slowly beneath the Earth's surface) and dolerite are exposed (Stalmans and Beilfuss 2008). The Cheringoma Plateau is composed mainly of limestone and grauwackes, resulting in sandy, leached soils with low pH and phosphorus content, often with an impermeable subsurface horizon. In contrast, the Midlands are underlain by gneisses, pegmatites, and dolerite dykes, producing sandy, fersiallitic soils—brown and red in colour—which are better suited to supporting wildlife.

Rainfall within GNP is elevation-dependent: the Cheringoma Plateau receives over 1,000 mm annually, the Rift Valley floor averages between 700 and 900 mm (e.g., 840 mm at Chitengo, the main camp and research station), and Mount Gorongosa receives over 2,000 mm (Stalmans and Beilfuss 2008). These rainfall gradients underpin a complex hydrology, with

numerous rivers draining from the highlands into Lake Urema, the park's hydrological nucleus, which in turn overflows into the Púnguè River system. Periodic flooding of the valley floor influences both soil development and vegetation dynamics.

Vegetation across the park is diverse, shaped by a combination of soil type, elevation, and water availability (Stalmans and Beilfuss 2008; Wild and Barbosa 1967). This environmental heterogeneity supports exceptional biodiversity, positioning GNP as a valuable analogue for understanding ecological processes within rift valley ecosystems (Stalmans et al. 2019; Tinley 1977).

Ecologically, GNP harbours a mammalian fauna similar in many aspects to those recorded in Plio-Pleistocene fossil sites, especially in terms of bovid tribe composition. Bovids, being key indicators for palaeoenvironmental reconstructions, allow direct comparisons between fossil and modern ecosystems. Among the twelve fossil sites examined here (see Figure 5-2), the Shungura Formation in the Omo Valley exhibits the closest similarity to GNP, both ecologically and geologically.

The Shungura Formation has a complex stratigraphy of fluvial, deltaic, and lacustrine deposits (Bobe and Reynolds 2022). The Basal Member begins with lacustrine sediments, followed by an extensive fluvial sequence, transitioning to deltaic deposits in units G-11 to G-13. Upper Member G resumes lacustrine deposition, while Member H reintroduces deltaic conditions, later returning to fluvial sedimentation through to the middle of Member L. The uppermost units, from L-7 to L-9, once again reflect lacustrine deposition (Reynolds and Bobe 2022). Taphonomic conditions shift notably in these upper units (Bobe and Eck 2001), much like the dynamic depositional patterns observed in GNP.

Palaeosols in Members A and B of the Shungura Formation indicate a warm, humid climate with high and stable precipitation, comparable to GNP during its rainy season (Tinley,

1977). Subsequent members record a trend towards increased aridity and more variable rainfall (Bobe and Reynolds 2022), paralleling the seasonal dry periods in GNP.

Stable carbon isotope analyses of palaeosol carbonates from this Formation reveal a transition from woodland- and bushland-dominated landscapes to wooded grasslands around 2 Ma (Levin et al. 2011). Despite this shift, the lower Omo Valley retained more wooded environments than contemporaneous regions, a pattern also reflected in the vegetational diversity of GNP. In both areas, habitat transitions are shaped by local hydrological regimes, creating ecological niches that maintain a mosaic of vegetation types.

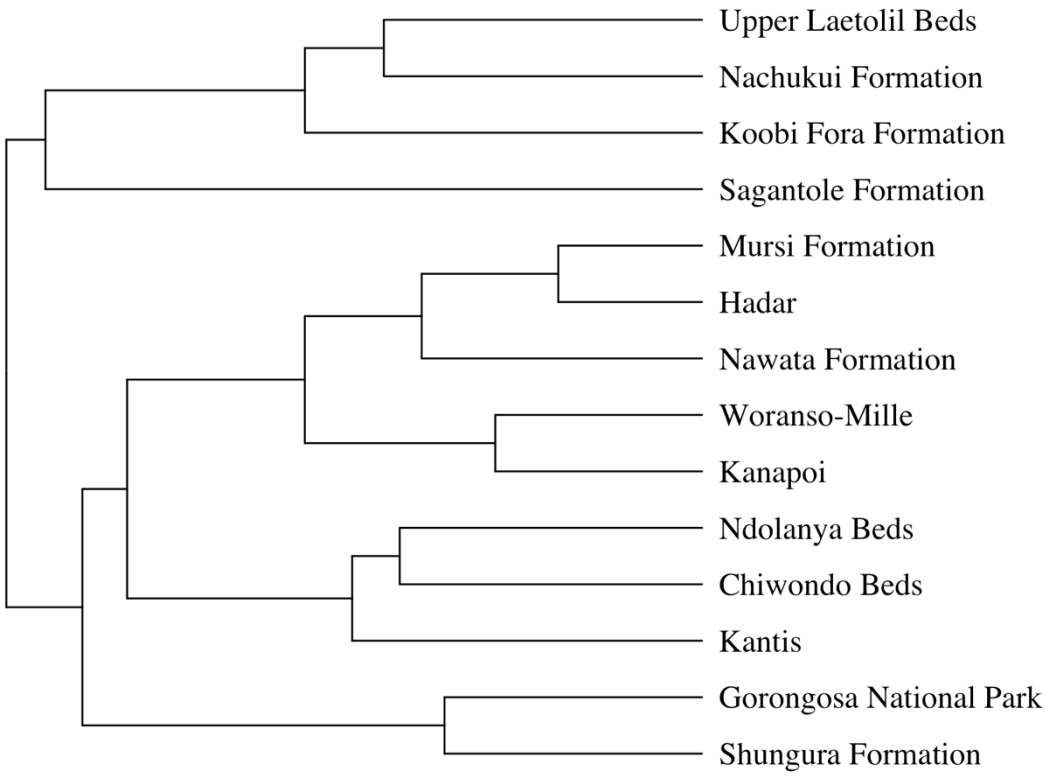


Figure 5-2. Correspondence analyses of palaeontological specimens of bovid tribes from fossil sites in the EARS and modern bones from Gorongosa National Park.

5.5. Research limitations in recording bone assemblages and species diversity

The dataset of osteological specimens for this research was collected over seven years (2016–2023) from the highly heterogeneous environments of GNP. In terms of hours in the field collecting data, this thesis exceeds the pioneering work in Amboseli, where researchers collected data during short field seasons over many years, but sometimes with long interruptions between visits. It also surpasses the time spent on data collection at Virunga National Park. In this regard, this thesis offers a unique and important contribution to the studies of neotaphonomy in Africa. It should be noted, however, that comparisons with fossil sites have to be assessed with the fact that most palaeontological sites yield data that accumulated over thousands or even millions of years. However, when compared to fossil sites such as Nachukui, Mursi, or the Shungura Formation, the Gorongosa dataset remains limited in temporal resolution. Fossil assemblages from sites like Mursi or Shungura often reflect high levels of time-averaging capturing faunal information spanning millions of years. This highlights the importance of sample size and continuity in long-term neotaphonomic studies. These studies would further examine whether the faunal remains documented in the Shungura Formation across different members and stratigraphic levels accurately represent the contemporaneous fauna, and to what extent they reflect the species diversity of past ecosystems.

Furthermore, methods of data collection over the years had to be modified in account of the logistical constraints specific to Gorongosa's complex terrain and seasonality. The park's environmental heterogeneity and extended rainy seasons—often making roads impassable—limited consistent seasonal data collection. As a result, all data presented in this thesis were collected during dry seasons, precluding comparative analysis of carcass distribution between wet and dry periods. Initially, the fieldwork was based on a plan to survey all major habitat types across Gorongosa National Park. Although the principal investigator had extensive prior

experience with the GNP landscape, the plan had to be adjusted to reflect on-the-ground realities. For example, in recent years, the rainy season extended unexpectedly into May, delaying fieldwork due to continued flooding. Access to certain habitats, particularly miombo woodlands in the eastern part of the park and areas west of Muanza District, was severely limited by unmaintained roads. Consequently, the number of transects and plots was adapted to the terrain and accessibility each year. Nevertheless, after seven years of repeated fieldwork, the research team was able to identify key areas suitable for long-term transects and plots, which can now be monitored twice a year—in both dry and wet seasons.

One component of the original research design—surveying caves and their entrances—could not be implemented due to the COVID-19 pandemic. This part of the study was to be conducted in collaboration with a speleological team and relied on improved access to the Cheringoma Plateau. However, pandemic-related restrictions significantly reduced staffing and road maintenance within the park, preventing access to the caves. As a result, no data from caves or their entrances were included in this thesis. Nevertheless, this aspect of the original plan serves as a basis for new research projects and will be implemented in the near future.

Another planned element involved recording taphonomic marks on bones from the moment of death through to complete skeletonisation, allowing for precise identification of modification agents. This component was postponed due to the difficulty of locating fresh carcasses across the expansive terrain. While GPS-collared carnivores such as wild dogs and lions were tracked to increase the likelihood of locating fresh kills, the effort was largely unsuccessful. Unlike other regions where multiple carcasses may be found in a single day, carcass availability in Gorongosa varies significantly throughout the year. During the study period, very few fresh carcasses were encountered, limiting the opportunity to document bone modification patterns. As such, only a small number of bones with surface modifications were recorded and are reserved for future analysis.

Finally, tooth enamel samples were taken for stable isotope analysis (carbon and oxygen) to be processed at the Max Planck Institute for Chemistry in Germany. However, due to delays in processing, the data were not available in time for inclusion in the final analysis and discussion presented here. This work will continue as part of future research efforts. Some of the data not included in this thesis are being incorporated into collaborative projects with local Mozambican researchers across various programs, including bachelor's, master's, and doctoral studies. These initiatives fall under the mandate of the Gorongosa Restoration Project, which aims to build scientific capacity among Mozambicans. This represents a pioneering research effort in Mozambique—one that will ultimately be led by Mozambicans and passed on to future generations of Mozambican scientists.

In sum, while these limitations affected the scope of this thesis, they also informed necessary adaptations and ultimately contributed to the success of the research. Importantly, they underscore the value of ongoing, long-term neotaphonomic studies in Gorongosa's ecosystems. This thesis lays the groundwork for future research involving broader collaborations and training of students in neotaphonomy, to continue addressing the gaps identified here.

5.6. Filling the gaps and Future directions

In this thesis, I highlighted four main gaps that need to be addressed. These include the significant transformation of modern African ecosystems compared to past environments, and the lack of direct and accurate analogues for conditions in the Miocene, Pliocene, or Pleistocene. I also pointed out that some African neotaphonomic studies are limited in their methodological approaches. For instance, there is a lack of integration between the survey techniques employed by Behrensmeyer and colleagues (Behrensmeyer et al. 1979; Western and Behrensmeyer 2009) and those by Blumenschine (Blumenschine 1986b), and I suggest that a combined approach would provide more comprehensive data on events occurring from the moment of death (e.g., predation) through to skeletonisation, dispersal, and the burial or destruction of osteological remains. Survey methods, such as transect lines and/or plots across entire ecosystems or in targeted locations like pans, are not applied systematically across study sites, limiting cross-site comparisons (Behrensmeyer 1993; Tappen 1995; Western and Behrensmeyer 2009).

With technological advancements, more tools have become available, allowing for greater flexibility in data collection than was possible in studies conducted decades ago. These tools include the use of camera traps (Silveira, Jácomo, and Diniz-Filho 2003; Wadley 2020), drones, radio collars (Bertram 1982), and GPS tracking devices (Fischer et al. 2018; Isbell et al. 2018), which may help monitor carcasses more effectively and facilitate cross-site comparisons.

Addressing these gaps will advance the field of neotaphonomy and help answer key questions, such as which parts of a carcass are consumed first, and how consumption patterns affect bone survivorship in the landscape. This understanding can help explain why some parts are preserved in the fossil record while others are not.

In this thesis, I addressed some of these gaps by working in the heterogeneous environment of Gorongosa National Park, which comprises a high diversity of vegetation and around fifteen distinct landscapes. Five of these were studied in the three empirical chapters of the thesis (Chapter Two). Beyond using vulture activity to locate carcasses, as done by Blumenschine, I also incorporated GPS radio collars on lions and wild dogs to improve the likelihood of locating fresh carcasses. However, some data are not presented in the thesis due to limited sample size but will serve as a basis for future studies.

Previous studies on live–dead fidelity relied primarily on data from aerial surveys and bone walks, such as those conducted in Amboseli (Behrensmeyer 1993; Behrensmeyer et al. 2003, 1979). In contrast, Chapter Two of this thesis also used camera trap data as an indirect method for censusing medium-to-large-sized mammals. This is the first study to combine data from three different survey methods for neotaphonomic research. The findings revealed that bone walks and aerial surveys recorded less than 50% of the species captured by camera traps in heterogeneous environments. This suggests that some fossil records may reflect less than half of the actual past biodiversity (Chapter Two). The absence of certain species in the fossil record is likely influenced by ecological variables that affect specimen preservation.

This issue was first tested empirically by Tappen (1995) in Virunga National Park, where variables such as habitat type, proximity to rivers, and tree distribution were examined to determine their influence on bone deposition in savanna environments. However, none of these variables fully explained bone distribution and preservation patterns. Building on Tappen's work, I included additional variables and applied Generalised Linear Models (GLMs), taking advantage of Gorongosa well-mapped ecological features, including landscapes, rivers, pans (seasonal marshes), roads, and lakes (Chapter Three). This research exemplifies how modern technology can advance neotaphonomic research, with tools that allow measurement of distances and mapping of features to be used as explanatory variables.

These findings support geological interpretations that some fossils may have been deposited in river or lake beds, rather than along their margins, as has often been assumed. This provides a foundation to test whether ecological influences vary by species group. For example, some fossil sites like the Mursi Formation contain few primate fossils. It remains unclear whether this scarcity is due to ecological variables or differs from patterns seen in other mammalian orders. Notably, the rarity of primates in some fossil records is also evident in bone surveys, despite their high abundance in modern ecosystems (Behrensmeyer 1993; Behrensmeyer et al. 1979; Tappen 1992, 1995). Chapter Four addresses this issue, revealing that primates are preserved differently compared to other mammalian orders (Chapter Four).

Despite these advancements, many questions remain, and further research is needed. For instance, due to time constraints and security concerns, osteological surveys were not conducted in caves or at their entrances—areas known to yield high numbers of specimens, particularly of small mammals. Including such areas in future surveys would help close this gap.

From my bone surveys, I recorded 2,313 bones from 270 carcasses representing 19 species, across 38 transects and 96 plots (Chapter Two and Chapter Three). However, collecting more specimens would yield more robust results.

The lack of systematic carcass monitoring from the time of animal death until bone burial or complete decomposition is a gap that remains to be addressed. I was able to record some instances of this process, but sample size remains too small to draw compelling conclusions. Consequently, we remain uncertain whether carcasses are buried or decompose differently across various landscapes. We are also still unsure about the key determinants of bone survivorship in the landscapes of Gorongosa National Park (GNP).

Considering that GNP is recovering from nearly 95% of its fauna having been depleted, with both natural repopulation and active reintroductions (Stalmans et al. 2019)—including of carnivores—long-term research on neotaphonomy is essential to capture the bone assemblages' response to mammalian population growth and carnivore reintroductions.

In this thesis, we addressed ecological variables: landscape type, proximity to roads, lakes, and rivers. However, other factors are also critical, and future studies should consider incorporating soil characteristics (e.g., type, pH, and salinity) and predator distribution via GPS collars to better understand their influence on bone preservation.

Additionally, the use of automated detection methods (e.g., camera traps and GPS tracking devices) to study interactions between crocodiles (Mascarenhas-Junior, Sousa Correia, and Simões 2023) and other predators with primate carcasses—and to assess the role of primates in carcass distribution and bone deposition—emerges as a key direction for future research based on this thesis.

5.7. Supplementary materials

Table S 5-1. Plio-Pleistocene fossil sites in the EARS. Data from the PaleoTurkana Database (Bobe and Carvalho 2019) and Reynolds and Bobe (2022).

Site	Country	Chronology (Ma)	Dominant Habitat	Vegetation (C_3/C_4)	Key Fauna	Geological Context	Palaeoenvironmental Significance
Woranso-Mille	Ethiopia	~3.8–3.2	Mosaic: grasslands + riparian woodland	Mixed C_3/C_4	*Theropithecus oswaldi* and bovids	River–lake systems, moderate complexity	Mixed, aquatic-influenced ecosystem
Laetoli – Upper Laetolil Beds	Tanzania	~3.8–3.6	Arid open woodland	Predominantly C_4	Large-sized herbivores	Volcanic tuff-dominated	Dry, seasonal bushland
Shungura Formation	Ethiopia	~3.6–1.0	Woodland and grassland within fluvial–deltaic systems	Mixed C_3/C_4	Bovids, hippos, crocs	Thick sedimentary sequences	Environmental reconstruction over time
Gona – Sagantole Formation	Ethiopia	~4.3–2.9 Ma	Heterogeneous; open–closed habitats	Mixed (C_3–C_4)	*Eurygnathohippus, Tragelaphus*, crocs, hippos	Volcanic + fluvial-lacustrine	High ecological diversity; *Ardipithecus* habitat
Nachukui Formation	Kenya	~4.3–0.7	Wooded grassland → open grassland (post-2 Ma)	Transition from C_3 to C_4	Diverse bovids	Alternating fluvial-lacustrine	Key for tracking long-term environmental shifts
Ndolanya Beds	Tanzania	~2.6	Semi-arid bushland	C_4 dominant	Large-sized grazers	Volcaniclastic	Drier and more open than earlier beds
Mursi Formation	Ethiopia	Early Pliocene	Closed forest with low energy water sources	Dominantly C_3	Suids, deinotheres	Fluvial–lacustrine	Dense vegetation, rare, forested setting
Koobi Fora Formation	Kenya	~4.3–0.6	Varied: rivers, lakes, floodplains	Increasing C_4 post-2 Ma	Diverse grazers and browsers	Volcanic + tectonic with complex stratigraphy	Key to hominin–environment dynamics
Kantis	Kenya	~3.5–3.3	Open grassland with woodland patches	Mostly C_4; some C_3	*Eurygnathohippus, Notochoerus*, giraffids	Volcanic mudflows + fluvial sands	More arid than Hadar/Dikika; elevation-driven
Kanapoi Formation	Kenya	~4.2–3.9	Wooded grasslands + aquatic zones	Mixed (C_4 dominant in diet)	Crocs, fish, molluscs	Fluvial-deltaic over basalt	Ideal for *Au. anamensis*

Hadar Formation	Ethiopia	~3.8–2.9	Lakes, rivers, floodplains	Variable C_3/C_4	Bovids	Rapid sedimentation, tectonically active	Classic mosaic habitat for early hominins
Chiwondo Beds	Malawi	~2.5–1.0	Regionally variable mosaic	C_3 dominant	Bovids, suids, giraffids	Rift valley margin	Southernmost evidence of diverse hominin habitats

Table S 5-2. Palaeontological specimens of bovid tribes from fossil sites in the EARS and modern bones from Gorongosa National Park.

Site	Aepycerotini	Alcelaphini	Antilopini	Bovini	Reduncini	Tragelaphini
Chiwondo Beds	19	107	32	25	15	14
Hadar	182	52	6	60	49	35
Kanapoi	70	70	22	37	4	147
Kantis	32	52	12	25	1	3
Koobi Fora Formation	221	544	240	217	1204	625
Mursi Formation	177	11	4	52	67	82
Nachukui Formation	328	441	163	93	369	214
Ndolanya Beds	1	65	40	2	2	9
Sagantole Formation	69	10	17	42	49	701
Shungura Formation	4	14	7	25	96	39
Upper Laetolil Beds	224	546	212	18	3	10
Woranso-Mille	228	94	20	34	10	153
Gorongosa National Park*	12	8	8	6	165	29

*Number of bovid tribes based on MNI of modern bones.

Chapter Six. Conclusion

This thesis has provided a new perspective on the implications of bones and ecology in the southern African Rift Valley for our understanding of human evolution. It began by exploring the gaps in African neotaphonomy, particularly the ecological and palaeoecological significance of modern bone assemblages in open-ground environments for interpreting live-dead fidelity, with implications for our understanding of fossil bone assemblages and palaeoecology. In that chapter, I proposed six main approaches to advance neotaphonomic research: i) combining bone surveys with carcass monitoring; ii) using camera traps to document the living community and track carcass fate; iii) employing standardised data collection methods to enable inter-site comparisons; iv) incorporating key ecological variables such as water features, predator presence, vegetation type, and road proximity as predictors of bone deposition and carcass distribution; v) monitoring carcasses systematically from death until burial; and vi) using data from radio-collared predators to locate fresh kills in heterogeneous ecosystems.

In Chapter Two, I showed that systematic bone counts along 23 transects and 96 plots, combined with four biennial aerial surveys and a 300 km² grid of 60 camera traps in Gorongosa National Park, revealed that species diversity in the dead assemblages represents less than 50% of the original living community, and that, for those species present in both communities, the relative abundances in the bone assemblages closely mirror those of the living community, particularly when applying species rank order data.

Chapter Three explored whether ecological variables like lakes, rivers, pans, roads, and habitat types—influenced the deposition of bones from medium- to large-sized mammals in Gorongosa National Park. A Negative Binomial Model analysis revealed that bone deposition

is higher near roads and decreases further away, while it increases with distance from Lake Urema and pans and decreases closer to these water sources. The insights of this chapter suggest that fossil assemblages of middle- and large-sized mammals most likely formed in waterbeds located further from low energy water sources rather than directly at their margins. Chapter Four investigated the ecological factors driving the disparity between primate carcass abundance and live census data by testing whether i) landscape type, proximity to roads, and water sources (pans, rivers, and lakes) predict primate carcass occurrence relative to other mammals, and ii) primate bone abundance significantly differs from that of other mammals in annually flooding versus non-flooding landscapes. Based on bone assemblages of chacma baboons (*Papio ursinus*) and other mammal species, I found that permanent water sources (rivers and lakes) are significant drivers of primate bone accumulation. I also showed that primate bones are more commonly deposited in Rift Valley Riverine and Floodplain landscapes. These findings have implications for understanding the accumulation of primate bones in the African fossil record and suggest that the sparse fossil records of primates in some palaeontological sites such as Mursi do not necessarily reflect low primate abundances in the ancient landscapes.

Chapter Five presents the main findings, contributions, limitations, and future directions of this thesis, and puts the data in the context of key palaeontological sites in the East African Rift System. The research fills critical gaps in neotaphonomy by providing the first southern African study focused on live–dead fidelity and ecological diversity using bone assemblages. Conducted in Gorongosa National Park—an ecologically diverse setting—the study integrates bone surveys, aerial counts, and camera traps. This multi-method approach revealed that over 50% of vertebrate species detected by camera traps were missed by both aerial and bone surveys, highlighting limitations of specific methods. The research also advances analytical

approaches by considering interactions between environmental variables, showing that habitat type influences how factors like water availability affect bone distribution.

However, several limitations are acknowledged. Data collection was restricted to the dry season due to flooding and terrain, limiting seasonal comparisons. Access to some habitats, such as miombo woodlands, was constrained, and some planned surveys, including surveys at cave entrances, were not possible due to COVID-19 restrictions.

Future work should involve year-round bone sampling, narrower spatial coverage, and consistent application of standardised bone survey methods. Incorporating remote sensing and automated technologies (GPS trackers and camera traps) will strengthen ecological interpretations and improve inter-site comparisons.

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APPENDICES

Appendix A



Figure A- 1. Local community involvement in bone documentation during the field work: Assessing the MNE and MNI of a hartebeest carcass. The two interns in the photo helped to document the specimens. Photo by Arquimedez André.



Figure A- 2. River crossing by chacma baboons during the dry season, when most rivers are shallow. Photo by Lee Bennett.



Figure A- 3. Fresh waterbuck carcass monitoring in the Rift Valley Riverine & Floodplain in GNP. Photo by Susana Carvalho



Figure A- 4. Bone dispersal of a waterbuck in the Rift Valley Colluvial Fan of Gorongosa National Park: Recorded in sodic soil during bone survey in plots.



Figure A- 5. Wild dogs captured by a camera trap placed at a site with a waterbuck carcass



Figure A- 6. Teaching session of Gorongosa International field School about Conservation Paleobiology in GNP.



Figure A- 7. Herbivores concentrated along river margins, grazing on fresh grass in the Rift Valley riverine and floodplain landscape.



Figure A- 8. Four people evenly spaced conducting bone surveys in Rift Valley Riverine & Floodplain. Photo by René Bobe.



Figure A- 9. Systematic monitoring of carcasses and recording of scavenging activity in Rift Valley Riverine & Floodplain in GNP. Photo by Susana Carvalho.



Figure A- 10. Data collection on bone patches in the Grassland of Gorongosa National Park.



Figure A- 11. Wildebeests observed during the 2024 aerial survey in the Rift Valley Colluvial Fan, Gorongosa National Park. The red bar is the sign from the helicopter setting the range of aerial count. Photo by Dadzie Tarua.

Appendix B. Peer-reviewed publications & published abstracts where the candidate is a co-author

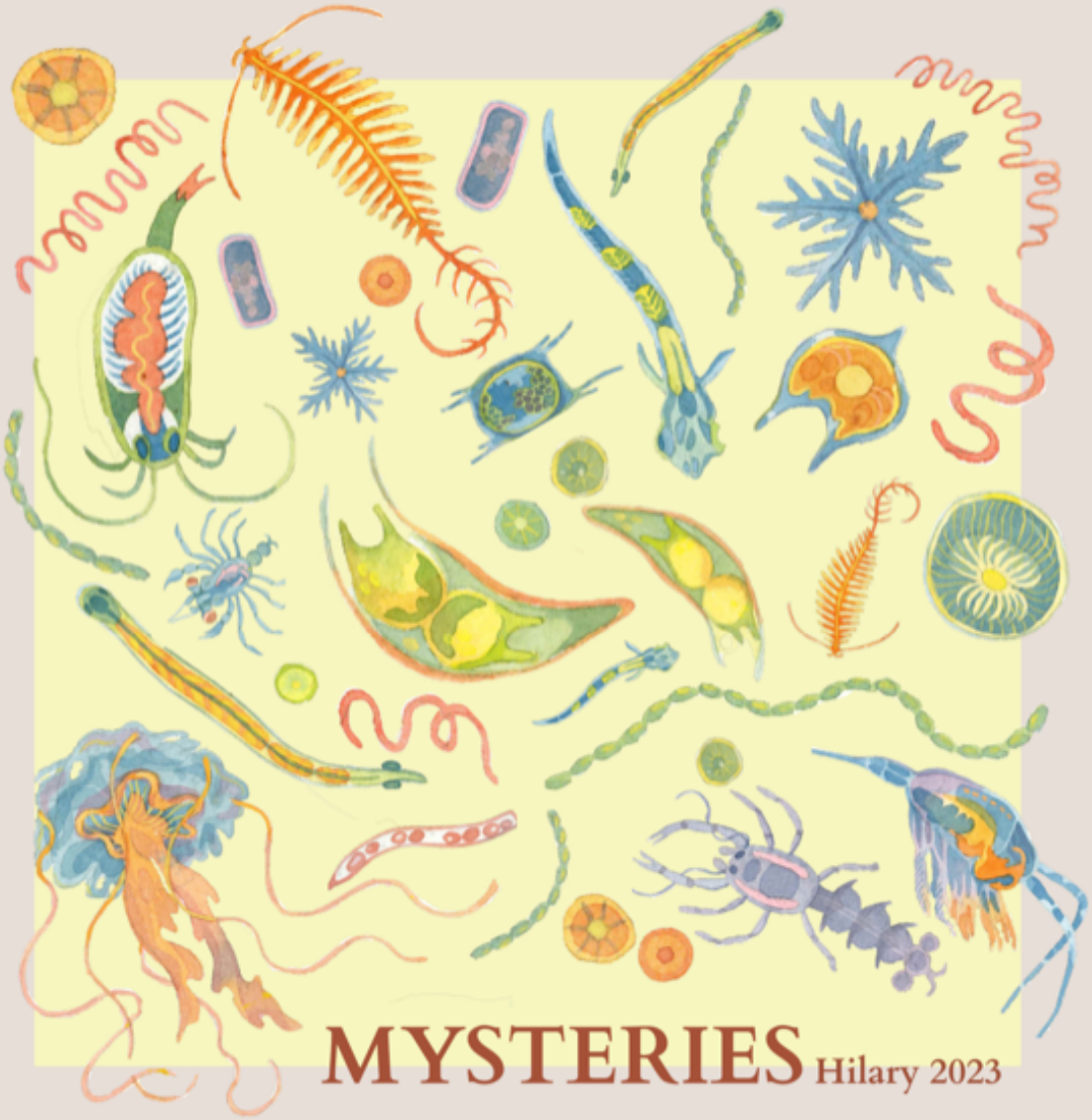
DIVERSITY, RELATIVE ABUNDANCE AND DISTRIBUTION OF MAMMALS ACROSS GORONGOSA HABITATS

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Species abundance distributions and changes over time can be monitored through the documentation of osteological remains in modern ecosystems. At Gorongosa National Park in Mozambique we are documenting osteological remains of mammals, including primates as baboons (*Papio cynocephalus*), guenons (*Cercopithecus* sp.), vervets (*Chlorocebus pygerythrus*), to establish patterns of diversity, abundance, and distribution, and to test how these variables change over time. These bone surveys form a base for the interpretation of climate and ecosystem changes. We carried out 23 transects, 40-50m wide and 3-4 km long across five habitats of Gorongosa: 1) Rift Valley Riverine & Floodplain Landscape, 2) Argillaceous and Limestone Landscapes, 3) Rift Valley Colluvial Fan Landscape, 4) Rift Valley Alluvial Fan Landscape, and 5) Midlands Rocky Riparian & Midlands Alluvial Landscape. Samples were photographed and GPS coordinates were taken. Bones representative of each animal species were collected for osteological reference. Most of the samples remained in place for later annual monitoring to determine the timing of bone decomposition and the interpretation of the fossilization process. We collected 93 specimens from 13 wild mammal species, including 4 baboon specimens. Midlands Rocky Riparian & Midlands Alluvial Landscape had lower diversity, and the other four habitats had approximately equal diversity. These surveys provide a basis for the long-term monitoring of species abundance across Gorongosa landscapes, and contribute to conservation efforts.

the Oxford Scientist

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MYSTERIES Hilary 2023

Something to consider before eating brains p5

Neo-taphonomy: From modern bones to the fossil record in Africa p11

The mystery of Guam disease p29

Neo-taphonomy: From modern bones to the fossil record in Africa

By Jacinto Mathe

Who we are and where we came from are two fundamental questions in life, and the answers to those questions still constitute a mystery. Although we can look to the fossil record for answers, these do not capture the whole truth. Not all materials fossilise, and so we have to infer information about ancient habitats (known as "paleoenvironments"), taxa, and diets from an incomplete record.

Instead of relying on this imperfect history, we can make educated guesses about ancient ecology and our ancestors' behaviour from analysis of today's life and environment. Paleoecology—the study of how organisms interact with their environments across different timescales—can teach us how life passes from the biosphere (the world's ecosystems) to the lithosphere (the Earth's crust), and what contributes to the preservation of materials such as bones.

Knowing life's transition from the biosphere to the lithosphere is essential to infer our identity and origin through fossil records.

This leads us to neo-taphonomy. Neo-taphonomy focuses on the events and changes occurring in living organisms immediately after death. It is a tool for understanding paleoecology from current life and environment. Through this approach, we can use the corpses of recently deceased animals to deepen our understanding of decomposition and preservation of organic remains, considering environmental and biological factors. The common organic remains we find in our fossil records comprise bones and teeth.

Bones and teeth are the best specimens of the past as these are the most prevalent fossils found. But it can often be difficult to recognise these artefacts as many forces may affect these fragile materials, such as erosion, faunal activities, and ice and heat damage. Neo-taphonomy makes demystifying these materials one step easier.

Much of what we know currently about the evolution of our own species came from fossil records found in Africa. For example, the famous hominin 'Lucy' (*Australopithecus afarensis*) was discovered in Hadar, Ethiopia, and an additional site in South Africa has been titled the "Cradle of Mankind". This makes neo-taphonomic work from Africa key for accurately interpreting evidence regarding ancient human behaviour, as well as the paleoecology and paleoenvironment.

And so, although we will never have a perfect understanding of our past, studying modern bones in relevant environments can start to reveal some of the mysteries of our early evolution.

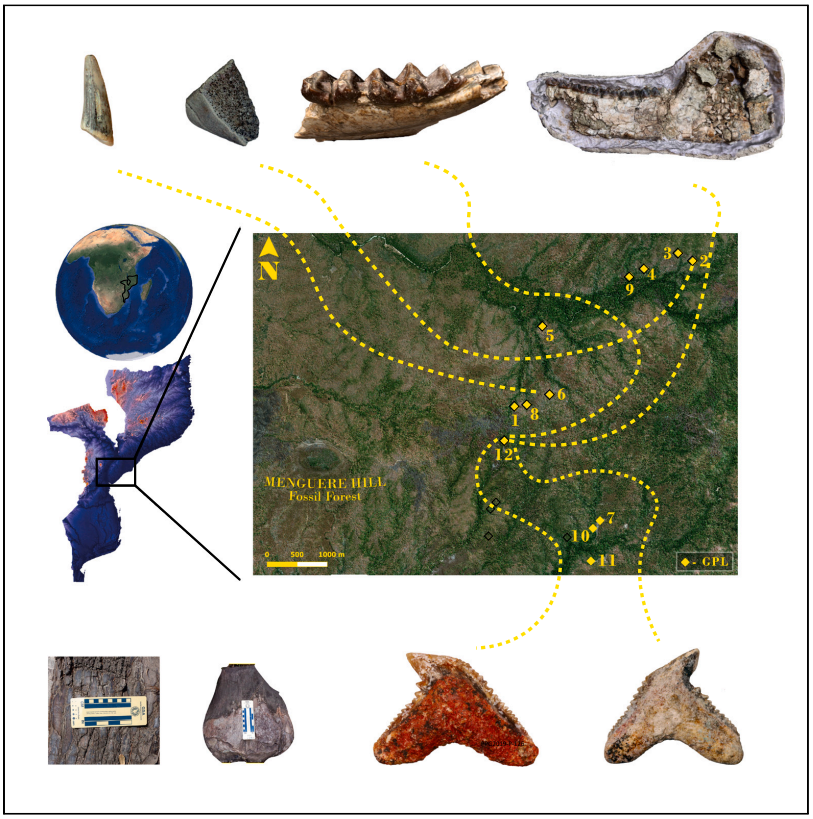
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Article

The first Miocene fossils from coastal woodlands in the southern East African Rift



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Highlights

First Miocene fossil sites discovered in the southern East African Rift

First cosmogenic nuclide dating of fossil sites in the region

New sites fill major biogeographic gap in evolution of African ecosystems

Multiple lines of evidence of ancient coastal forest and woodland ecosystems

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Article

The first Miocene fossils from coastal woodlands in the southern East African Rift

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SUMMARY

The Miocene was a key time in the evolution of African ecosystems witnessing the origin of the African apes and the isolation of eastern coastal forests through an expanding arid corridor. Until recently, however, Miocene sites from the southeastern regions of the continent were unknown. Here, we report the first Miocene fossil teeth from the shoulders of the Urema Rift in Gorongosa National Park, Mozambique. We provide the first 1) radiometric ages of the Mazamba Formation, 2) reconstructions of paleovegetation in the region based on pedogenic carbonates and fossil wood, and 3) descriptions of fossil teeth. Gorongosa is unique in the East African Rift in combining marine invertebrates, marine vertebrates, reptiles, terrestrial mammals, and fossil woods in coastal paleoenvironments. The Gorongosa fossil sites offer the first evidence of woodlands and forests on the coastal margins of southeastern Africa during the Miocene, and an exceptional assemblage of fossils including new species.

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Carbon, nitrogen, and oxygen stable isotopes in modern tooth enamel: A case study from Gorongosa National Park, central Mozambique

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The analyses of the stable isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and oxygen ($\delta^{18}O$) in animal tissues are powerful tools for reconstructing the feeding behavior of individual animals and characterizing trophic interactions in food webs. Of these biomaterials, tooth enamel is the hardest, most mineralized vertebrate tissue and therefore least likely to be affected by chemical alteration (i.e., its isotopic composition can be preserved over millions of years), making it an important and widely available archive

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Caves of Inhaminga: the speleological heritage of the Cheringoma Plateau, Mozambique

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Abstract: Speleological expeditions have been conducted in Gorongosa National Park (GNP), Mozambique, under the Paleo-Primate Project Gorongosa (PPPG) since 2016. The main purpose of this work is to inventory, explore and characterize the karstic caves in the limestone formations, and to assess their archaeological and palaeontological potential.

In 2022 and 2023, expeditions were held to the northern region of the Cheringoma plateau, covering an area located in Inhaminga, Sofala Province (outside the GNP). Following previous bibliographical and documentary research, this karstic area was inspected with the help of local guides, who pointed out the locations of thirteen caves, eight of which were previously undocumented. These caves were explored and described with regard to their general and specific features, including appraisals of sedimentary deposits and related heritage.
Keywords: Stone Age, Africa, pottery, mammal bones.

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Introduction and framework

The Cheringoma Plateau stands in a geographical setting with great potential for the study of human evolution, at the south end of the East African Rift System (EARS) (cf. Bobe *et al*., 2020), in central Mozambique. Located east of the Urema Graben, the plateau comprises a karstified Eocene nummulitic limestone formation, remnant of the former coastal plain (Tinley, 1977).

The western flank of the plateau features impressive karst canyons sculpted by water drainage toward the Rift Valley. According to Laumanns (2001), these limestones were initially karstified in post-Eocene times and then filled with conglomerates and sand during a marine transgression that took place during the Miocene, followed by a second karstification phase in the Pleistocene. Erosion on the east slopes of the Rift promoted the removal of part of the sediment infill and sculpted rocky arches and canyons (Steinbruch, 2010: 280). The Urema Rift, which began to form between 4 and 2 Ma (million years ago) (MacGregor, 2015), played a significant role in this geological process. The limestone in the plateau is largely covered by sands and clays, with outcrops and other exposed surfaces mostly visible in the canyons and their upper borders. According to Steinbruch (2010), the Cheringoma Plateau reaches an altitude of 352m, with gentle slopes, less than 5° to the seaside, 5° to 7° towards the southeast and between 5° and 10° to the Urema Rift.

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Genomic variation in baboons from central Mozambique unveils complex evolutionary relationships with other *Papio* species

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Abstract

Background: Gorongosa National Park in Mozambique hosts a large population of baboons, numbering over 200 troops. Gorongosa baboons have been tentatively identified as part of *Papio ursinus* on the basis of previous limited morphological analysis and a handful of mitochondrial DNA sequences. However, a recent morphological and morphometric analysis of Gorongosa baboons pinpointed the occurrence of several traits intermediate between *P. ursinus* and *P. cynocephalus*, leaving open the possibility of past and/or ongoing gene flow in the baboon population of Gorongosa National Park. In order to investigate the evolutionary history of baboons in Gorongosa, we generated high and low coverage whole genome sequence data of Gorongosa baboons and compared it to available *Papio* genomes.

Results: We confirmed that *P. ursinus* is the species closest to Gorongosa baboons. However, the Gorongosa baboon genomes share more derived alleles with *P. cynocephalus* than *P. ursinus* does, but no recent gene flow between *P. ursinus* and *P. cynocephalus* was detected when available *Papio* genomes were analyzed. Our results, based on the analysis of autosomal, mitochondrial and Y chromosome data, suggest complex, possibly male-biased, gene flow between Gorongosa baboons and *P. cynocephalus*, hinting to direct or indirect contributions from baboons belonging to the "northern" *Papio* clade, and signal the presence of population structure within *P. ursinus*.

Conclusions: The analysis of genome data generated from baboon samples collected in central Mozambique highlighted a complex set of evolutionary relationships with other baboons. Our results provided new insights in the population dynamics that have shaped baboon diversity.

Keywords: Evolutionary genetics, Primate genomics, *Papio*, Population genomics

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Background

Baboons (genus *Papio*) are the primate genus beside humans with the largest distribution across Africa [1]. Over the last two million years they came to occupy a variety of different habitats, from the gallery forests of western Africa all the way to the rocky Cape Peninsula in southern Africa, extending their presence also outside

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Goldschmidt 2023 Abstract
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Inter- and intra-tooth variability in enamel-bound nitrogen isotopic composition of modern African mammals from Gorongosa National Park, Mozambique

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Nitrogen isotopes ($\delta^{15}N$) are a well-established tool for reconstructing diet and trophic level because $\delta^{15}N$ values increase with each step up the food chain. $\delta^{15}N$ measured in collagen provides insight into the dietary behavior of species in modern ecosystems and the recent geological past. However, $\delta^{15}N$ analyses are challenging in fossil materials due to degradation of organic matter. Unlike bone or dentin, N-containing material in tooth enamel is protected from alteration by its highly mineralized structure, and thus an isotopic fingerprint can be preserved over deeper geological timescales. Enamel's low organic content long prevented $\delta^{15}N$ analyses in this material, but recent advances in the oxidation-denitrification method have made this possible. Using this method, data from a controlled feeding experiment, and from mammals in Gorongosa National Park (GNP, Mozambique) show that $\delta^{15}N_{enamel}$ reflects diet and preserves trophic level spacing [1, 2].

Here we present inter- and intra-tooth analysis of $\delta^{15}N_{enamel}$ of modern teeth from GNP. We analysed $\delta^{15}N_{enamel}$ from 302 tooth enamel samples including 16 herbivores and six carnivores. Complete dentition was analyzed for $\delta^{15}N_{enamel}$ to investigate variability between teeth formed during different periods of a mammal's life (e.g., before and after weaning). In each individual, the tooth reflecting its adult diet was serially sampled to investigate seasonality. Additionally, stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes were analyzed from the same aliquot of tooth enamel to evaluate dietary preferences of individuals with different feeding behaviours.

This study enables the evaluation of inter- and intra-tooth variability in enamel-bound $d^{15}N$ and shows that the proxy reflects trophic level and dietary behavior in a well-studied modern natural ecosystem. Overall, our results show expected patterns reflecting seasonality and different developmental periods in an animal's life, illustrating the high potential of multi-isotope approaches for paleontological applications using diagenetically robust tooth enamel.

[1] Leichliter J.N. *et al.* Nitrogen isotopes in tooth enamel record diet and trophic level enrichment: Results from a controlled feeding experiment. Chem. Geol. 563:120047 (2021).

[2] Lüdecke T. *et al.* Carbon, nitrogen, and oxygen stable isotopes in modern tooth enamel: A case study from Gorongosa National Park, central Mozambique. Front. Ecol. Evol., 10:1107 (2022).

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Sex-mediated gene flow of grayfoot chacma baboons (Papio ursinus griseipes) in a highly seasonal habitat in Gorongosa National Park

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RESEARCH ARTICLE

West Side Story: Regional Inter-Troop Variation in Baboon Bark-Stripping at Gorongosa National Park, Mozambique

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Keywords: *acacia* | bark-stripping | behavioral variation | chacma baboon | habitat survey | non-technological material traces

ABSTRACT

Objectives: Baboons possess sophisticated physical and social cognitive abilities; hence, the lack of evidence to date of large-scale behavioral variation in these primates is puzzling. Here we studied a candidate for such variation—the stripping of bark from *Acacia robusta* trees for consumption of the sap and soft tissue underneath—in Gorongosa National Park, Mozambique.

Materials and Methods: We surveyed an area inhabited by ~60 troops of chacma baboons, recording the availability and characteristics of the target trees, as well as the presence or absence of bark-stripping at 45 habitat plots distributed across a grid covering an area of ~300 km^2.

Results: Camera traps confirmed the presence of baboons at all habitat plots, and we identified regional clumping in the distribution of the behavior, a pattern consistent across two consecutive years. Proportion and mean height/width of *A. robusta* did not predict whether bark-stripping behavior was present at a given site, nor did broader ecological variables such as habitat type and distance to the nearest water source. However, stripping sites had significantly higher numbers of *A. robusta* than non-stripping sites, and within a given bark-stripping site, baboons preferred to strip taller and wider trees among those available.

Discussion: The prominent geographical clustering we uncovered may have been driven by opportunity (i.e., the prevalence of *A. robusta* at a given site), but is also consistent with a possible (non-mutually exclusive) cultural interpretation. We propose avenues for future research on Gorongosa's baboons to better quantify the relative contributions of ecology, genetics, and social

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Sex-mediated Gene Flow in Grayfoot Chacma Baboons (*Papio ursinus griseipes*) in Gorongosa National Park, Mozambique

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Abstract

Dispersal behavior influences gene flow and the spatial distribution of genetic diversity, which is crucial for a species' evolutionary trajectory and population persistence under environmental changes. We used gene flow as a proxy to investigate dispersal patterns in the grayfoot chacma baboon (*Papio ursinus griseipes*) in Gorongosa National Park (GNP), central Mozambique. The baboons inhabit a mosaic landscape with a seasonally variable environment. Thirty-two years ago, GNP was the epicenter of a major war that severely reduced apex predators, resulting in limited mammalian predation on baboons. We aimed to characterize genetic diversity, examine the extent and direction of sex-biased gene flow at different time frames and investigate changes in population size and recent migration events. We collected 121 non-invasive DNA samples and analyzed uni- and bi-parentally inherited markers, comprising mitochondrial DNA, autosomal and Y-linked microsatellites, at two geographic locations (GNP and Catapú Forest Reserve) 150 km apart.

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Maria Joana Ferreira da Silva and Paula Tralma are shared first co-authors.

Susana Carvalho and Felipe I. Martínez are shared senior authors.



Badges earned for open practices: Open Data. Experiment materials and data are available in the repository at GenBank (under Accession numbers PP398582–PP398684, and Dryad repository https://doi.org/10.5061/dryad.gb5mkkwxv).

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