Small game forgotten: Late Pleistocene foraging strategies in eastern Africa, and remote capture at Panga ya Saidi, Kenya

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Abstract

The Late Pleistocene (~125-12 thousand years ago) record of eastern Africa is critical for assessing the origin, evolution and history of human behavior. Faunal remains are a resource for understanding changes in paleoenvironments and the foodways of ancient people in eastern Africa, yet zooarchaeological information for this timeframe has been constrained by few and frequently biased samples, leading to interpretations that emphasize the hunting of large ungulates. New research in a mesic peri-coastal area of Kenya reveals a distinct food acquisition strategy at Panga ya Saidi, a cave that foragers intermittently occupied over the past 78,000 years. Zooarchaeological data from Panga ya Saidi, together with published ethnographic, animal behavioral, and zooarchaeological data, are used to argue that archaeologically invisible tools such as snares, traps, and/or nets were regularly used by Middle and Later Stone Age foragers to remotely capture small game in the site's forested environs, while encounter hunting was occasionally used to target larger game in nearby grasslands. The earliest circumstantial evidence for remote capture of fauna in eastern Africa raises questions about technological innovations, planning, and the people potentially involved in the food quest.

Keywords: Hunter-gatherers, zooarchaeology, faunal remains, taphonomy, eastern Africa, Middle Stone Age, Later Stone Age

1. Introduction

The Late Pleistocene (~125-12 thousand years ago [ka]) is a critical timeframe for understanding the cognitive and behavioral development of humans and the demographic expansion of humans across the African continent and globally. While research on this temporal window long focused on the African origins of *Homo sapiens* and the dispersal of humans across Eurasia and beyond, a growing body of work is now focused on examining interregional variation in records for our species across the African continent (Scerri et al., 2018). Late Pleistocene human fossil evidence in Africa, while sparse, points to anatomical diversity and deep and lasting population structure, an interpretation supported by genetic data (Bergström et al., 2021; Mirazón Lahr, 2016; Schlebusch and Jakobsson, 2018; Stringer, 2016). Based on material culture, archaeologists define two Late Pleistocene traditions: the Middle Stone Age (MSA) and the Later Stone Age (LSA). These traditions are composed of regionally defined industries with locally variable MSA-LSA transitions, often centering around 50 thousand years ago (ka), though also extending back to ~67ka and into the Holocene (Scerri et al., 2021; Shipton et al., 2021; Tryon, 2019). The LSA is characterized by a greater ubiquity and variety of human behavioral evidence than had appeared earlier in the MSA, including symbolic material culture such as beads and pigments (Miller and Wang, 2022); shifts toward lithic miniaturization, blade-based technology, and composite tools (Grove and Blinkhorn, 2020; Shipton et al., 2021; Tryon, 2019); and diversified subsistence strategies (Thompson, 2020). The LSA may reflect both demographic shifts (Archer, 2021; Lipson et al., 2020; Tryon, 2019) and adaptations to Late Pleistocene climatic variability, with regional ecological heterogeneity (Blome et al., 2012; Robinson, 2022).

Late Pleistocene African archaeology has historically focused on the southernmost part of the continent and its abundance of exceptionally well-preserved and well-researched sites with early evidence of cognitively complex human behavior (de la Peña, 2020; Wadley, 2021, 2015; Will et al., 2019; Wurz, 2020). In eastern Africa, the number of investigated sites is smaller. Nevertheless, the region is increasingly a focal point for studies of Late Pleistocene human behavior, particularly given its importance for *H. sapiens* dispersal routes across Africa and into Eurasia (Beyin, 2021; Blinkhorn and Grove, 2018; Tryon, 2019; Tryon and Faith, 2013). This region's Late Pleistocene faunal records are limited in terms of their preservation, recovery, and identifiability, and they have been primarily used to reconstruct paleoenvironments, which can now be leveraged to approach important questions of human mobility, dispersals, and demography (Faith et al., 2016; Robinson, 2022; Tryon and Faith, 2016). Yet behavioral approaches to the past must also consider how faunal remains speak to people's choices: divisions of labor, prey selection, technologies employed in the food quest, and culinary practices. Until recently, most eastern African Late Pleistocene records were insufficient to enable scholars to address these fundamental questions related to early African foodways.

We present a comprehensive review of Late Pleistocene faunal records and zooarchaeological analyses in eastern Africa (defined here as the Horn of Africa, Kenya, and Tanzania), which underscore the paucity of available information. These data lead to a narrow range of interpretations, constrained by sampling biases and selective analogical frameworks, shaped by prevailing intellectual trends at the times of analysis. Our review demonstrates that the eastern African coast and islands, and in particular the site of Panga ya Saidi (PYS) in southeastern Kenya, are distinctive in several respects from most eastern African Late Pleistocene sites. PYS preserves a lengthy sequence of intermittent occupations over the past ~78,000 years, with important evidence for human innovation and symbolic expression (including personal ornamentation, pigment use, and intentional burial), and has produced a chronologically-resolved faunal assemblage with stable isotope data that are informative about local paleoecology and environmental shifts, from the Late Pleistocene through the Late Holocene (Culley et al., 2021; d'Errico et al., 2020; Faulkner et al., 2021; Goldstein et al., 2022; Helm et al., 2012; Martinón-Torres et al., 2021; Roberts et al., 2020; Shipton et al., 2021, 2018, 2013).

Here, we offer new faunal analyses from PYS, and argue that these data cannot be fully understood within the frameworks that have traditionally dominated eastern African zooarchaeology. Instead, we look to zooarchaeological scholarship in southern Africa, and analogically relevant (Wylie, 1985) ethnographic research on small-game procurement from elsewhere in Africa, to interpret this diverse faunal assemblage. In so doing, we offer a possible roadmap for future research at this and other Late Pleistocene sites.

2. Late Pleistocene faunal records in eastern Africa and key limitations

There are limited faunal datasets for Late Pleistocene eastern Africa, particularly when compared against the abundant records for forager subsistence in the Holocene. **Table 1** and **Appendix A (Table S1)** summarize the available faunal data for 28 Late Pleistocene sites (including PYS), located in present-day Somalia, Ethiopia, Kenya, and Tanzania (**Figure 1**). From this dataset, some key limitations emerge.

2.1 Sampling and preservation bias

The first limitation of zooarchaeological data from eastern Africa is the selective nature of many Late Pleistocene assemblages. Several come from surface collections of fossil-bearing localities, as at the Kibish Formation in the Omo River Valley (Assefa et al., 2008; Trapani, 2008), Rusinga Island and nearby Lake Victoria shores (Faith et al., 2015; Tryon et al., 2012), and the Ndutu Beds at Olduvai Gorge (Eren et al., 2014). Surface collection methods tend to prioritize large, visible, and taxonomically informative teeth, bones, and horncores. Chronologies and cultural relationships are often less secure than in excavated contexts. But many excavated faunal remains also lack contextual information, chronological control, and/or curatorial records, especially when the primary excavations – generating the bulk of faunal remains – occurred in the early-mid 20th century, as at Mumba, Nasera, and Kisese II Rockshelters (Inskeep, 1962; Kohl-Larsen, 1943; Mehlman, 1989; Tryon et al., 2019) and Gamble's Cave II (Leakey, 1931).

In many of these early excavations, methods prioritized hand-collection of large, mostly complete, readily identifiable bones and teeth, rather than sieving and recovering smaller fragments, including limb bone shafts now valued as critical to taphonomic studies. For example, at Mumba Rockshelter, an enormous discard pile includes abundant faunal material from the 1930s excavations (Prendergast et al., 2007). At Mumba, Nasera, and Kisese II Rockshelters, interpretations of these selective assemblages have relied almost exclusively on identifications of teeth (Mehlman, 1989; Tryon et al., 2019). Small mammal and fish remains, best recovered through fine-mesh sieving and/or flotation, are rarely reported in useful numbers from Late Pleistocene excavations, with notable exceptions at Enkapune ya Muto (Marean, 1992a), and the recently excavated Rifle Range Site, Guli Waabayo, Fincha Habera, and Shinfa-Metema 1 (Davis, 2019; Jones et al., 2018; Jones and Brandt, 2022; Ossendorf et al., 2019).

Even in well-controlled excavations of rockshelter or cave deposits, where methods prioritize full recovery of faunal remains, adverse preservation conditions can negatively impact retrieval. Taphonomic circumstances – including potential carnivore activity, sediment compression, and acidic burial conditions – often lead to deletion of bone relative to lithics and other cultural material, and in other cases, bone is so heavily covered in calcium carbonate deposits as to be unrecognizable. Thus, in many Late Pleistocene contexts, faunal remains are so poorly preserved as to impede identification, leading to low Number of Identified Specimens (NISP) values, which limits analytical power (Badenhorst et al., 2022). This is true for the Bulbula River sites (Lesur et al., 2016), Laas Geel (Gutherz et al., 2014), Mochena Borago (Brandt et al., 2012) Goda Buticha (Pleurdeau et al., 2014), and Enkapune ya Muto (Ambrose, 1998; Marean, 1992a). In other sites with poor preservation, NISP values are higher but identifications are only possible to body part and carcass size, and rarely taxon, limiting some kinds of interpretations. This is the case at Magubike Rockshelter (Masele and Willoughby, 2021), Mlambalasi Rockshelter (Collins and Willoughby, 2010), and open-air Loiyangalani (Masele, 2021, 2020; Thompson, 2005).

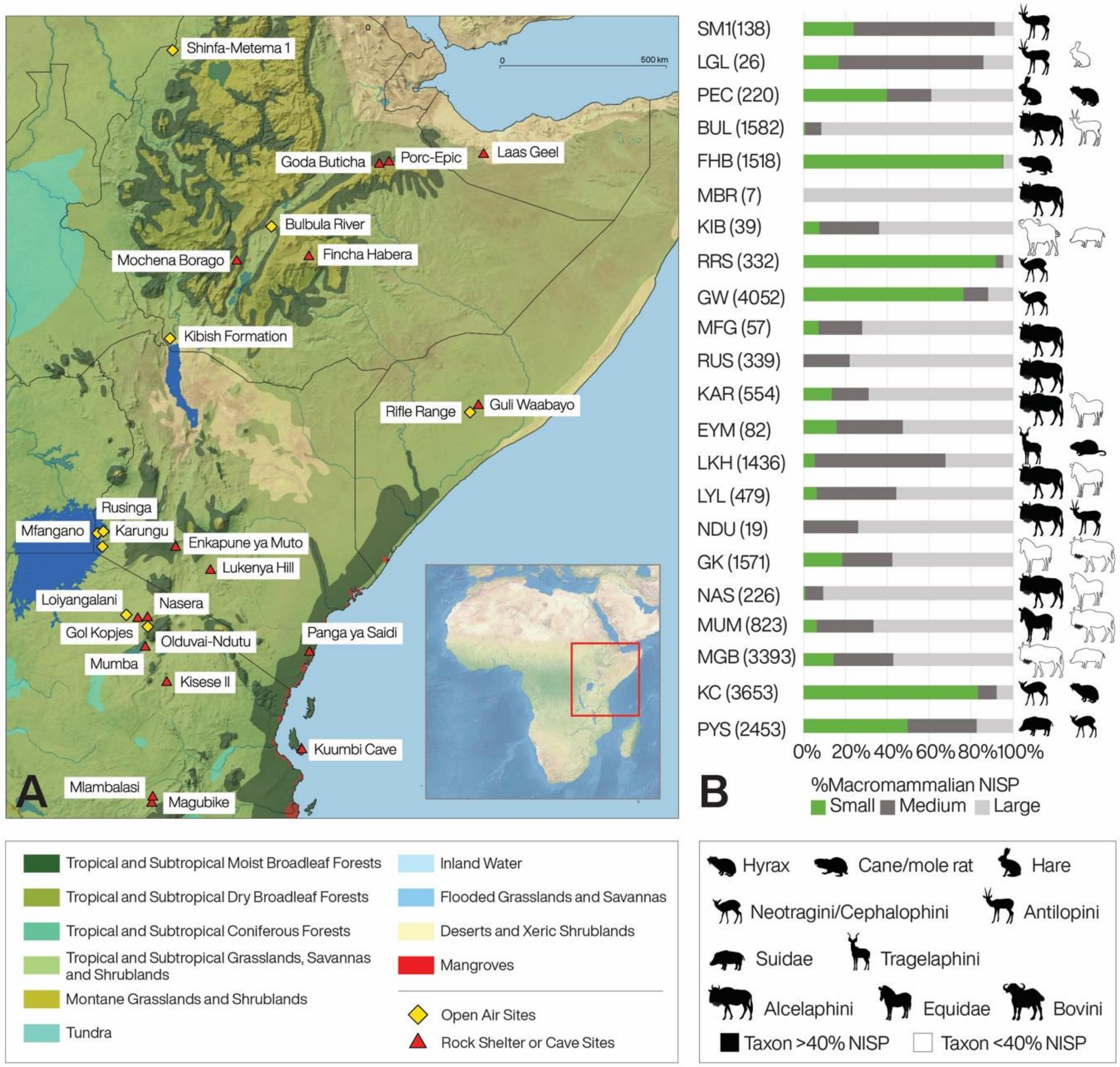

Figure 1. **(A)** Map of eastern Africa with present-day vegetation and locations of Late Pleistocene sites with published faunal assemblages. **(B)** Relative abundance of small, medium, and large

mammals, expressed as a percent of the total macromammalian Number of Identified Specimens (NISP) at each site, listed in parentheses. Icons show the two most-abundant taxa at each site. Not all sites shown in **(A)** have faunal data applicable to (B). Site abbreviations: SM1, Shinfa-Metema 1; LGL, Laas Geel; PEC, Porc-Epic Cave; BUL, Bubula River; FHB, Fincha Habera; MBR, Mochena Borago; KIB, Kibish Formation; RRS, Rifle Range Site; GW, Guli Waabayo; MFG, Mfangano; RUS, Rusinga; KAR, Karungu; EYM, Enkapune ya Muto; LKH, Lukenya Hill; NDU, Ndutu Beds, Olduvai Gorge; GK, Gol Kopjes; NAS, Nasera Rockshelter; MUM, Mumba Rockshelter; MGB, Magubike; KC, Kuumbi Cave; PYS, Panga ya Saidi. See **Table 1** and **Appendix A (Tables S1, S2)** for details of sites and explanations of mammal size groups.

2.2 Biogeographic bias

A second limitation is that Late Pleistocene faunal assemblages are biogeographically biased. Most have been recovered from a narrow set of environments in eastern Africa, principally the Rift Valley and immediately adjacent areas, mainly from caves or rockshelters (**Figure 1**). Present-day environments for these sites fall into four main categories. First, there are caves or rockshelters found in ecotonal forest-savanna environments along the Rift Valley escarpment and highlands, as at Goda Buticha (Pleurdeau et al., 2014), Mochena Borago (Brandt et al., 2012), Porc-Epic Cave (Assefa, 2006), and Enkapune ya Muto (Ambrose, 1998). Second are lowland riverine or lacustrine plains, characterized by open and semi-open vegetation, as at the Bulbula River sites (Lesur et al., 2016), Laas Geel rockshelter (Gutherz et al., 2014), the Rifle Range and Guli Waabayo inselberg sites (Jones et al., 2018; Jones and Brandt, 2022), the Kibish Formation (Assefa et al., 2008; Trapani, 2008), Victoria Basin fossil beds (Faith et al., 2015; Tryon et al., 2012), and Mumba Rockshelter (Mehlman, 1989). A third group of sites are found in higher-elevation grasslands, as in the Athi-Kapiti Plains of Kenya at the Lukenya Hill sites (GvJm19, GvJm22, GvJm46, and GvJm62) (Marean, 1992b), and in the Serengeti Plains of Tanzania at Nasera Rockshelter, Gol Kopjes, Loiyangalani, and the Ndutu Beds at Olduvai Gorge (Eren et al., 2014; Gifford-Gonzalez, 2011; Masele, 2020; Mehlman, 1989). Finally, a fourth group of sites are located in semi-wooded uplands, as at Kisese II Rockshelter in the Irangi Hills and at Magubike and Mlambalasi Rockshelters in the Iringa Highlands (Collins and Willoughby, 2010; Masele, 2017; Masele and Willoughby, 2021; Tryon et al., 2019).

These biases limit our understanding of Late Pleistocene foodways in important ways. They shape an understanding of the early human food quest that centers on hunting of large game in grasslands, which although important, leaves small game forgotten even though their capture, in a broader range of environments, is possible and attested in other parts of the continent (e.g., Klein, 1981; Wadley 2010). Aquatic resources, long shown to be important in Pleistocene southern and northern Africa (e.g., (Colonese et al., 2011; Marean, 2016), are rarely reported in eastern Africa (but see Davis, 2019; Stewart, 1989). Taken together, these biases affect our understanding of food procurement and preparations associated with Middle and Later Stone Age technologies.

Recent research, however, has emphasized a greater diversity of site locations, and accordingly enable scholars to study a greater array of food procurement strategies. These include the Afro-alpine environment of the MSA site of Fincha Habera (Ossendorf et al., 2019), and mesic coastal environments in southern Tanzania (Beyin and Ryano, 2020; Masao, 2015; Omi, 1986), at Kuumbi Cave on Unguja Island (Zanzibar) (Prendergast et al., 2016), and at PYS, under analysis here, in southeastern Kenya's peri-coastal zone (Shipton et al., 2018). Earlier research, too, uncovered faunal assemblages from comparatively closed and humid environments in the Great Lakes, including Ishango (Peters, 1990; Stewart, 1989), Katanda (Yellen, 1996), and Matupi Cave (van Neer, 1984; van Noten, 1977), and these merit revisiting in light of the themes raised here.

2.3 Chronological resolution

Third and finally, a major limitation of some Late Pleistocene assemblages is a lack of chronological resolution. Many deposits produce dates near or beyond the limits of radiocarbon dating, and many sites reviewed here were excavated prior to widespread use of the Accelerator Mass Spectrometry (AMS) radiocarbon method and other radiometric dating methods (e.g., optically stimulated luminescence). Several sites in our review have been recently dated (e.g., Fincha Habera, Goda Buticha, Guli Waabayo, PYS, Kuumbi Cave) or redated (e.g., Kisese II, Mumba, and Nasera Rockshelters) (Gliganic et al., 2012; Jones, 2020; Ossendorf et al., 2019; Pleurdeau et al., 2014; Ranhorn and Tryon, 2018; Shipton et al., 2018; Tryon et al., 2018). However, the lack of a region-wide high-resolution chronology for the Late Pleistocene hinders assessments of diachronic subsistence change, inter-assemblage comparisons, and links between faunal assemblages and dated paleoenvironmental archives.

3. Interpreting the faunal records

Despite being limited by sampling and preservation biases, particular biogeographic settings, and obstacles to chronologically linking fauna and cultural phenomena, archaeologists have been able to offer important insights on Late Pleistocene environments and human behavior in eastern Africa. These insights come through three major interpretational frameworks.

The first approach – developing in the 1970s and continuing in ever-more refined ways today – focuses on paleoenvironmental reconstruction, mainly based on relative taxonomic abundance (e.g., Gramly, 1976; Marean, 1992b; Marean and Gifford-Gonzalez, 1991; Mehlman, 1989) and the identification of extinct fauna (Faith, 2014; Faith et al., 2014, 2011; Rowan et al., 2015; Tryon et al., 2012). Such reconstructions have demonstrated the importance of open grasslands for Late Pleistocene eastern African hunters. **Figure 1** illustrates that at most published sites, the predominant fauna are medium to large ungulates that primarily inhabit open grasslands (**Table 1; Appendix A, Table S1, Table S2**). The abundance of grazers such as Alcelaphini, Antilopini, and warthog (*Phacochoerus* spp.), and the presence of taxa that are either extinct (such as *Damaliscus hypsodon*) or found outside their historical ranges (such as *Equus grevyi*), have been used to support interpretations of arid, open paleoenvironments and faunal communities markedly differing from present day (e.g., Faith et al., 2020b, 2015; Tryon et al., 2014, 2012, 2010).

The second interpretational lens builds upon the first by examining how people were shaped by their environments, an approach influenced by late 20th century behavioral ecology. For example, Marean (1997) developed models for Late Pleistocene to Holocene humans in eastern Africa by drawing on ethnographies of grasslands hunters elsewhere in the world, and zooarchaeological data from the Lukenya Hill sites (Marean, 1992b). Marean's work outlines different approaches to hunting (e.g., generalized encounters, specialized prey choices), and as constitutes one of the earliest appraisals of Late Pleistocene archaeofauna focused on human choices. Today, this approach is exemplified by Jenkins et al.'s (2017) analysis of procurement techniques along watercourses in the Victoria Basin. Other recent scholarship on human-environment interactions approaches questions of demography (Tryon and Faith 2016), human agency (or lack thereof) in megafaunal extinctions (Faith 2014), or the roles of refugia in human dispersal routes and cultural adaptations (e.g. Basell, 2008; Blinkhorn et al., 2022; Faith et al., 2016, 2015; Groucutt et al., 2015; Roberts et al., 2020; Roberts and Stewart, 2018).

A third interpretational lens in zooarchaeology has emphasized taphonomy and the relative contributions of humans, carnivores, and other agents to assemblage formation. The taphonomic approach, while established in African zooarchaeology by the 1970s and important to Plio-Pleistocene archaeology (Gifford, 1981; Domínguez-Rodrigo and Pickering, 2003), was reinvigorated at the turn of the 21st century by questions of *H. sapiens*' 'behavioral modernity' in the Middle and Late Pleistocene (McBrearty and Brooks, 2000). Today, identifying 'modernity' is increasingly problematized (e.g., Scerri et al., 2018), yet taphonomy remains critical to assessing the validity of faunal interpretations, and is an important focus of Late Pleistocene zooarchaeology in eastern Africa (e.g., Collins and Willoughby, 2010; Jenkins et al., 2017; Masele, 2020; Masele and Willoughby, 2021; Ossendorf et al., 2019; Prendergast et al., 2016; Thompson, 2005).

Moving from food to foodways, however, requires a social approach that has thus far eluded much of Pleistocene eastern African zooarchaeology. With exceptions (Marean, 1997, 1992a), studies usually lack more than passing mention of people's foraging choices, procurement technologies, butchery and other culinary practices, or implications for group organization and labor divisions, fundamental questions in social zooarchaeology (Gifford-Gonzalez, 2018; Russell, 2011; Sykes, 2014). By contrast, much of the scholarship on Holocene zooarchaeology attempts to tackle these issues for foragers and their neighbors, often with reference to ethnographic or ethnohistoric data (e.g., Gifford-Gonzalez, 2003, 1998; Marean, 1992a; Marshall and Stewart, 1995; Mutundu, 1999; Prendergast, 2010; Prendergast and Mutundu, 2009; Quintana Morales and Prendergast, 2017; Stewart, 1989). In part, these differences may reflect relatively well-preserved Holocene faunal assemblages, the potential for herder-hunter interaction, and more diverse food-related material culture, such as grinding stones and pottery.

But new research at Late Pleistocene sites is leading to an appreciation of diverse forging lifeways. For example, Davis (2019) presents the first detailed interpretations of MSA fishing economies, at Shinfa-Metema 1 in the Blue Nile Basin. Jenkins et al. (2017) combine skeletal part analysis, mortality profiles, and site formation processes to demonstrate targeted, mass capture of an extinct alcelaphine in the Victoria Basin. Langley et al. (2016) consider the potential for poison use by terminal Pleistocene hunters in Zanzibar. Finally, the abundance of small mammals at some sites (**Figure 1**) – giant mole rats (*Tachyoryctes macrocephalus*) at Fincha Habera (Ossendorf et al., 2019), dik-dik (*Madoqua* spp.) at the Rifle Range Site and Guli Waabayo (Jones et al., 2018; Jones and Brandt, 2022), and duikers (Cephalophini) and suni (*Neotragus moschatus*) at Kuumbi Cave (Prendergast et al., 2016) – is beginning to prompt discussion of prey capture techniques.

Here, in order to interpret the faunal record of PYS in terms of foraging choices and capture techniques, we look to southern Africa for inspiration, with its robust tradition of Late Pleistocene zooarchaeology (for syntheses, see Clark and Kandel, 2013; Marean, 2016; Mitchell, 2013; Plug, 2017). We draw on Wadley's (2010) work on remote capture and on relevant (*sensu* Wylie, 1985) ethnographic analogies. Working in a biogeographically underrepresented area – the coastal forest mosaic of eastern Africa – we use this framework to explore the range of procurement strategies that may have been employed during the Late Pleistocene. We also consider the group members potentially involved in the food quest, noting that in the ethnographic record, women and children tend to be actively involved in remote capture.

4. Invisible technologies and archaeological inferences

In her assessment of Sibudu Cave – a landmark site for the MSA in South Africa – Wadley (2010) used faunal and material cultural data, together with faunal data from other sites (e.g., Klein, 1981) and ethnographic observations, to construct an argument about Late Pleistocene use of snares and traps. Wadley's (2010) foremost concerns were first, emphasizing the complex cognition involved in such remote capture, in terms of planning, device construction, and acceptance of delayed returns; and second, considering a wider range of approaches to and actors involved in the food quest.

Remote capture is distinguished from encounter hunting, in which game are killed when encountered, often with spears or bows and arrows, with or without poison; as well as from other techniques such as ambushes. Big-game encounter hunting is high-effort and high-risk, with failure rates >96% but potentially large meat yields (Hawkes et al., 2001). Hunters are therefore selective in order to maximize returns on investment, targeting specific prey and prime-age individuals. Ethnographers often focus on large-game hunting because it is valued by present-day informants, particularly men, who benefit socially from it (Hawkes and Bliege Bird, 2002). Similarly, in the literature reviewed above, interpretations usually center on encounter hunting. This is logical given the dominance, at most sites, of medium to large ungulates. But it may also reflect a limited set of analogical frameworks, heavily reliant on the experiences of foragers presently living in the semi-arid Eyasi Basin (Hadza) and Kalahari Basin (Ju'/hoansi and others), and on socially and ethnographically privileged aspects of their food quests.

Remote capture requires initial labor inputs to make and set devices, but later allows free time and reliable returns, and can therefore support the seasonal and less reliable pursuit of large game. An experiment among Hadza showed that snaring small game was 12 times more successful than small-game encounter hunting, and 40 times more successful than big-game encounter hunting (Hawkes et al., 1991); yet Hadza do not usually snare (Marlowe, 2010). Remote capture is documented in the Kalahari Basin (Silberbauer, 1981), but is more common in forested environments, such as the highland Mau Escarpment (Okiek) and the lowland Congo Basin (Aka, Bofi) (Blackburn, 1982; Lupo and Schmitt, 2005, 2002). Device monitoring is compatible with other seasonal and high-input/reliable-return activities in forests, such as honey-hive construction and management (Blackburn, 1982). Snares, traps, nets, and pitfalls can be made, set, and tended by diverse group members: men and women, children and elders (Biesele and Barclay, 2001; Kent, 1993; Lupo and Schmitt, 2002; Silberbauer, 1981).

Remote capture is best suited to prey that are otherwise difficult to target through encounter hunting. Ideal prey are solitary or paired, rather than moving gregariously in herds; they follow predictable, repeated trails where devices can be set; they have small ranges, enabling regular checks on devices near camps; they live in dense woodlands or forests where pursuit is challenging; and they may be shy, nocturnal, and/or dangerous, and thus elusive. Examples in eastern and southern Africa include dwarf bovids and bushpig (**Table 2**). While dwarf bovids can also be targeted with bows and arrows, or by throwing sticks or rocks (McCall and Thomas, 2012;

Yellen, 1991), their closed habitats may make them difficult to pursue in this way, and they may not be worth the effort due to low meat yields.

Since remote capture devices perish in the tropics, we must infer their past use from circumstantial evidence, principally from the faunal record. **Table 3** outlines zooarchaeological expectations in scenarios of remote capture and of encounter hunting, recognizing that these are not mutually exclusive strategies and both may have contributed to the formation of a faunal assemblage. Remote capture is nonselective and likely to lead to high species richness and evenness; animals that may not be top-choice prey, such as small carnivores or primates, may be also taken (Lupo and Schmitt, 2002). Likewise, the age distribution will be nonselective, with mortality profiles closer to a 'catastrophic' profile (infants, juveniles, adults, and older individuals) than to a 'prime-adult' profile (Stiner, 1990), though profiles are unlikely to exactly mirror living population structure (Lupo and Schmitt, 2002; Wadley, 2010). Most importantly, the dominant prey in an assemblage will be behaviorally well-suited to remote capture.

At Sibudu Cave, the circumstantial evidence for remote capture during the Howieson's Poort occupations (~63 ka) includes: high species richness; the presence of numerous small mammals including carnivores; and dominance of blue duiker and bushpig (Clark and Plug, 2008; Wadley, 2010). Subsistence during the Final MSA (~38 ka), however, is argued to not to have involved remote capture (Collins, 2016), suggesting later strategic and technological changes, potentially in response to drier conditions (Robinson and Wadley, 2018). Arguments for remote capture have been made at numerous other Late Pleistocene southern African sites: by Klein (1981) at Byneskranskop I, Die Kelders Cave, Elands Bay Cave, Klasies River Mouth, and Nelson Bay Cave; by Dusseldorp and Langejans (2015) for Marine Isotope Stage (MIS) 5 (~100-80 ka) occupations at Blombos Cave and Klasies River; and tentatively by Reynard et al. (2016) for the Howieson's Poort at Klipdrift Shelter. The implications of small prey abundance for MSA technological innovation, niche broadening, and resource stress remain a subject of debate in southern Africa (Clark, 2011; Dusseldorp, 2012; Dusseldorp and Langejans, 2013; Lombard and Phillipson, 2010; McCall and Thomas, 2012), a discourse stimulated by Wadley's (2010) arguments. However, while inferences about remote capture may be circumstantial, the archaeofaunal correlates *are* observable and measurable, given appropriate sites and assemblages.

Along the eastern African coast and islands, ethnohistoric and archaeological data suggest that snaring and trapping have been common approaches to subsistence for centuries and potentially millennia (Ingrams, 1931; Prendergast et al., 2017b; Walsh, 2007). Here, we investigate the possible deep-time origins of these practices at PYS. The PYS faunal assemblage is well-suited to this task due to the site's location in a peri-coastal forest mosaic, its temporal coverage spanning the Late Pleistocene to Holocene, and methods that aimed for high contextual resolution and excellent faunal recovery through both dry-sieving and wet-sieving following flotation. Since assemblages with traits fitting the remote-capture model could also have been accumulated by raptors or carnivores using the cave environment, the first step is a detailed taphonomic study to assess the extent of human agency.

5. Zooarchaeological analysis at Panga ya Saidi

5.1 Site overview

PYS is part of a limestone cave complex in the Dzitsoni Uplands, ca. 15 km from the Indian Ocean (Kilifi District, southeastern Kenya). Today, this region is part of the Zanzibar-Inhambane Regional Mosaic, with lowland moist forest and lowland dry forest forming the primary vegetation (White, 1983), which is highly fragmented since much of the land is now used for agriculture (Shipton et al., 2013). Insight into past environments comes from combined zooarchaeological and stable isotope data from PYS (Roberts et al., 2020), which demonstrate that the site was located in a relatively stable forest-savanna ecotonal setting for much of the Late Pleistocene and Holocene, but with a shift starting ~67 ka toward more open, grassy environments during MIS 4 and MIS 3, and a return to more humid, forested conditions at the Pleistocene/Holocene (MIS 2/1) transition. Roberts et al. (2020) suggested that the near-coastal conditions provided a relatively stable refugium throughout the Late Pleistocene, in contrast with the Rift Valley and adjacent areas which, as shown above, witnessed faunal extinctions. Robinson’s (2022) region-wide comparison of faunal stable isotope values further underscores both the distinctiveness of the PYS environment and its role as a Late Pleistocene refugium, which may help explain its long-term attractiveness for human habitation.

Since 2010, PYS has been excavated by teams from the Max Planck Institute for the Science of Human History (formerly based at the University of Oxford) and the National Museums of Kenya (Helm et al., 2012; Shipton et al., 2018, 2013). Excavations extending over c. 7 m^2 in area and 3 m in depth have revealed a sequence comprised of 19 layers spanning the last 78,000 years (**Figure 2**) based on radiocarbon and optically stimulated luminescence dating (Shipton et al., 2018). This sequence captures MSA to LSA technological shifts (Shipton et al., 2021) and documents symbolic expression through intentional human burial (Martinón-Torres et al., 2021), as well as via beads, ochre, and worked bone and shell (d’Errico et al., 2020).

Holocene deposits at PYS yielded a variety of material including: Later Stone Age lithic technology (Goldstein et al., 2022); Iron Age material culture found at coastal towns, such as pottery and glass beads (Shipton et al., 2018); increased evidence for marine and freshwater resource exploitation (Faulkner et al., 2021); botanical and faunal remains including crops and domestic and commensal animals (Crowther et al., 2016; Culley et al., 2021; Prendergast et al., 2017b); the burial of a person with an ancient DNA sequence relatable to ancient and present-day foragers (Lipson et al., 2022; Skoglund et al., 2017; Wang et al., 2020), and isotopic values consistent with reliance on wild fauna (Roberts et al., 2020). Collectively, these finds provide insight into forager-agropastoralist relations in the region as it underwent dramatic change (Boivin et al., 2014, 2013; Crowther et al., 2018; Helm et al., 2012; Quintana Morales and Prendergast, 2017).

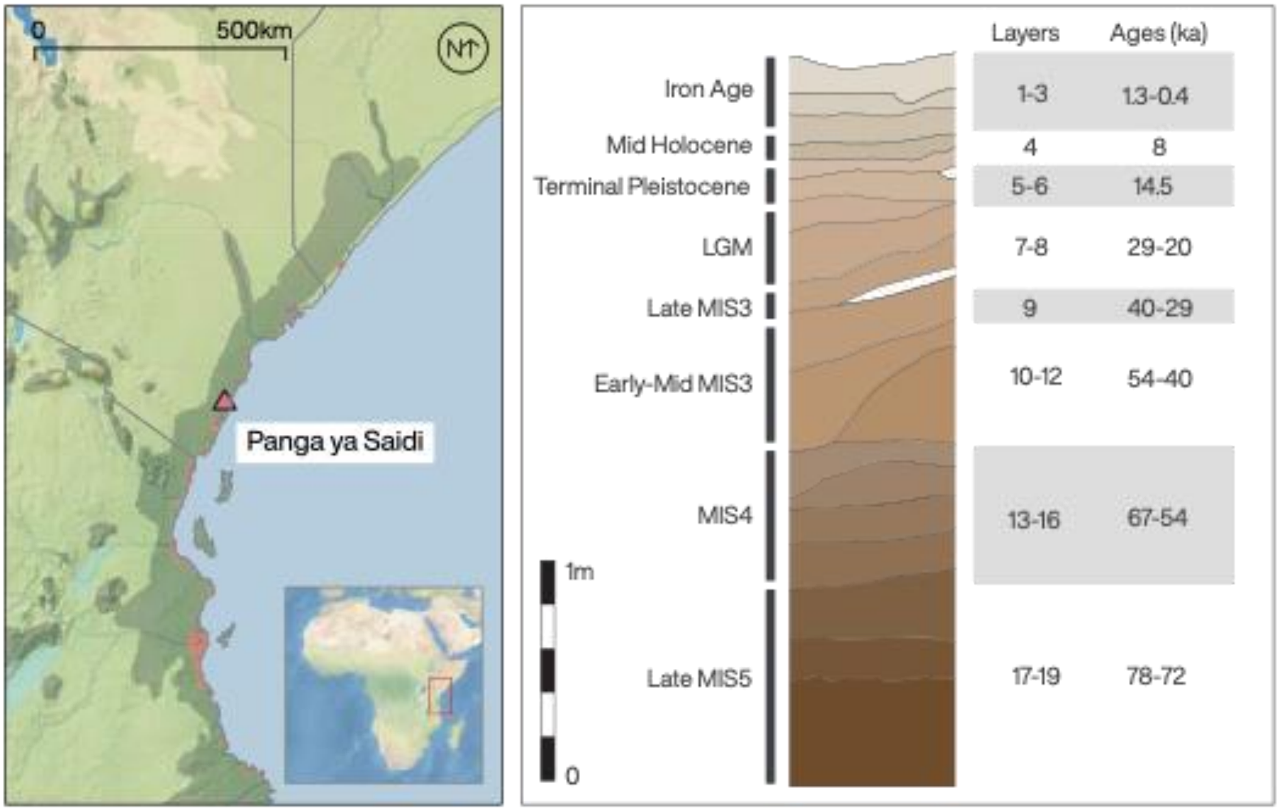

Figure 2. (A) Map of the southeastern coast of Kenya with present-day vegetation and location of Panga ya Saidi; for vegetation descriptions, see Figure 1 legend. **(B)** Panga ya Saidi stratigraphic sequence and the temporal groupings used in this paper.

The PYS sequence can be summarized and layers can be grouped as follows, based on stratigraphic studies including geoarchaeology and radiocarbon dates (Shipton et al., 2018) and artifacts including lithic technology (Shipton et al., 2021) and symbolic material culture (d'Errico et al., 2020). Layers 19-17 (late MIS 5; ~78-72 ka) are characterized by MSA occupation. Lithic technology is large relative to younger layers, it includes the Levallois technique, and is dominated by limestone. Occupation intensity was very low in the upper part of Layer 17 interface (~72-67 ka), while Layers 16-13, dating to MIS 4 (~67-54 ka), show miniaturized lithic technology and gradually increasing signs of human activity.

A sharp erosional relief separates the MIS 4 deposits from those of MIS 3, which in turn can be subdivided into three groups based on additional interfaces: Layers 12-11 (early MIS 3; ~54-48 ka), Layer 10 (mid MIS 3; ~48-40 ka) and Layer 9 (late MIS 3; ~40-29 ka). For the present faunal analysis, Layers 12-10 are lumped and Layer 9 is kept separate. The MIS 3 deposits are characterized by intensive human activity, with abundant material culture including lithics – with backed crescents appearing for the first time – as well as worked bone, shell, and eggshell, and ash lenses interpreted as disintegrated hearths.

Layers 8-7 date to the Last Glacial Maximum (LGM) during MIS 2 (~29-20 ka), and similarly to MIS 3, are a time of clear human activity in the cave. Blades become common at this point and for the remainder of the sequence. Layers 6-5 date to the terminal Pleistocene (~14.5 ka), and the thinner overlying deposits include an early to middle Holocene component (Layer 4, ~8 ka) characterized by increased use of chert, overlain by several thin Late Holocene occupations, with dates and some material culture consistent with coastal Middle Iron Age (Layer 2-3, ~1.3 ka) and Later Iron Age (Layer 1, ~0.4 ka) cultural traditions; here, as elsewhere, Layers 1-3 have been grouped (Goldstein et al., 2022). Notably, while marine resources were used for symbolic material culture throughout the Pleistocene occupations (d'Errico et al., 2020), their exploitation as food only develops in the terminal stages of the Pleistocene (Faulkner et al., 2021).

5.2 Zooarchaeological methods

The present analysis focuses on tetrapod (mammal, bird, reptile) remains recovered from excavations of Trench 3 in 2011 (6.4 kg of bone) and its expansion, Trench 4, in 2013 (14.7 kg of bone). Mollusc and fish remains are reported elsewhere (Faulkner et al., 2021). Trenches 3 and 4 preserve a long stratigraphic sequence, with Trench 4 extending into MSA deposits. Faunal data from individual contexts are aggregated into layers, and layers into temporal groups following the sequence described above (**Appendix A, Table S3**): Layers 1–3 (Iron Age), Layer 4 (mid-Holocene), Layers 5–6 (terminal Pleistocene), Layers 7–8 (LGM), Layer 9 (late MIS 3), Layers 10–12 (early-mid MIS 3), Layers 13–16 (MIS 4), and Layers 17–19 (MIS 5).

Zooarchaeological analysis by M.E.P. took place in 2012 and 2014 at the National Museums of Kenya (NMK) in Nairobi, with access to ample and highly relevant regional comparative collections. Faunal remains were sorted into three groups: maximally identifiable (maxID; all teeth, and bone fragments preserving highly diagnostic features); minimally identifiable (minID; e.g., limb shaft, rib, and vertebral fragments); and not identified (NID) in light of fragmentation, preservation, analyst experience, and time. About 10% of the assemblage, by weight, was classified as maxID and each of these identified specimens was given a unique database record and catalog number; groups of identified specimens were bagged together. In a subset of nine high-priority contexts (**Appendix A**), minID specimens were also identified and assigned catalog numbers in the same fashion. In other contexts, minID specimens were bagged separately but left unanalyzed due to time constraints. NID specimens were weighed.

Cataloged specimens were identified, at minimum, to skeletal element (or element type, e.g. limb bone) and to a taxonomic group or size class. Taxonomic identification was largely based on NMK osteological collections, supplemented by photographs of reference collections and by published guides (e.g., Walker, 1985). Size classes were used for bovids and other mammals, adapted after Brain (1981) (**Appendix A, Table S4**). In the Iron Age subassemblage, some identifications were later confirmed or changed following collagen fingerprinting and ancient DNA analyses (Culley et al., 2021; Prendergast et al., 2017a).

Estimates of the Minimum Number of Individuals (MNI) were derived for each temporal grouping (aggregating layers), using the database and considering laterality, body size, and where relevant, estimated age. These estimates are deliberately conservative. It may have been possible to calculate MNI for each layer, but at the risk of double-counting individuals whose remains shifted after deposition. MNI estimates calculated post-analysis from the database are also likely far lower than would be the case if it had been possible – given adequate space and time – to lay out all limb specimens in order to identify unique elements and individuals. Inclusion of limb shafts can elevate MNI in assemblages affected by density-mediated attrition (e.g., Marean and Spencer, 1991).

Identification of bone surface modifications (BSM) such as cut marks, percussion marks, carnivore tooth marks, and rodent gnaw marks formed an important part of the analysis at PYS, especially given initial questions about human agency in the formation of the earliest faunal deposits. All cataloged bones were examined with 10x-20x hand lenses under strong oblique light in order to identify BSM, following criteria outlined in Domínguez-Rodrigo et al. (Domínguez-Rodrigo et al., 2007). Other modifications including burning, weathering, polishing (anthropogenic and natural), and damage from water, insects, roots, and fungi were noted; identification of biochemical damage follows (Domínguez-Rodrigo and Barba, 2006). Breakage was recorded following Villa & Mahieu (1991). Cortical preservation was scored as good (complete cortical surface intact and visible), moderate (>2/3 of cortical surface intact and visible), or poor (<2/3). Limb diaphyseal circumferences were recorded using Bunn's (1981) typology: Type I (x<50% of circumference), Type II (100>x>50%), and Type III (x=100%). Potentially worked bones, teeth, and (egg)shell were identified, separated, and are reported elsewhere (d'Errico et al., 2020).

6. Results

6.1 Assemblage overview

A total of 5,239 nonhuman faunal specimens (Number of Identified Specimens, NISP) were identified in Trenches 3 and 4, representing a minimum of 366 individuals (MNI) (**Table 4; Appendix A, Table S5**). Just over half (52%, by weight) of the assemblage was identified. Many identified remains belong to microfauna, leading to inflation of NISP and MNI values especially in the Iron Age (Layers 1-3). For those contexts, microfauna – including rodents, shrews, bats, birds, and small reptiles such as snakes – were studied in Trench 3 but not Trench 4; therefore, even though microfauna are numerous, they are in fact underrepresented. Cave use seems to have been infrequent during the Iron Age, and the densely packed, fresh-looking rodent bones in Layers 1-3 may originate from raptor or snake activities in the cave. In all of the analyses presented in this paper, except for the analysis of faunal densities by weight (**Figure 3A**), microfauna are excluded. Instead, analyses presented here focuses on the macromammalian assemblage, which largely comes from the Late Pleistocene deposits in Layers 4-19. For detailed discussion of Holocene faunal remains, see Prendergast et al. (2017) and Culley et al. (2021).

In the lowermost Layers 17-19 (MIS 5), bats and monkeys are abundant, and their presence, along with a few other potentially cave-dwelling taxa such as crocodile and pangolin, suggests periods of low occupation intensity or cave abandonment, consistent with geomorphological and magnetic susceptibility data for Layers 17 and 19 (Shipton et al., 2018). While not consistently catalogued during analysis, a large number of crab dactyls were also noted in the deepest levels, and these are cave inhabitants today, as observed during excavation. Carnivore remains are rare and scattered throughout the sequence. These are mainly limited to small taxa such as mongoose, but also include a single isolated tooth and one bone of hyena in MIS 4 and early-mid MIS 3 deposits, and a likely leopard bone in MIS 4 deposits.

Other indicators also suggest a clear pattern of low human activity in the earliest and most recent deposits, and intermittent but important human activity from MIS 4 to the middle Holocene. Faunal and lithic densities based on weight (**Figure 3a**) generally track one another, and are notably high during MIS 3 and MIS 2 (LGM), which is also when other indicators of human activity – including charcoal, possible hearths, and cultural materials such as bone tools and beads

– are commonly found (d’Errico et al., 2020; Shipton et al., 2018). Where densities diverge, it may be explained by large, heavy limestone lithics in the deepest deposits. Burnt bone, while present even in the deepest (MIS 5) deposits, is most abundant in the middle of the sequence, another indicator of human subsistence activity (**Figure 3b).** The mid-sequence is also where abundant but highly fragmented macromammalian remains are found – which are often less identifiable than the small fauna common to earlier and later deposits (**Figure 3c**). From Layer 14 through Layer 4, ungulates – bovids and suids – dominate (>50% of NISP), and these would have been transported to the cave (**Figure 3d**). Large bovids are common in the middle of the sequence, and relatively rare in the earliest and most recent deposits; small-bodied bovids are common throughout most of the sequence; nearly identical patterns are seen when all macromammals, not only bovids, are considered (**Figures 3e, 3f**).

Overall, the picture that emerges is one of low occupation intensity in the oldest and youngest deposits, with abundant ‘background fauna’ that may have entered the cave on its own or as the prey of other animals. By contrast, from MIS 4 through the terminal Pleistocene, faunal and other indicators indicate intermittent, but clear, human use of the cave.

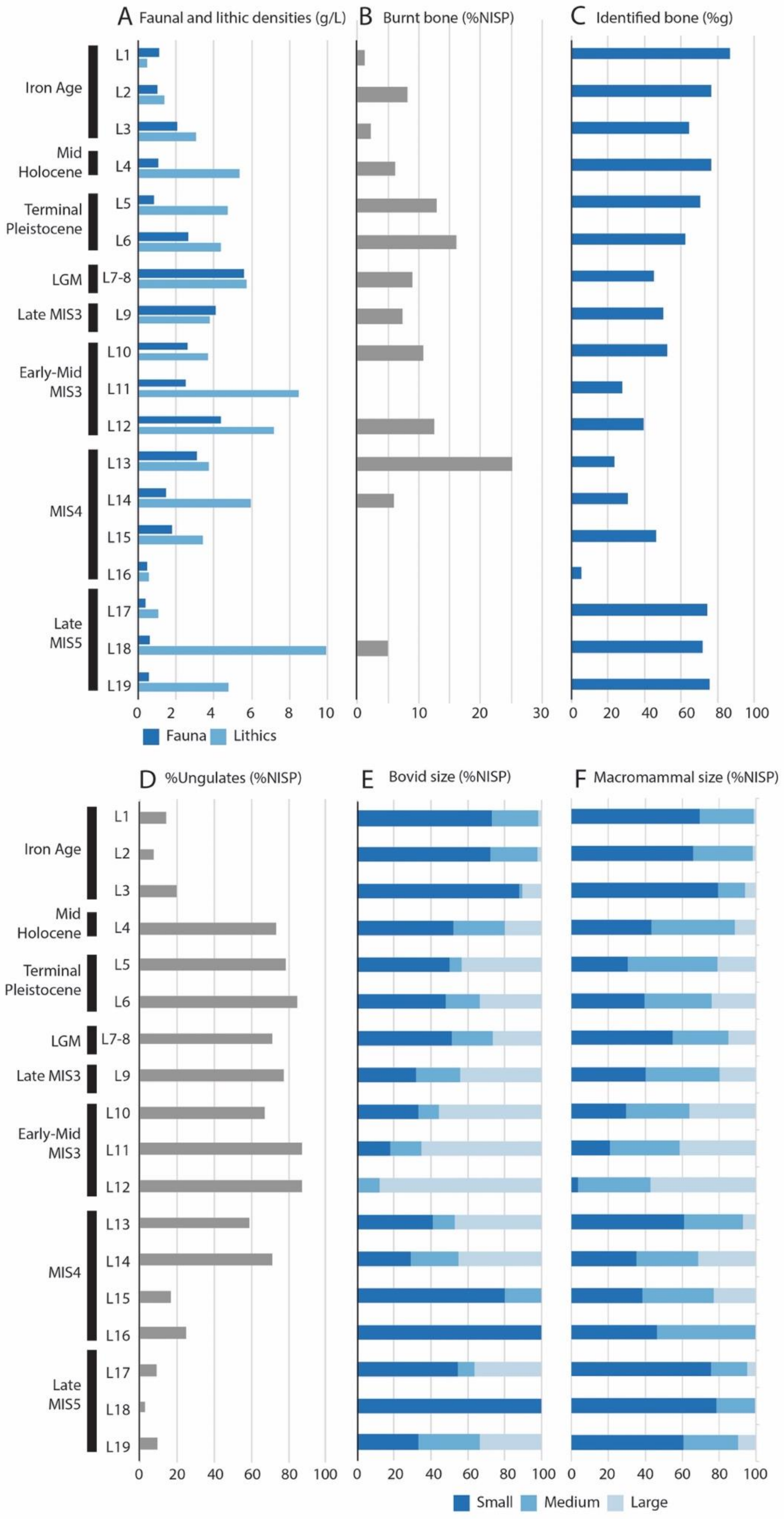
A Faunal and lithic densities (g/L)
B Burnt bone (%NISP)
C Identified bone (%g)
Iron Age
Mid Holocene
Terminal Pleistocene
LGM
Late MIS3
Early-Mid MIS3
MIS4
Late MIS5
L1
L2
L3
L4
L5
L6
L7-8
L9
L10
L11
L12
L13
L14
L15
L16
L17
L18
L19
0 2 4 6 8 10
0 10 20 30
0 20 40 60 80 100
Fauna
Lithics
D %Ungulates (%NISP)
E Bovid size (%NISP)
F Macromammal size (%NISP)
0 20 40 60 80 100
Small
Medium
Large

Figure 3. Overview of trends in the PYS Trench 3-4 faunal assemblage. A, densities of tetrapod faunal remains and lithics (grams per liter of excavated sediment), including microfauna. B, frequency of burnt bone, as a percentage of all identified tetrapods (NISP, Number of Identified Species), excluding teeth and microfauna; C, percentage of the tetrapod faunal assemblage that was identified, by weight; D, frequency of ungulates (suids and bovids) among identified tetrapods (NISP); E, relative abundance of size groups among identified bovids; F, relative abundance of size groups among identified macromammals; carnivores, rodents, and shrews are excluded.

6.2 Taphonomy and assemblage formation

The PYS sequence shows highly variable faunal preservation conditions. In nine selected contexts, all maxID and minID specimens were identified (NISP = 1,765) and a full taphonomic analysis was conducted (**Table 5; Supplementary Table S6**). In order to assess faunal assemblage formation at PYS, quantitative indicators of faunal abundance, cortical preservation, breakage patterns, and BSM for this subset and the broader assemblage have been combined with qualitative notes, regularly taken during analysis for individual specimens and whole contexts.

In the deepest deposits (L19-L17), faunal remains are sparse (0.5 g/L) and poorly preserved. Heavy fragmentation and a lumpy, thick coating of sedimentary matrix made these remains difficult to identify. Just a quarter (26%) of NISP were rated as having good cortical preservation. Where surfaces are visible, they frequently exhibit faint, multidirectional, elongated scratches typical of mechanical abrasion (6.8% of macromammalian NISP, 8.2% of limb shaft NISP); remains may have been exposed to trampling by animals or people prior to burial. Many identified specimens are fragmentary limbs of bats and other microfauna, including rodents; gnawing is observed at a greater frequency than anywhere else at PYS (3.4% of macromammalian NISP). Water affected parts of the assemblage (**Figure S1**): some bones experienced chemical dissolution, inferred from softening and bleaching of bone, while others have worn or rounded surfaces and edges. At least 15% of NISP bear pits and channels typical of biochemical marks created by bacteria or fungi, and another 3% of NISP – at minimum – bear star-shaped pits made by insects (biochemical and insect marks were not recorded consistently, so rates may be higher). The fact that these adverse preservation conditions exist alongside relatively well-preserved bones in L17-L19 suggests that there were highly localized microenvironments in the cave. For example, water drips or channels, and/or patches of bat guano, may have created locally acidic conditions.

Signals of human activity are low but present during MIS 5. Burnt bone is identifiable and can usually be distinguished from the brown to black oxide staining that characterizes much bone in the deepest deposits. In L18, 5% of NISP are burnt, sometimes under conditions hot enough to produce calcination, evident in a bluish white color. Abundant green breakage (83% of observed breakage planes in L17-L19) implies most bones were broken while fresh. Cut marks are on 4.5% of macromammalian NISP, whereas tooth marks are less common at 1%. These frequencies rise to 5.8% and 2.1%, respectively, if ambiguous marks are counted. Collectively, the data suggest multiple agents – including carnivores, rodents, and people – were involved in assemblage formation and modification during MIS 5 at PYS, and that this assemblage formed over a long period of infrequent human activity.

During MIS 4 (L16 to L13), similarly patchy preservation conditions persisted, with many of the same traits described above for some – but not all – remains: heavy fragmentation, frequent coating in a thick sedimentary matrix (nearly 40% of cortical surfaces were rated as 'bad'), and in a few cases, evidence of dissolution or rounding by water. In comparison with MIS 5, abrasion is rare (2.2%), and remains low for the remainder of the sequence. Bat and crab remains are abundant in some contexts, and rare in others. Nearly all breaks are fresh rather than diagenetic (94%). Burnt bone increases toward the top of the deposits, from 6% of NISP in L14 to 25% of NISP in L13. Cut and tooth marks occur at low frequencies (0.9%).

During MIS 3 (L12 to L9), bone preservation conditions steadily improve, though the variability and patchiness of earlier deposits remains true here as well. In L12, degrees of bone fragmentation, and incidences of dissolution and rounding, are similar to those of underlying deposits. L11, however, preserves larger, more intact bone specimens, with improved surface visibility and identifiability. The profile of animals represented also changes during early MIS 3, with more large ungulates, and only rare bat, rodent, or crab remains. Burnt bone is common in L12 (13%), but absent in L11; frequencies are influenced by small samples.

Preservation improves substantially in L10 and L9, which are characterized by abundant macromammalian remains and especially limb shafts of medium and large ungulates, which overwhelmingly have green breakage planes (80% of observations in L9). Surfaces are often clearly visible; only 19% of cortical surfaces were rated 'bad' in L9. Chemical dissolution and water polishing are rare. Burnt bone remains common (11% of NISP in L10, 7% in L9), and in L9 this may be linked to a disintegrated hearth (context 413c). Despite the visibility of surfaces and the abundance of limb shafts, cut marks remain infrequent (2% of limb shaft NISP; or 3.6% if including ambiguous marks). There are even fewer carnivore tooth marks (1.6%; or 2.4%), suggesting these are not major agents of assemblage formation. Given the indicators pointing to a human role in assemblage formation, the low incidence of cut marks is surprising; but it is notable that at other coastal sites where small mammals dominate and human agency is clear, cut marks are similarly infrequent (Prendergast et al. 2016, Prendergast et al. 2017).

Deposits dating to the LGM (L8-L7) contain some of the best-preserved fauna at PYS. As in L10 and L9, these deposits have abundant limb shafts of medium and large ungulates, again mainly broken while fresh (87% of observed breakage planes). Microfauna are rare aside from a single cluster of bat remains. Surface preservation is better than elsewhere in the site (just 10% of surfaces rated 'bad'), and BSM are better documented: cut marks are present on 3.8% of shafts (or 6.5% if including ambiguous marks), while tooth marks are rare (0.7%, or 1.3%). Burnt bone is common (9%) and sometimes exhibits calcination.

Similarly good preservation continues into the terminal Pleistocene (L6-L5), but remains are relatively few, indicating a drop in occupation intensity. This is supported by an increase in remains of cave-dwellers – bats, rodents, and crabs – though an intrusive burrow (context 409) may be a source of some of these. Burnt bone is abundant in L6 (16%) and L5 (13%), while cut marks are few (1.3% of limb NISP) and tooth marks absent; all of these frequencies are influenced by small samples, however, and the visibility of BSM is also influenced by a thin sedimentary matrix – distinct from that of deeper deposits – that coats many of the surfaces.

Many of these trends continue into the middle Holocene (L4): faunal remains are sparse, large mammals are fewer, and microfaunal remains increase. Bone preservation conditions are good, surfaces are similarly coated in a thin matrix, and BSM remain low, with 3.2% of NISP (n=2) bearing cut marks and 1.6% (n=1) bearing tooth marks and rodent marks; these samples are extremely small. As one moves into the Middle Iron Age (L3) and Later Iron Age (L2-L1), the presence of microfauna increases dramatically, with rodents, bats, birds, crabs, and – for the first time – fish becoming common. Bone surface preservation is excellent, and microfauna often appear fresh, likely recent. Burrowing by rodent and/or raptor deposition of pellets are possible explanations. The mixing of fresh-looking bone with more ancient-looking bone suggests significant postdepositional disturbance, especially in L1-L2. The presence of a human burial in L1, dated to ~400 BP (context 402), is one likely cause of this disturbance.

Indications of human agency, in the form of burnt and cut-marked bones, are present even in the deepest layers of PYS, where occupation intensity was low (**Table 5**). Human activity at PYS is most intensive from MIS 3 through the LGM, when densely packed large mammal remains bear signatures of subsistence activities. Surface preservation in many of these contexts is excellent, and most bones were broken while fresh. While fresh (or 'green') breakage cannot indicate the agent of breakage, a paucity of carnivore tooth marks or notches suggests these were not important bone accumulators at PYS. Signatures of human activity are more common in the form of burnt bone, but butchery activities are difficult to detect, with cut marks usually appearing on less than 2% of NISP, except during parts of MIS 5, MIS 3, and the LGM, when these rates reach up to 5% (or higher if including ambiguous marks). The paucity of cut-marks is discussed further below in a consideration of carcass sizes.

6.3 Taxonomic identifications

Identifications to taxon were often limited by fragmentation and a paucity of highly identifiable fragments such as teeth and limb epiphyses or complete bones. As a result, most NISP (93%) are identified at the family level or higher, and ample use was made of bovid size classes (14% of NISP) and mammal size classes (37% of NISP) (**Table 4; Appendix A, Table S5**). As noted above, remains of potential cave-dwellers were recovered particularly in the earliest and most recent deposits. Here we focus on ungulates and other taxa that may have been captured – intentionally or not – and consumed by people.

Macromammalian ungulate (bovid and suid; not hyrax) remains are found throughout the sequence and are relatively abundant from MIS 3 through the LGM. Suids (NISP = 167) include both warthog (NISP = 42, MNI = 8) and bushpig (NISP = 13, MNI = 4), and during the MIS 3 to LGM, warthog become relatively abundant, which together with stable isotope data has been interpreted in terms of increasingly open habitats (Roberts et al., 2020). Of those specimens identified as bovids (NISP = 860), only 14% (122) could be identified to tribe. Tribe-level identifications – particularly when combined with stable isotope values – agree with the suid data by showing that while PYS was always located near a tropical forest-grassland ecotone, there are low-amplitude but clear shifts toward open environments from late MIS 4 until the Pleistocene-Holocene transition (Roberts et al., 2020).

Two interrelated trends stand out amongst bovid remains. First, it is clear that small bovids – which include suni, dik-dik, klipspringer, oribi, and bush duiker – are the focus of subsistence at PYS, and indeed all but klipspringer persist in the region today. Small bovids are more than half of NISP throughout the assemblage except during later MIS 4 and MIS 3, when medium and large bovids are more common (**Figure 3e**). Second, for those remains that could be identified to bovid tribe, there are clear diachronic shifts in relative abundance (**Figure 4**). Small mostly browsing bovids, Neotragini (suni, dik-dik, klipspringer) and Cephalophini (duikers), are present throughout and dominate in the earliest and latest parts of the sequence. They are however less abundant during MIS 3 through the LGM, relative to medium and large grazing Alcelaphini (topi/hartebeest, wildebeest), Reduncini (reedbuck, waterbuck), and Bovini (buffalo). Tragelaphini (bushbuck, eland) are present in low numbers mainly at the beginning and end of the sequence, consistent with their preference for more closed habitats.

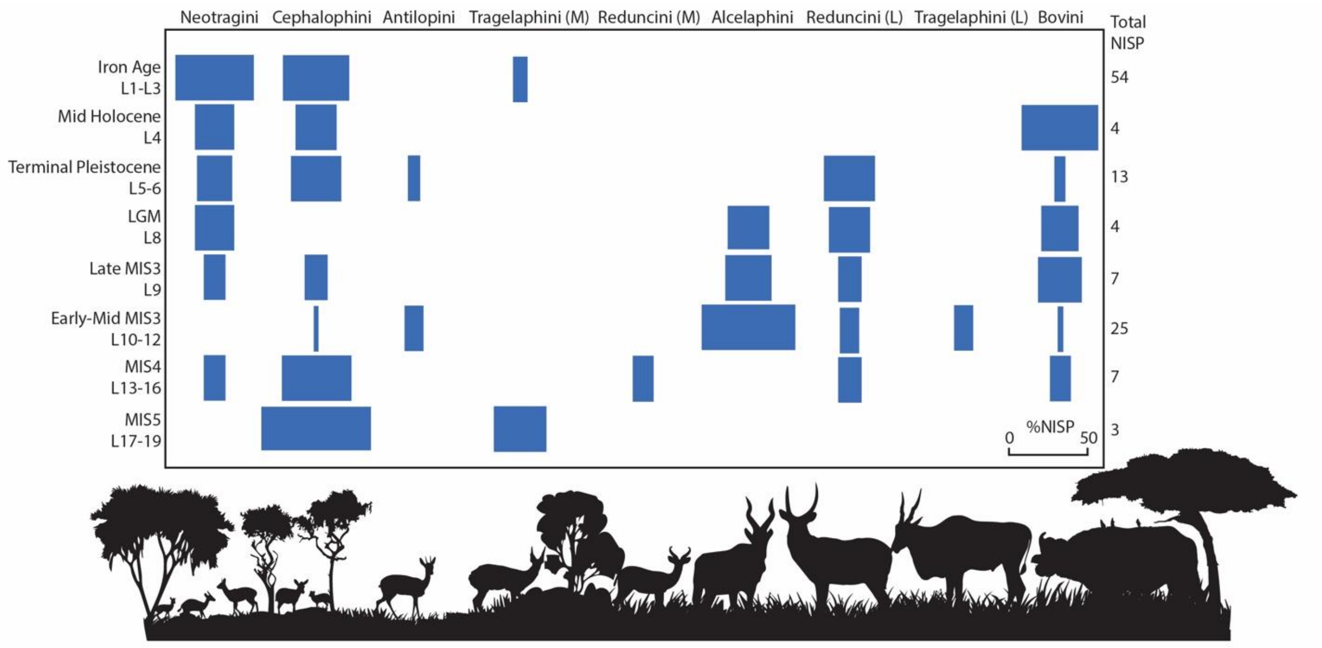

Figure 4. Relative abundance of bovids, expressed as %Total NISP for each temporal grouping. Representative species of each tribe are illustrated and show a continuum from small (left) to large (right) carcass sizes. In general, this continuum also trends from mainly browsing bovids (Neotragini, Cephalophini) to mostly grazing bovids (Alcelaphini, Bovini), but not perfectly so, since Tragelaphini, for example, are mainly browsers; see discussion in Roberts et al. (2020).

We caution that the sample sizes illustrated in Figure 4 are small. The differences in faunal representation over time, however, are statistically significant. Ten taxonomic groups (Neotragini, Cephalophini, Tragelaphini, Antilopini, Bovini, Reduncini, Alcelaphini, *Potamochoerus*, *Phacochoerus*, and Cercopithecini/Colobini) were compared across temporal grouping, using the free R software (R Core Team, 2013). First, NISP data were organized in a contingency table for each taxonomic group, using the temporal groupings seen in Figure 4. Next, we analyzed these values using a chi-square test and a randomized Fisher test. The Fisher test is more reliable in the case of small sample sizes and null values (i.e., some bovid tribes are absent in some temporal groups). Finally, we computed p-values for both tests using a Monte Carlo simulation, replicated 2000 times. The chi-square test yielded significant differences over time in representation based on NISP ($\chi2=228.66$, df=63, $p < 2.2e-16$), as did the randomized Fisher test ($p < 0.001$). When focusing only on the seven bovid groups, the same Fisher test also found a significant difference ($p < 0.001$).

Small mammal and reptile remains are common at PYS (**Figure 3e**) and may represent human food in some cases. Primate remains (NISP = 57) are found throughout the sequence, but abundant in the earliest part of the sequence. These include monkeys (Cercopithecini and

Colobini, NISP=45), baboon (*Papio* sp., NISP=5) and galago (*Otolemur* sp., NISP=2). While it is likely that many of these primates were present in the cave of their own accord, or as the prey of other animals, cut marks on colobus remains in L11 (early MIS 3) suggest that at least some were eaten by people. Hyrax are also present (Hyracoidea, NISP = 85), and although they are occupants of this cave today, one bone in L8 (LGM) bears a possible cut mark, and five bones are burnt in L10 through L5. Giant pouched rat (NISP = 6) and tortoises (NISP = 49) are also found, but not cut-marked. Monkeys, hyraxes, pouched rats and tortoises were, and in some cases are, eaten on the coast (Prendergast et al., 2017b, 2016; Walsh, 2007), and we consider this to be possible at PYS.

6.4 Assessing bone surface modifications by carcass size

Analysis of bone surface modifications, already touched upon in Sections 6.2 and 6.3, can be informative about the agents of accumulation, and here are assessed according to carcass size (**Table S2, Figure S2**). Unfortunately, sample sizes are small. An assessment of the limited number of toothmarked specimens suggests they are more abundant in the earliest (MIS5-MIS4) and middle (Late MIS3-LGM) deposits at the site, and that the few identified marks are found on all carcass sizes. Human-imparted marks – cut marks and burning – are more abundant throughout the deposit. While cutmarks tend to be relatively abundant in large and medium carcasses, this likely reflects the higher degree of butchery required for these carcasses. Burnt bone, on the other hand, is common in small carcass sizes. At least initially, these data – limited by sample size and by the ambiguity of many of the cut and tooth marks – suggest humans had an important role in accumulation of the fauna, and that human activities (butchery and fire use) were associated with all carcass sizes. The abundance of burnt remains of small game, and the paucity of tooth marks, challenges an interpretation that these carcasses were largely accumulated by carnivores.

6.5 Skeletal part representation

Inferences about complete *versus* selective transport of fauna must take into account the taphonomic processes that can introduce bias. The PYS faunal assemblage may be subject to density-mediated attrition, i.e. the loss of less-dense skeletal elements and portions, a pattern common to many archaeological sites (Lam et al., 2003). This can be seen through survivorship indices illustrated in **Figure 5** and tabulated in **Appendix A, Table S7**. Survivorship is defined as the Minimum Number of Elements (MNE) represented at the site, as a percentage of the expected number of elements based on the MNI. For ease of illustration, skeletal elements are grouped following Clark (2011) into broad categories: skull, axial, forelimb, hindlimb, distal limb, and feet. Some caveats merit repeating here: only a subset of contexts were fully studied including minID specimens, which are critical to skeletal part representation; and it was not possible to lay out all elements on surfaces, which would have enabled higher and more accurate MNE and MNI estimates. These data should therefore be taken as preliminary, to be confirmed with an expanded study.

Although there is variation across carcass sizes and over time, some trends are clear throughout the assemblage. Skulls – represented mainly by teeth – are relatively abundant, and indeed are often the element that provided the highest MNI. Foot and distal limb bones, while appearing numerous, are underrepresented relative to expectations based on MNI. Axial bones – generally less dense – are virtually absent, never exceeding a survivorship rate of 6%. Survivorship is more evenly distributed across the skeleton for smaller bovids. By contrast, large bovids are often represented by little more than crania, except in MIS 3 and LGM deposits, where they are not only abundant but also more evenly represented. Suid remains are especially fragmented and mostly limited to teeth, distal limbs, and feet.

The dominance of skull and limb bones, and the absence of axial remains, speaks to patterns of density-mediated attrition that are further supported by the ratio of limb epiphyseal specimens (generally spongy) to limb diaphyseal specimens (generally dense). Additionally, the abundance of shaft circumferences <50%, especially among medium and large ungulates, indicates heavy fragmentation of limb bones. Since carnivore modification of bone – in the form of tooth pits or scores, or notches typical of static loading – is rare at PYS, a more logical explanation is that humans broke open bones for marrow or grease extraction, or trampled them after cooking. Another likely agent of breakage is sediment compaction over the long timescales represented at PYS.

The strongly adverse burial conditions in deeper contexts of the cave – which led to chemical dissolution including softening and bleaching of bone – may also have created an environment in which less-dense portions could not survive. Given these possible explanations, it would be prudent to consider taphonomic factors rather than selective transport as the primary drivers of the skeletal part patterns seen at PYS (Faith and Thompson, 2018), especially until more detailed taphonomic analyses can be undertaken on a larger PYS assemblage.

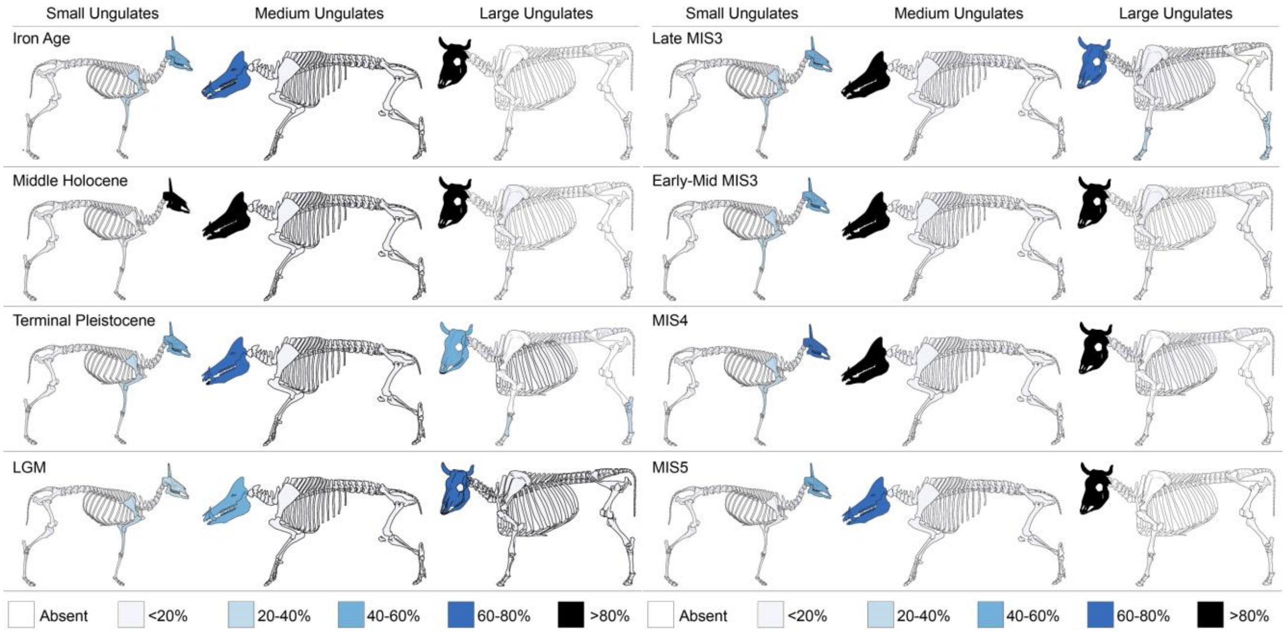

Figure 5. Survivorship of skeletal elements of small, medium, and large ungulates at PYS. This is expressed as the Minimum Number of Elements (MNE) present at the site, as a percentage of the expected number of elements, given MNI (Minimum Number of Individuals). Medium ungulates includes all suids, and medium-sized bovids; large and small ungulates are only bovids. For size classifications, groupings of elements, and tabulated data see **Appendix A**.

6.6 Mortality patterns

Analysis of mortality patterns was limited by sample sizes of specimens that inform about age at death: complete teeth or limb epiphyses. Tooth wear coding and reference data are not available for most wild African bovids. While subjective descriptions of tooth wear were recorded, these are not considered sufficiently reliable here. Instead, only postcranial remains are used, and the limits of this dataset include that reference data on fusion are not widely available; postcrania are uninformative about age after fusion has occurred; and in a scenario of density-mediated attrition, epiphyses and remains of juveniles and neonates are unlikely to preserve. Given the poor resolution of this data, three very broad categories were used: adult (fused epiphysis); subadult (unfused or fusing epiphysis); and neonatal (generally recognizable as small and unfused diaphyseal shafts of a highly porous texture).

All these caveats taken into account, a preliminary pattern does emerge in which there is more diversity in age-at-death among small bovids, which include adult, subadult, and neonatal individuals, than among medium and large bovids, which are mostly represented by adults (**Figure 6**). This contrast holds true throughout most of the sequence. While this trend should be confirmed with larger samples, this initially suggests that people were intentionally targeting adult medium and large ungulates, whereas capture of small game was less selective.

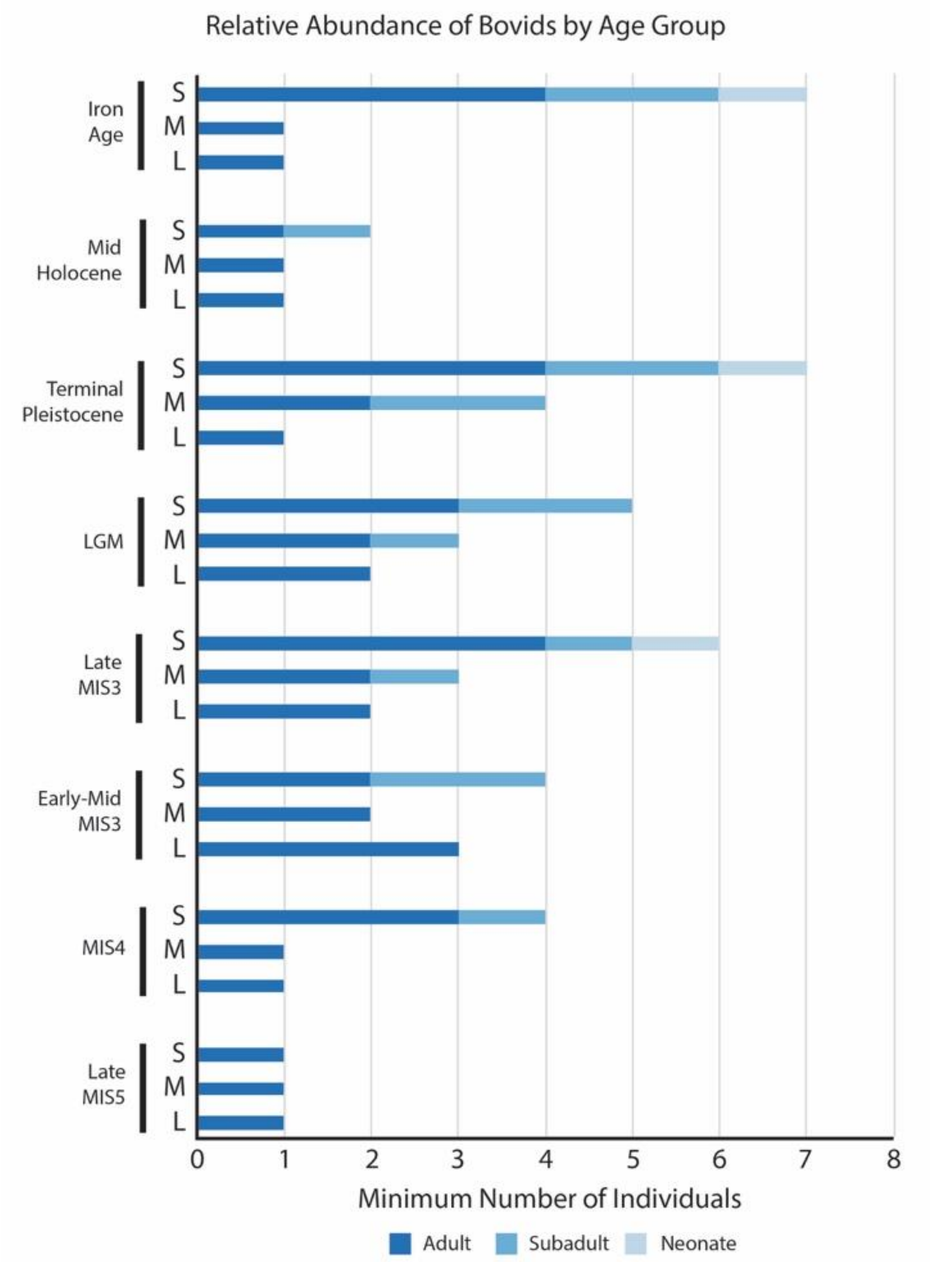

Figure 6. Relative abundance of adult, subadult, and neonatal bovids, expressed as MNI and separated by size class (S, small; M, medium, L, large), for a limited subset of individuals for which an approximate age could be determined.

7. Discussion

The PYS faunal remains provide an unprecedented opportunity to trace continuity and change in dietary choices over the last ~80,000 years of human history in coastal eastern Africa. Taphonomic data show a complex history of assemblage formation involving multiple agents and periods of low or intermittent human activity, especially in the earliest and most recent deposits, but they also establish people as primary accumulators of macromammalian fauna in most archaeological contexts. Previous zooarchaeological and stable isotope data demonstrated that the PYS faunal assemblage reflects mild environmental fluctuations from late MIS 5 to MIS 1 – from more closed to more open conditions and back – in what has been a stable, ecotonal forest-savanna environment for much of the Late Pleistocene (Roberts et al., 2020). Here, we consider how people may have responded to these shifts and opportunities by varying their prey choices and capture strategies.

First, we consider measures of taxonomic abundance as relates to our theoretical frameworks (**Table 2**). If remote capture is used, one can theoretically expect high taxonomic diversity, while encounter hunting may be characterized by specialization in a few taxa – typically large, gregarious ungulates, as is seen in many of the grasslands sites listed in **Table 1** where alcelaphines or zebra are >40% of NISP: Bulbula River B1s1, all of the Lukenya Hill and Victoria Basin sites, and Gol Kopjes and Nasera in the Serengeti (Mochena Borago is excluded here due to its small sample). However, a degree of specialization can also be seen at sites where we might argue, based on animal behavioral traits (see below), that remote capture was likely used – as at PYS, Kuumbi Cave, Guli Waabayo, and the Rifle Range site, where dwarf antelopes dominate the fauna (40-92% of NISP), or Fincha Habera, overwhelmingly dominated by giant mole rat. These patterns of apparent small-game specialization are shaped by unique environments: at Fincha Habera, an Afro-alpine ecosystem; at Rifle Range and Guli Waabayo, unique inselberg microenvironments; and at Kuumbi Cave, an island with substantial forest.

Comparing richness and evenness data across Late Pleistocene faunal assemblages is problematized by gaps and biases mentioned earlier. It is well-documented that richness generally increases with sample size (e.g., Badenhorst et al., 2022). It is also strongly shaped by preservation, availability of relevant reference collections, the confidence of each zooarchaeologist in making specific taxonomic identifications, and the taxonomic levels at which such identifications are published. Evenness, too, is highly sensitive not only to sample size, but to richness itself, leading to problems when comparing evenness across very distinct faunal assemblages; for this reason, an index was chosen that is less sensitive to these biases (Faith and Du, 2018).

With these caveats in mind, a comparison of all sites reviewed here (**Supplementary Table S8**) suggests that PYS is among the five richest sites in our review, with an NTAXA value of 29, well above the median and mean NTAXA values of 15 and 16, respectively, and sharing company with Guli Waabayo, Mumba Rockshelter, Kisese Rockshelter II, and Karungu, all relatively large and well-identified assemblages. The PYS assemblage is also slightly more even than is typical for the sites reviewed here. While this could be used to support an argument for nonrandom capture, as is typical of remote devices, we note that remote capture was likely also used at sites with very low evenness indices – such as Rifle Range Site and Guli Waabayo – where small, shy, and solitary fauna dominate (Jones et al. 2018, Jones and Brandt 2022).

Second, we can consider the traits of prey represented at PYS. Those best suited to remote capture tend to be difficult to acquire through other means, either because they are small, solitary, shy, and/or dangerous (**Table 2**). They also tend to have small home ranges within the vicinity of the site, making the setting of traps or snares worthwhile. Indeed, the prey best-represented throughout most of the PYS sequence – Cephalophini and Neotragini – all fit this profile well (**Table 3**). The dangerous bushpig, also well-suited to remote capture, is also common at PYS. By contrast, fauna best acquired via encounter hunting – including the larger, sometimes gregarious, and seasonally migratory Alcelaphini and Reduncini – are most common in the phases at PYS when more arid, open grasslands would have prevailed. Even during these times, Neotragini and Cephalophini remain common. Since few specimens can be confidently identified to tribe or lower taxonomic category (**Figure 4**), we can use broader carcass size categories to check these interpretations. Consistent with the above observations, small bovids, and small mammals overall, are common throughout the PYS sequence, but are most relatively abundant in MIS 5-4 and from the LGM to recent times (**Figures 3e, 3f)**.

Mortality profiles at PYS must be taken as tentative, given small underlying samples. Nonetheless, initial data show differences between small bovids, where ages-at-death include important numbers of infant and subadult individuals, and medium and larger ungulates, which are almost exclusively adults at death (**Figure 6**). This could suggest that capture of smaller prey was nonselective – as is typical of remote capture – whereas hunting of larger prey was selective. However more robust age-at-death data are needed to confirm this.

These interpretations contrast with those that can be made at most eastern African Late Pleistocene sites (**Table 1**). Many assemblages represent encounter hunting of large, gregarious ungulates in open grasslands environments. At about 40% of the sites in our review, either alcelaphines or zebra comprise greater than 40% of identified ungulate specimens. Four sites, besides PYS, stand out as notable exceptions: Fincha Habera, where 94% of identified MSA faunal remains are giant mole rat; the Rifle Range Site and Guli Waabayo, where approximately 90% of identified ungulate remains are Neotragini; and Kuumbi Cave, where 83% of identified remains are small mammals. While the capture method is left unresolved for Fincha Habera, comparisons based on burning patterns there are made with the capture and roasting of birds at Sibudu (Ossendorf et al., 2019). For the remaining sites, remote capture techniques are suggested (Jones et al., 2018; Jones and Brandt, 2022; Prendergast et al., 2016).

During the Holocene, key changes in mobility and the food quest are noted at PYS. Lithic analysis indicates increasingly intermittent occupations, and it is possible the cave was being used as a special-purpose site (Goldstein et al., 2022). Iron Age faunal remains include small numbers of domestic sheep, goat, and cattle (Culley et al., 2021), and African crops such as sorghum, pearl millet, and finger millet (Crowther et al., 2018, 2016), implying contact with or cave use by people from agricultural settlements, well documented in the Dzitsoni region (Helm et al., 2012). Marine molluscs and fish also formed part of the Holocene diet, indicating exploitation of habitats located 7-15 km away, suggesting both greater mobility and novel capture techniques (Faulkner et al., 2021). Despite these important shifts, however, PYS was continually used as a camp for people who were exploiting small mammals, likely through remote capture.

African records challenge the notion that broad-spectrum foraging must be a response to climate and/or demographic change. Somali records show that this pattern crosscuts Pleistocene-to-Holocene environmental and cultural shifts (Jones and Brandt, 2022), and the PYS record pushes this pattern back into MIS 5, putting the site on par with similar ones in South Africa, which share stable peri-coastal/coastal environments. Such environments, in fact, may have been key to many Late Pleistocene foragers' success. At PYS, the ecotonal setting – with access to both forest and savanna grasslands – enabled a mix of prey acquisition strategies that fluctuated over time according to whether more open or closed environments were most accessible (Roberts et al., 2020; Shipton et al., 2018). However the site's immediate ecology and topography would have consistently enabled remote capture. The cave lies in the Dzitsoni Uplands, c. 100-200 m asl, with forested hilltops and limestone outcrops – dotted with springs and streams – overlooking the lowland savanna, creating steep drops and crevices in the immediate vicinity of the site (Helm et al., 2012). These conditions would have created natural trapping areas along narrow or precipitous game trails, which people could have exploited through their cultural innovations. Such diverse food quest strategies, across altitudinal gradients and from forest to plains, are well-documented among the Okiek, whose Mau Escarpment home bears many resemblances to the surroundings of PYS, and whose territoriality, seasonality, and material culture all offer analogical frameworks worth investigating in future work at PYS (Blackburn, 1974, 1971; Dale et al., 2004). Accounts of coastal hinterland foragers are less informative in this respect, possibly due to demographic shifts that have led to a lack of written information about past forager lifeways (e.g., Spear, 1981; Stiles, 1982; Walsh, 1990), and to an ethnographic focus on large-game hunting (e.g., Ville, 1995).

8. Conclusions and directions for future research

The Late Pleistocene of Eastern Africa is an increasingly critical area of study for key demographic and cultural transitions of *Homo sapiens*, revealed through fossil, genetic, and archaeological data (e.g., Lipson et al., 2022; Miller and Wang, 2022; Mirazón Lahr, 2016). In the past decade, both the publication of new sites – such as PYS and Fincha Habera – and the reinvestigation of long-known ones – such as Lukenya Hill, and Mumba, Nasera, and Kisese II Rockshelters – have led to an appreciation of the diversity of site settings and forager lifeways during a time when behaviors emerged that we recognize as not unlike our own (Tryon, 2019). PYS contributes to this scholarship with a deep, chronologically resolved faunal sequence that not only testifies to the site’s ecological distinctiveness and long-term stability vis-à-vis other sites in the region (Roberts et al., 2020; Robinson, 2022), but also to the diversity of approaches taken toward the food quest, approaches that likely involved archaeologically invisible tools, and the labor of group members who are often ignored in studies of the past.

Here, seeking inspiration from the richer South African zooarchaeological record and drawing upon ethnographic and animal behavioral data, we have used a combination of taphonomic analysis, faunal abundance measures, and mortality profiles to make an inferential argument about prey capture technologies. We suggest that remote capture was likely used to acquire small mammals recovered at PYS throughout the ~80 ka sequence, whereas encounter hunting of larger ungulates was only frequent during more arid phases. This paves the way for future research to support or challenge the remote capture hypothesis, with additional faunal samples acquired since 2017 at PYS. Such expanded research might include additional biomolecular work to refine and expand the number of specimens identified to taxon; using larger and more rigorously aged samples to generate robust mortality profiles; and potentially, analyzing traces on artifacts that may have been used to construct remote capture devices. The approach advanced here might also be geographically expanded to analyze Late Pleistocene assemblages from more closed and near-aquatic environments in, for example, D.R. Congo or Malawi (Peters, 1990; Stewart, 1989; Thompson et al., 2021; van Neer, 1984; van Noten, 1977; Yellen, 1996).

A consideration of remote capture opens up new archaeological questions, testable with further research. One centers on technological innovation. Scholarship on the MSA and LSA often focuses on lithic technology, but this cannot be fully understood without taking into account archaeologically invisible technologies that may be essential to generate the faunal record, such as snares and nets. To some extent, these may be inferable from more perishable – but sometimes preserved – technologies, such as bone tools that may have been used in weaving (e.g., Langley et al., 2016). Another fruitful avenue is to integrate lithic and faunal data to examine mobility and demography (e.g., Tryon and Faith, 2016). Technological analyses from PYS indicate important changes in site use and mobility over time, with bone tools appearing in the LSA part of the sequence (d'Errico et al., 2020; Goldstein et al., 2022; Shipton et al., 2021). Further research might analyze faunal and technological datasets together to examine strategies of mobility, occupation intensity, and food acquisition strategies.

Foodways can be partially reconstructed when not only food acquisition, but also culinary practices have been considered. Future research might explore how food-sharing, butchery, roasting, boiling, and other aspects of cuisine would be shaped by a diet focused largely on small prey. A holistic approach must also remember largely archaeologically invisible parts of the food record, such as plants and honey, and consider how collection of these foods might have been integrated into a larger system. For example, honey-hive maintenance and snaring small game were complementary activities among Okiek living along the Mau Escarpment in Kenya, an analogous forest-to-savanna ecotonal environment to that of PYS (Dale et al., 2004). Ultimately, delineating the food quest has implications for understanding long-term planning and scheduling that are fundamentally modern parts of the human condition.

Finally, we cannot ignore the implications of these findings for social lives. Investment of skill, labor, and time in creating remote capture devices, and planning, setting, and maintaining them, implies not only a high level of cognitive complexity, and an understanding of the habitats and behavior of targeted prey (Wadley, 2010), but also a relationship to place, memory, and by extension, the potential for ownership not only over capture technologies, but territories (Dale et al., 2004), a topic not yet investigated prior to the terminal Pleistocene in eastern Africa. Remote capture is a kind of delayed return system, where payoffs for labor investments are delayed (Woodburn, 1982). At the same time, it is also, once built, a relatively low-intensity system to maintain, and thus can be complementary with other kinds of economic activities, including higher-risk encounter hunting as well as the daily work of collecting plant foods, wood, water, honey, or other resources. Ethnographic data suggest that the making, setting, and checking of snares, traps, and nets is often the labor of people whose activities may be overlooked in the archaeological record: women, children, and elders (Kent, 1993; Lupo and Schmitt, 2002). Social zooarchaeology considers these actors by creating a series of 'bridging arguments' between ancient bones and ancient lives, in order to make reasonable inferences about invisible technologies and people (Wadley, 2010). While such an approach has thus far been elusive in studies of Pleistocene eastern Africa, in large part due to gaps and biases in the archaeofaunal record, we hope that this work, together with a growing number of new and reinvestigated sites, will prompt more holistic approaches in the future.

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Appendix A

Supplementary Note

Faunal assemblage formation at Panga ya Saidi
Figure S1. Examples of preservation conditions at Panga ya Saidi
Figure S2. Presence of burnt, cutmarked, and toothmarked bone at Panga ya Saidi

Supplementary Tables:

Table S1. Summary of the literature: published zooarchaeological data from eastern African Late Pleistocene sites.
Table S2. Number of Identified Specimens (NISP) for macromammalian fauna at Late Pleistocene eastern African sites.
Table S3. Archaeological contexts, layers, and temporal groupings at Panga ya Saidi.
Table S4. Basis of size class determinations for macromammalian remains.
Table S5. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) identified at Panga ya Saidi, Trenches 3-4 (tetrapods only).
Table S6. Bone surface modifications by carcass size in the Panga ya Saidi faunal assemblage, Trenches 3 and 4 (macromammals)
Table S7. Ungulate (bovid and suid) skeletal part representation at Panga ya Saidi.
Table S8. Taxonomic diversity indices for Late Pleistocene macromammalian fauna.

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Table 1. Summary of macromammalian data from Late Pleistocene contexts in Eastern Africa

Dates and faunal data presented for Late Pleistocene contexts only, where possible to separate; see Supplementary Tables S1 and S2 for details. SO, Somalia; ET, Ethiopia, KE, Kenya; TZ, Tanzania; ka, thousands of years ago; NISP, Number of identified Specimens

					Ungulate groups (%Wild ungulate NISP); groups >40% bolded											
Site (Country)	**Dates**	**MM NISP**	**SMM (%NISP)**	**UNG (NISP)**	**Neotragini**	**Cephalophini**	**Antilopini**	**Aepycerotini**	**Tragelaohini**	**Reduncini**	**Alcelaphini**	**Hippotragini**	**Bovini**	**Suidae**	**Equidae**	**Primary faunal reference**
Rifle Range Site (SO)	26-6 ka	207	92%	157	**91%**	1%	2%		3%		1%	1%		2%	1%	Jones et al. 2018
Guli Waabayo (SO)	20-9 ka	2062	76%	767	**87%**		4%		3%		1%	1%		4%	1%	Jones 2020
Laas Geel Shelter 7 (SO)	43-13 ka	80	17%	19	5%		**63%**					5%	21%	5%		Gutherz et al. 2014
Bulbula River B1s1 (ET)	14-13 ka	1850	1%	425			24%				**64%**		11%	1%		Lesur et al 2016
Fincha Habera (ET)	47-31 ka	1537	95%	7					29%	**57%**			14%			Ossendorf et al. 2019
Goda Buticha (ET)	43-31 ka	340	N/A	N/A			+		+	+			+	+	+	Pleurdeau et al. 2014
Kibish Formation MIII (ET)	~104 ka	41	8%	34	6%				15%	18%	3%	6%	26%	26%		Assefa et al. 2008
Mochena Borago (ET)	53-38 ka	9	0%	6							**67%**	17%	17%			Brandt et al 2012
Porc-Epic Cave (ET)	>43-33 ka	243	40%	145	8%		19%	2%	17%	8%	19%		12%	7%	7%	Assefa 2006
Shinfa-Metema 1 (ET)	>60-40 ka	188	24%	9			**70%**	10%						10%		Davis 2019
Enkapune ya Muto (KE)	40-29 ka	83	16%	9					**44%**		22%	11%		11%	11%	Marean 1992a
Karungu (KE)	45-33 ka	560	13%	462			5%		2%	1%	**47%**	3%	8%	5%	28%	Faith et al 2015
Lukenya Hill GvJm19 (KE)	14-6 ka	132	15%	124	2%	3%	6%		2%	1%	34%	5%		2%	**44%**	Marean 1992b
Lukenya Hill GvJm22 (KE)	18-14 ka	676	3%	672	1%		11%			1%	**63%**	1%		3%	18%	Marean 1992b
Lukenya Hill GvJm46 (KE)	21-19 ka	536	2%	536			6%				**81%**				13%	Marean 1992b
Lukenya Hill GvJm62 (KE)	21-12 ka	97	26%	77	6%	5%	4%			5%	**50%**				29%	Marean 1992b
Mfangano (KE)	45-33 ka	57	7%	53	4%		9%			6%	**58%**		11%	4%	8%	Tryon et al. 2012
Rusinga (KE)	45-33 ka	343	0%	334			7%		1%	5%	**73%**	1%	3%	3%	6%	Tryon et al. 2012
Panga ya Saidi (KE)	78-0.4 ka	2960	50%	284	20%	20%	2%		5%	6%	10%		5%	32%		present work
Gol Kopjes (TZ)	N/A	1582	19%	475			18%				**59%**			3%	19%	Gifford-Gonzalez 2011
Kisese II Rockshelter (TZ)	47-4 ka	N/A	N/A	N/A	+	+	+	+	+	+	+	+	+	+	+	Tryon et al. 2019
Kuumbi Cave (TZ)	20-11 ka	3653	83%	296	9%	**43%**	1%		1%	5%			1%	9%	31%	Prendergast et al. 2016
Loiyangalani (TZ)	~65 ka?	>1405	6%	N/A			+		+		+		+	+	+	Masele 2020

Magubike Rockshelter (TZ)	280-32 ka	3396	14%	N/A	+		+	+			+		+	+	+	Masele 2017
Mlambalasi Rockshelter (TZ)	undated	105	N/A	N/A												Collins & Willoughby 2010
Mumba Rockshelter (TZ)	~60-<37 ka	841	6%	770	5%		8%	3%	17%	2%	21%	8%	5%	18%	14%	Mehlman 1989
Nasera Rockshelter (TZ)	>46-16 ka	240	1%	236			5%		3%	1%	14%	4%	1%	2%	**68%**	Tryon & Faith 2016
Olduvai Ndutu beds (TZ)	>62 ka	22	0%	4					33%				33%		33%	Eren et al. 2014

NOTES:

NISP, Number of Identified Specimens; "+" indicates presence where NISP data are unavailable.

MM = Macromammal NISP, which excludes Chiroptera, Soricomorpha, and small Rodentia (Muridae). Fauna only identified as "vertebrate" are also excluded.

SMM = Small macromammals, which includes Bovids Sizes 1-1.5 and Mammal Sizes 0.5-1.5 (e.g., Neotragini, Cephalophini, Hyracoidea, Lagomorpha, smaller primates, and larger rodents).

UNG = ungulates, which includes all wild bovids that could be identified to tribe; all suids; all equids; and excludes unidentified bovids, and ungulates that are not bovid, suid, or equid.

Table 2. Present-day traits of ungulates documented or potentially documented at Panga ya Saidi
Sources: Estes (1991), Kingdon (1997)

Family/ Tribe	Scientific name	Common name	Present-day range	Present-day habitat	Activity period	Behavioral traits
Bovidae/						
Alcelaphini	*Alcelaphus buselaphus*	hartebeest	Patchy distribution throughout eastern African savannas	Prefer grasslands near boundaries with woodlands or scrub,	Primarily diurnal	Gregarious females, territorial and solitary males. Large mobile aggregations reported.
	Damaliscus lunatus	topi	Patchy distribution in coastal eastern Africa, Great Lakes	Seasonally flooded grasslands, often near woodlands boundaries.	Primarily diurnal	Highly variable organization depending on habitat. In floodplains, large mobile herds, long distance migrations. Others dispersed in smaller home ranges.
	Connochaetes taurinus	wildebeest	Inland patches of savanna grasslands	Short grasslands near permanent water	Primarily diurnal	Territorial. Highly gregarious mobile herds, migrating to short grasses & water; smaller, more dispersed resident herds.
Bovini	*Syncerus caffer*	Cape buffalo	Patchy distribution throughout eastern African savannas	Savannas and mosaics with grasses and patches of thicket or forest, and access to water.	Diurnal, continuous activity	Highly gregarious, living in large mixed herds. Nonterritorial. Dry season mobility to access water.
Cephalophini	*Philantomba monticola*	blue duiker	coastal eastern Africa and inland southern Tanzania	Forests (lowland, montane, riverine, littoral); moist thickets	Strictly diurnal, crepuscular	Bonded pairs, small permanent home ranges, <0.5 km2.
	Cephalophus adersi	Ader's duiker	Zanzibar and coastal Kenya only	Coastal forest & thicket	Diurnal	Solitary, bonded pairs, territorial, small home ranges. Shy, alert, quick to flee.
	Sylvicapra grimmia	bush duiker	Most of eastern Africa, except arid parts of N Kenya and Horn	Areas with cover in savannas, woodlands; highly versatile, able to live in diverse habitats	Diurnal and nocturnal	Highly territorial with little overlap between male-patrolled ranges
Neotragini	*Neotragus moschatus*	suni	Coastal eastern Africa and inland forested patches	Coastal forests, thickets, forest-savanna mosaics	Diurnal and nocturnal	Bonded pairs, territorial, small home ranges.
	Madoqua kirkii	Kirk's dik-dik	Most of eastern Africa	Bush, thicket	Diurnal and nocturnal	Solitary, bonded pairs, territorial, small home range

	*Ourebia ourebi**	oribi	Savannas of coastal and inland (Rift Valley) eastern Africa, largely absent in Horn	Short grasslands	Diurnal	Solitary, bonded pairs, territorial in small home range. Occasionally aggregating in larger groups. Shy, alert, quick to flee.
	Oreotragus oreotragus	klipspringer	Patchy distribution across eastern Africa, mainly along Rift Valley	Variable habitats with steep, rocky ground, short vegetation	Diurnal and nocturnal	Solitary. Bonded pairs and small groups: female with male and offspring. Territorial in small home range
Reduncini	*Kobus ellipsiprymnus*	waterbuck	Patchy distribution throughout eastern African savannas, always near water	Well-watered grasslands, near woodlands boundary	Diurnal	Territorial. Dispersed during wet season; congregates near water in dry season
	Redunca redunca	Bohor reedbuck	Most of eastern Africa, except arid parts of N Kenya and Horn	Floodplains grasslands with some cover	Nocturnal grazing	Monogamous or polygynous pairs. Solitary and dispersed during wet season, aggregating during dry season.
Tragelaphini	*Tragelaphus scriptus*	bushbuck	Most of eastern Africa, except arid parts of N Kenya and Horn	Bush, forest edges; wide range of habitats but always requiring cover.	Noctural grazing and browsing	Solitary, nonterritorial, sedentary. Each adult has a small home range, some overlap among these.
	Taurotragus oryx	eland	Patchy distribution across eastern Africa, excluding N Kenya and Horn	Highly adaptable, diverse habitats, prefers woodlands and savannas	Diurnal and nocturnal	Gregarious and nonterritorial with fluid group sizes: small groups in dry season, aggregating during rains. Younger animals highly mobile, older ones residential.
Suidae						
	Phacochoerus africanus	common warthog	Most eastern African grasslands	open grasslands and woodlands	Diurnal	family units living in 'clan areas' of about 4 km2
	Potamochoerus porcus	bushpig	Most of eastern Africa, except arid parts of N Kenya and Horn	Woodland/forest, prefer dense vegetation	Primarily nocturnal	Small groups (female with young plus single male). Highly territorial. Larger home ranges than warthogs, c. 10 km2

*The oribi is often classified as Neotragini, but some now classify together with gazelles as Antilopini; Kingdon establishes a separate tribe.

Table 3. Zooarchaeological expectations for distinct capture methods
Based primarily upon Wadley's (2010) review of ethnographic and archaeological literature

Category of information	Expectations for remote capture	Expectations for encounter hunting
Measures of taxonomic abundance	High taxonomic diversity High richness/evenness indices	Potential for specialization in a few taxa Low richness/evenness indices
Characteristics of abundant taxa	Prey best suited to remote capture: Predominantly small taxa (<10-15 kg) Not exclusively ungulates Solitary & shy (individuals & pairs) Non-migratory, restricted home ranges Home range within site vicinity Potentially dangerous (e.g., bushpig)	Prey best suited to hunting: Size diversity, including medium to large Mostly ungulates Gregarious (herd structure) Migratory, large home ranges Home range potentially at a distance Potentially docile
Inferred habitats of abundant taxa	Closed (forest, woodland) habitats	Potentially diverse habitats, including open ones
Mortality profiles	Higher diversity of ages-at-death Catastrophic profile Many infant and juvenile animals	Lower diversity of ages-at-death Prime-adult profile Few younger and older animals
Skeletal part representation*	Evidence of complete skeletons	Evidence of selective transport

*Where density-mediated attrition can be ruled out or addressed through analytical methods

Table 4. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI)[1] identified in Trenches 3-4 at Panga ya Saidi

	Iron Age (L1-L3) [2,3]		Middle Holocene (L4)		Terminal Pleistocene (L5-L6)		LGM (L8)		Late MIS3 (L9)		Early-Mid MIS3 (L10-L12)		MIS4 (L13-L16)		MIS5 (L17-L19)		TOTAL	
Taxonomic Attribution	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
CLASS AVES																		
Charadriiformes, Aff. Turnicidae (button quail)	2	1															2	1
Galliformes, Phasianidae indet.	5	3					2	1			1	1					8	5
Passeriformes, Aff. Ploceus sp. (weaver)	7	2															7	2
Strigiformes, Aff. Tyto sp. (owl)	18	2			1	1											19	3
Bird indet.	11	-			2	-	1	-					3	1	1	1	18	2
CLASS MAMMALIA																		
Artiodactyla/Bovidae																		
Alcelaphini																		
Alcelaphus (hartebeest) or *Damaliscus* (topi)											7	1					7	1
Cf. *Alcelaphus/Damaliscus*							1	1	2	1	6	-					9	2
Connochaetes taurinus (wildebeest)											1	1					1	1
Antilopini																		
Cf. *Ourebia ourebi* (oribi)					1	1					3	1					4	2
Bovini																		
Bos taurus (domestic cattle)	2	1															2	1
Syncerus caffer (buffalo)							1	1									1	1
Cf. *Syncerus caffer* (buffalo)			2	1	1	1			2	1	1	1	1	1			7	5
Caprini																		
Ovis aries (domestic sheep)	1	1															1	1
Capra hircus (domestic goat)	1	1															1	1
Cf. Caprini (domestic goat or sheep)	1	-															1	
Cephalophini																		
Cephalophini, small (duiker)											1	1					1	1
Sylvicapra grimmia (bush duiker)	9	1			2	1			1	1							12	3
Cf. *Sylvicapra grimmia* (bush duiker)	13		1	1	2								3	1	2	1	21	3
Neotragini[4]																		
Neotragini (dik-dik, suni, klipspringer) or oribi[4]	12	-							1	1							13	1

Cf. *Madoqua* sp. (dik-dik)							1	1					1	1			2	2
Cf. *Neotragus moschatus* (suni)			1	1	2	1											3	2
Oreotragus oreotragus (klipspringer)	15	1			1	1											16	2
<u>Reduncini</u>																		
Cf. *Redunca redunca* (reedbuck)													1	1			1	1
Kobus ellipsiprymnus (waterbuck)					2	1	1	1	1	1	2	1	1	1			7	5
Cf. *Kobus ellipsiprymnus* (waterbuck)					2	-					1	-					3	-
<u>Tragelaphini</u>																		
Tragelaphus scriptus (bushbuck)	5	1															5	1
Cf. *Tragelaphus scriptus* (bushbuck)															1	1	1	1
Large Tragelaphini (eland or greater kudu)											3	1					3	1
<u>Indeterminate</u>																		
Bovid Size 1 (dik-dik to duiker-sized)	79	6	10		47	3	51	3	24	3	21	1	12	1	5	1	249	18
Bovid Size 1-2 (klipspringer/bush duiker/oribi-sized)	24	2	1	-	7	-	25	1	14	-	5	1	6	-	2	-	84	4
Bovid Size 2 (caprine to bushbuck size)	28		6	1	11	2	28	2	16	1	13	1	4		1	1	107	8
Bovid Size 2-3 (bushbuck to waterbuck size)			1	-	9	1	5	-	14	1	6	-	6	-			41	2
Bovid Size 3 (waterbuck size)	5	-	3	-	37	-	34	-	40	-	59	-	19	-	4	1	201	1
Bovid Size 3-4 (waterbuck to buffalo size)	2	-			4	-	2	-	8	-	5	-			1	-	22	-
Bovid Size 4 (buffalo or eland)							1	-	2	-	2	-	1	-			6	-
Bovid size indet.	1	-			3	-			1	-	21	-	2	-			28	-
<u>Artiodactyla/Suidae</u>																		
Phacochoerus sp. (warthog)	1	1	3	1	11	1	3	1	15	2	9	2					42	8
Potamochoerus larvatus (bushpig)	2	1			8	1			2	1			1	1			13	4
Suid indet.	8	-	5	-	28	-	22	1	23	-	11	-	11	-	4	1	112	2
<u>Carnivora/Felidae</u>																		
Felis cf. *serval* (serval)	1	1			1	1											2	2
Cf. *Panthera pardus* (leopard)													1	1			1	1
<u>Carnivora/Herpestidae</u>																		
Cf. *Herpestes sangineus* (slender mongoose)	1	1															1	1
Cf. *Ichneumia albicauda* (white-tailed mongoose)	6	2															6	2
<u>Carnivora/Hyaenidae</u>																		
Hyaenidae (hyena)											1	1	1	1			2	2
<u>Carnivora/Indeterminate</u>																		
Small carnivore	9	-	1	1	1	-	1	1					1	1			13	3

Medium-sized felid or viverrid	1	1															1	1
Chiroptera																		
Microchiroptera indet.	2	1													2	1	4	2
Pteropodidae (fruit bats and flying foxes)	15	4	3	1	10	4	9	4	4	2	1	1	22	6	56	21	120	43
Cf. Pteropodidae (fruit bats and flying foxes)							5	-	1	-	1	-	5	-	123	-	135	-
Chiroptera indet.	1	-			1	-			9	-			11	-	6	-	28	-
Hyracoidea																		
Hyracoidea Cf. *Dendrohyrax validus* (tree hyrax)	9	2	2	1	11	2	23	3	13	2	22	3	3	1	2	1	85	15
Macroscelidea																		
Elephant shrew indet.	15	2											2	1	3	1	20	4
Pholidota																		
Smutsia temminckii (ground pangolin)															3	1	3	1
Primata																	0	
Cercopithecini (cercopithecine monkeys)	12	1	2	1											9	1	23	3
Colobus sp. (colobus monkey)							2	1	3	1					1	1	6	3
Colobus sp. or large Cercopithecini	2	1	1	1	2	1					1	1	1	1	9	-	16	5
Otolemur sp. (greater galago)	2	1															2	1
Papio sp. (baboon)					1	1					4	2					5	3
Medium primate indet.					1	-					1	-			2	1	4	1
Small primate indet.											1	1					1	1
Rodentia																		
Cricetomys gambianus (giant pouched rat)	2	1			1	1			1	1			2	1			6	4
Hystrix cristata (porcupine)	1	1															1	1
Medium-to-large rodent	2	-											1	-			3	-
Muridae (gerbils, rats and mice)	1524	132	1	1			1	1			1	1	8	1	12	2	1547	138
Sciuridae (squirrels)	2	1															2	1
Soricomorpha																		
Crocidura sp. (musk shrew)	20	7															20	7
Indeterminate																		
Small primate or carnivore					1	-	1	-	2	-	1	-			2	-	7	-
Micromammal indet.	185	-					3	-			1	-	3	-			192	-
Mammal Size 0.5	8	-			3	-	6	-	8	-	6	-	1	-	20	-	52	-
Mammal Size 0.5-1	4	-			1	-	3	-	8	-	2	-	16	-	82	-	116	-
Mammal Size 1	41	-	4	-	8	-	106	-	68	-	7	-	45	-	57	-	336	-

Mammal Size 1-2	25	-	10	-	9	-	177	-	138	-	3	-	56	-	35	-	453	-
Mammal Size 2	38	-	10	-	6	-	70	-	130	-	16	-	32	-	28	-	330	-
Mammal Size 2-3	9	-	6	-	19	-	77	-	66	-	22	-	35	-	31	-	265	-
Mammal Size 3			3	-	7	-	57	-	70	-	6	-	10	-	5	-	158	-
Mammal Size 3-4	1	-			1	-	4	-	6	-			2	-	1	-	15	-
Mammal size indet.	1	-							3	-	8	-	1	-	4	-	17	-
CLASS REPTILIA																		
<u>Crocodilia</u>																		
Crocodylus niloticus (Nile crocodile)															2	1	2	1
Medium reptile Aff. *Crocodylus niloticus* (Nile crocodile)															2	-	2	-
<u>Squamata/Serpentes</u>																		
Cf. *Python sebae* (African rock python)	6	1															6	1
Bitis arietans (puff adder)	6	1															6	1
Snake indet.	11	1	2	1	2	1	3	1	1	1	5	1	2	1	3	1	29	8
<u>Squamata/Varanidae</u>																		
Varanus niloticus (Nile monitor)	3	1			1	1											4	2
<u>Testudines</u>																		
Testudinidae (tortoise) or Cf. Testudinidae	6	2			1	1	11	1	13	1	7	1	5	1	6	1	49	8
<u>Indeterminate</u>																		
Small reptile indet.	2	1											1	-	1	1	4	2
CLASS INDETERMINATE																		
Small bird or bat							12	-	2	-							14	-
Microvertebrate indeterminate													1	-	1	-	2	-
Small vertebrate indet.	5	-			1	-	1	-	1	-	1	-	2	-	19	-	30	-
Medium vertebrate indet.															2	-	2	-
Large vertebrate indet.															10	-	10	-
TOTAL	**2230**	**190**	**78**	**12**	**270**	**28**	**750**	**25**	**713**	**21**	**296**	**25**	**342**	**24**	**560**	**41**	**5239**	**366**

[1] MNI estimates are calculated per chronological phase, combining archaeological layers (L) where relevant, and may be low underestimates/

[2] In L1-L3, microfauna were analysed in Trench 3 but not Trench 4; therefore, NISP and MNI counts, particularly for Aves, Chiroptera, Rodentia and Soricomorpha, are artificially low.

[3] For L1-L3, there are minor differences in NISP/MNI values from those published by Roberts et al. (2020), due to more precise biomolecular identifications available following Culley et al. (under review). These differences include one bovid reidentified as suid; indeterminate bovid remains with more specific identifications; and a slight increase in MNI.

MNI also increased for indeterminate bovids in Terminal Pleistocene, Late MIS3, and Early-Mid MIS3 phases relative to Roberts et al. (2020), following age determinations.

[4] Oribi was long classified as Neotragini but has been recently reclassified as Antiliopini (a higher-order group that also includes Neotragini and Cephalophini). Some remains identified as neotragines at PYS may belong to oribi, given morphological similarities.

Table 5. Bone surface modifications in the Panga ya Saidi macromammalian assemblage, Trenches 3 and 4.
All values expressed as Number of Identified Specimens (NISP). All frequencies (in parentheses) are expressed as a percentage of total NISP.

A. Denominators used in Table 5B.

	Iron Age (L1-L3)	Middle Holocene (L4)	Terminal Pleistocene (L5-L6)	Last Glacial Maximum (L8)	Late MIS3 (L9)	Early-Mid MIS3 (L10-L12)	MIS4 (L13-L16)	MIS5 (L17-L19)	TOTAL
Macromammal bone* NISP	334	63	185	682	633	143	228	292	2560
Macromammal limb** NISP	143	28	78	416	444	55	136	219	1519

B.

	Iron Age (L1-L3)		Middle Holocene (L4)		Terminal Pleistocene (L5-L6)		Last Glacial Maximum (L8)		Late MIS3 (L9)		Early-Mid MIS3 (L10-L12)		MIS4 (L13-L16)		MIS5 (L17-L19)		TOTAL	
Bone surface modifications	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Abrasion (%Macromammal NISP)							17	2.5%	12	1.9%	3	2.1%	5	2.2%	20	6.8%	57	2.2%
Abrasion (%Macromammal limb shaft NISP)							15	3.6%	11	2.5%			5	3.7%	18	8.2%	49	3.2%
Tooth pits or scores, including ?s (%Macromammal NISP)			1	1.6%			9	1.3%	15	2.4%			2	0.9%	6	2.1%	33	1.3%
Tooth pits or scores, definitive							5	0.7%	10	1.6%			2	0.9%	3	1.0%	20	0.8%

(%Macromammal NISP)																		
Rodent gnaw marks (%Macromammal NISP)			1	1.6%			2	0.3%	7	1.1%					10	3.4%	20	0.8%
Biochemical marks*** (%Macromammal NISP)	1	0.3%					85	12.5%	33	5.2%			5	2.2%	43	14.7%	167	6.5%
Insect marks*** (%Macromammal NISP)							9	1.3%	66	10.4%					3	1.0%	78	3.0%
Burnt bone (%Macromammal NISP)	16	4.8%	4	6.3%	27	14.6%	61	8.9%	46	7.3%	10	7.0%	47	20.6%	7	2.4%	218	8.5%
Cut marks, including ? (%Macromammal NISP)	4	1.2%	2	3.2%	3	1.6%	33	4.8%	16	2.5%	3	2.1%	3	1.3%	17	5.8%	81	3.2%
Cut marks, including ? (%Macromammal limb shaft NISP)	2	1.4%			2	2.6%	27	6.5%	16	3.6%	1	1.8%	2	1.5%	14	6.4%	64	4.2%
Cut marks, definitive (%Macromammal NISP)	3	0.9%	2	3.2%	2	1.1%	21	3.1%	9	1.4%	1	0.7%	2	0.9%	13	4.5%	53	2.1%
Cut marks, definitive (%Macromammal limb shaft NISP)	1	0.7%			1	1.3%	16	3.8%	9	2.0%	1	1.8%	1	0.7%	10	4.6%	39	2.6%

*Macromammal bone includes all remains except tooth and horncore from all mammals except rodents, bats, shrews, galago, and indeterminate micromammals

**Limb NISP includes all fragments of the six major limb bones (humerus, femur, radius, ulna, metacarpal, metatarsal)

***Database fields for insect and biochemical marks were introduced late in the analysis. These figures should be taken as low minimum numbers, especially for insect marks.