

## 20,000 years of small game hunting in southern Somalia

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### ABSTRACT

Archaeologists relate increasing forager reliance on small animals and broad-spectrum resource use to environmental and demographic changes in temperate regions during Marine Isotope Stage (MIS) 2, 29–14.7 thousand years ago (ka), and MIS 1, after 14.7 ka. However, little research has examined the factors that influenced small game hunting in the arid and semi-arid tropics of eastern Africa during this period. To address this research gap, we report on a large MIS 2/1 (N = 81,986) faunal assemblage from Guli Waabayo rock shelter in southern Somalia. Dates from the site show repeated Later Stone Age (LSA) forager occupation throughout the mostly arid MIS 2 and wetter African Humid Period (AHP; 14.7–5 ka). Evidence of a major lithic transition between MIS 2 and the AHP suggests changing LSA mobility patterns and economic systems corresponded with regional precipitation fluctuations. However, unusually high frequencies of small taxa (e.g., dik-dik, rock hyrax, monitor lizard) and fewer large and medium species (e.g., kudu and warthog) throughout the Guli Waabayo sequence crosscut both climatic and technological changes. These findings contrast with studies in other world regions that emphasize small game hunting in response to environmental reorganization, changing forager land use strategies, and large game overhunting.

### 1. Introduction

In temperate Eurasia and North America, archaeologists observe broad-spectrum subsistence strategies and a greater reliance on small animals among foragers beginning in Marine Isotope Stage (MIS) 2, 29–14.7 ka (thousand years ago), and increasing through MIS 1, after 14.7 ka (Badenhorst and Driver, 2009; Schmitt et al., 2002; Stiner et al., 2000; Stutz et al., 2009; Zhang et al., 2013). Most studies link small or lower-ranked game hunting to human population growth, reduced mobility, increased predation pressure on large mammals, and changing climatic conditions (but see Steiner et al., 2022). Although similar patterns are also observed in southern Africa (Chase et al., 2018; Jerardino, 2010, 2012; Steele and Klein, 2009), targeted studies of small animal hunting and its relationship to environmental conditions and Later Stone Age (LSA) social and economic systems in eastern Africa (Burundi, Djibouti, Eritrea, Ethiopia, Kenya, Rwanda, Somalia, Tanzania, and Uganda) remain few.

Climatic fluctuations and changing hunter-gatherer land use patterns in eastern Africa during this period provide an interesting backdrop for studying long-term patterns of small game hunting. In particular, the onset of the African Humid Period (AHP) ~14.7 ka following MIS 2

aridity (Gasse, 2001; Rachmayani et al., 2015; Thompson et al., 2002; Tierney and deMenocal, 2013) and an increased focus on resource-rich environmental niches by some early and middle Holocene foragers (Ambrose, 1986; Brandt, 1988) may have affected the availability of large game in certain parts of eastern Africa over time. However, the ways these changes related to small game hunting patterns are unclear.

Recent forager responses to environmental and settlement changes in Africa suggest an emphasis on small, locally available game might be predicted during periods when rainfall was low (e.g., MIS 2) and/or people began to live in larger, less mobile groups. Hawkes et al. (1991) argue that Hadza foragers in Tanzania improve hunting efficiency by incorporating a greater percentage of smaller taxa into their diets during periods of aridity or increased hunting pressure. Similar patterns are observed among San groups in southern Africa (Kent, 1993; Lee and Yellen, 1976; Yellen, 1991a).

Although zooarchaeological data from MIS 2/1 sites are rare in eastern Africa, faunal studies reveal some geographic variability—but little evidence of temporal change—in the extent to which LSA groups relied on small animals. At sites dated to ~14–13 cal ka in the semi-arid Zwai-Shala Lake Basin of south-central Ethiopia, small animals accounted for only 15.5% of all fauna by number of identifiable

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specimens (NISP) (Lesur et al., 2016). Rock shelter and cave site assemblages from the grasslands of Kenya and Tanzania also suggest a preference for hunting larger game, with small taxa comprising <27.2% (NISP) of all animal bones dated ~ 33.5–7.6 ka (Marean, 1992a, 1992b; Tryon and Faith, 2016). However, less emphasis on large animals is observed on the coasts and islands of eastern Africa. At Panga ya Saidi in the coastal forests of Kenya, small game accounts for 54.5% (NISP) of all fauna from levels dated ~ 25.3–7.6 ka (Roberts et al., 2020). An even greater emphasis on small game (90.4–84.0% NISP) is observed between ~20 and 11.3 ka at Kuumbi Cave on Zanzibar Island (Prendergast et al., 2016: S1 Table).

Relatively consistent hunting patterns throughout MIS 2 and the AHP elsewhere in eastern Africa contrast with faunal evidence from the open-air Rifle Range Site near Buur Hakaba inselberg in semi-arid southern Somalia. Jones et al. (2018) argue that LSA hunters at the site relied on small prey taxa more heavily during the AHP (69.5% NISP) than earlier, drier periods (27.5% NISP). These findings suggest increased small game hunting occurred with climatic amelioration, rather than aridity. Holocene human burials associated with ceremonial lesser kudu horn cores recovered from nearby Gogoshiis Qabe rock shelter at the Buur Heybe inselberg cluster (~25 km NE of Buur Hakaba) suggest changing hunting patterns at the Rifle Range Site might also correspond with increasing sedentism and ideas of territoriality among LSA hunter-gatherer groups at southern Somali inselberg environments with AHP-related climatic amelioration (Brandt, 1988). However, the small sample size of MIS 2 fauna from the Rifle Range Site limits diachronic interpretations of hunting patterns as they relate to climatic, social, and economic transformations over time.

To address this issue, we analyzed one of the largest (NISP = 81,988) and most well-dated faunal assemblages in eastern Africa. Using taxonomic and diversity data from Guli Waabayo rock shelter at Buur Heybe in southern Somalia (Fig. 1), we compared small game hunting patterns during the generally arid MIS 2 and wetter AHP. Findings from this study offer insights into when and why people hunted small animals in semi-arid eastern Africa and provide new perspectives on global discussions of small game hunting in relation to environmental and human changes in the past.

## 2. Inter-riverine southern Somalia

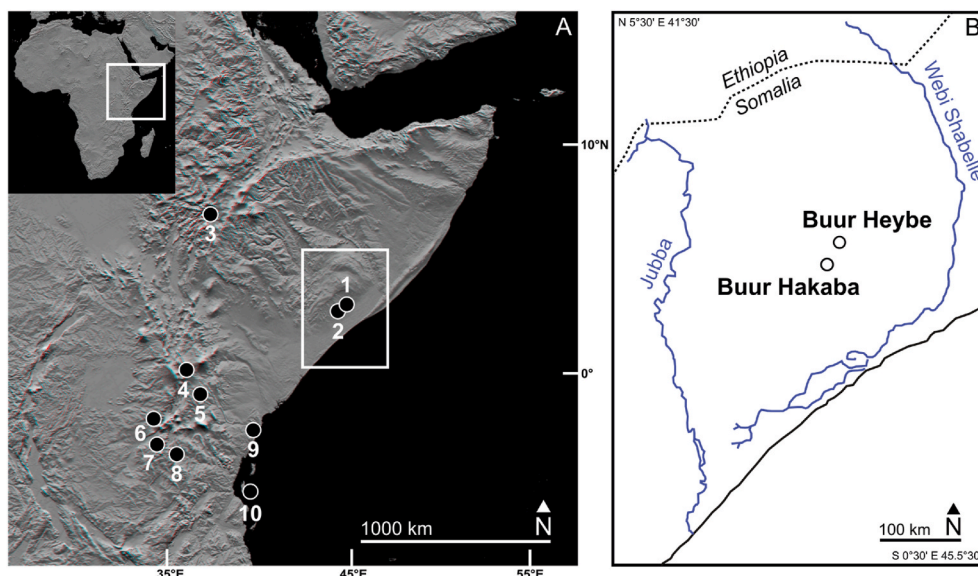
Situated between the Jubba and Webi Shebelle rivers (Fig. 1), the inter-riverine region of southern Somalia is a semi-arid bushland (White, 1983) that today receives 400–600 mm of rainfall per year, distributed

bimodally (Muchiri, 2007; Hutchinson, 1992). Precambrian granitic inselbergs (*buur*, in Somali) provide topographic and ecological diversity to the otherwise flat region. In Africa and elsewhere, the unique geology and topography of inselbergs are often associated with increased ecological productivity. In particular, the irregular, rocky surfaces of many inselbergs aid in soil accumulation and retention while also providing depressions where rainwater can collect (Burke, 2003; Jürgens and Burke, 2000; Müller, 2007; Porembski and Barthlott, 2000).

At the Buur Heybe inselberg cluster (Fig. 2), the tallest and most expansive inselberg in southern Somalia (~610 m a.s.l. and ~4.7 km<sup>2</sup>), perennial springs and fertile soils support plant species otherwise uncommon to southern Somalia and other semi-arid eastern African environments (Friis and Vollesen, 1989). Abundant vegetation and year-round water availability at many inselbergs support diverse animal communities, including small mammals like dik-diks, hyraxes, and mongooses (Kingdon, 1977, 1982, 2004). Reptiles such as tortoises, fresh-water turtles, plated lizards, monitor lizards, and snakes also occupy densely vegetated areas with fresh water like Buur Heybe (Madgwick et al., 1986). Archaeological data suggest southern Somalia's unique inselberg habitats influenced the choices people made in the past (Brandt, 1986, 1988; Jones et al., 2018, 2021). However, it is possible that major climatic changes during MIS 2 and 1 impacted the plants and animals available to foragers in the inter-riverine region over time.

### 2.1. Southern Somalia paleoclimate

Gulf of Aden and western Indian Ocean cores, Ethiopian lake cores, and other proxies indicate that the Horn of Africa was cooler and significantly drier during MIS 2 than MIS 3 (57–29 ka) and MIS 1 (DiNezio et al., 2018; Foerster et al., 2012, 2014, 2015; Hensel et al., 2020; Roberts et al., 2021; Schaebitz et al., 2021; Tierney and deMenocal, 2013; Tierney et al., 2017). Precipitation in the Horn decreased significantly 29 ka, followed by fluctuating rainfall patterns until 23 ka. The Last Glacial Maximum 23–20 ka marked a period of hyper-aridity that preceded a series of gradual precipitation increases between 20 and 18 ka. After a 3000-year arid period, climatic amelioration occurred during the first part of the AHP 14.7–12.9 ka (Foerster et al., 2015; Leplongeon et al., 2020; Ménot et al., 2020). Precipitation dropped abruptly during the Younger Dryas 12.9–11.7 ka and rose again precipitously 11.7–6 ka, marking the second half of the AHP (Costa et al., 2014; Foerster et al., 2015; Gasse, 2001; Holmes and Hoelzmann, 2017). This generally wet period was interrupted briefly by a short peak in



**Fig. 1.** A - Satellite image of eastern Africa showing Somalia's Inter-riverine Region (white box). Numbered circles represent sites with MIS 2/1 faunal assemblages mentioned in the text: 1) Guli Waabayo and Gogoshiis Qabe; 2) Rifle Range Site; 3) Zwai-Shala sites; 4) Ekapune ya Muto; 5) Lukenya Hill sites; 6) Nasera; 7) Mumba; 8) Kisese II; 9) Panga ya Saidi; 10) Kuumbi Cave. Modified from Jones et al. (2021) and Reid et al. (2019). B - Map of inter-riverine southern Somalia with locations of Buur Heybe and Buur Hakaba. Modified from Jones et al. (2021) and Reid et al. (2019).





Fig. 2. The Buur Heybe inselberg cluster (photo by S. Brandt).

aridity around 8.2 ka. In southern Somalia, Reid et al. (2019) used oxygen and carbon isotopic evidence preserved in archaeological ungulate teeth from Guli Waabayo and Gogoshiis Qabe rock shelters to argue that total annual precipitation during the AHP was comparable to today, but more evenly distributed throughout the year. For this study, we used evidence of regional and localized MIS 2/1 rainfall fluctuations as well as archaeological evidence from sites in inter-riverine southern Somalia to interpret faunal patterns from Guli Waabayo rock shelter. Our goal was to investigate the ways changing climatic and social dynamics impacted LSA hunting strategies and landscape use over the site's 20,000-year occupation. In doing so, we tested whether increased small game hunting and a greater reliance on inselberg environments coincided with climatic amelioration during the AHP (as suggested by Jones et al., 2018 after Brandt, 1988).

### 3. Excavations at Guli Waabayo rock shelter

Guli Waabayo rock shelter (Fig. 3 and Fig. 4) was one of many sites, including the Rifle Range Site at Buur Hakaba, excavated by J.D. Clark (1954: 230–250) during his World War II archaeological exploration of southern Somalia. Clark's (1954: 230–236) excavations at Guli Waabayo



Fig. 4. Guli Waabayo rock shelter (photo by S. Brandt).



Fig. 3. The Buur Heybe landscape with the location of Gogoshiis Qabe rock shelter. Guli Waabayo is out of frame to the east (photo by S. Brandt).

revealed a similar archaeological sequence to that reported earlier by Graziosi (1940) at nearby Gogoshiis Qabe.

In 1983, S. Brandt formed the Buur Ecological and Archaeological Project (BEAP) to test an ecological model of human mobility strategies (after Dyson-Hudson and Smith, 1978) through excavations at new and previously known sites in inter-riverine southern Somalia (Brandt, 1986, 1988; Brandt and Gresham, 1989, 1990). Two years later, BEAP conducted test excavations in an unexplored part of Guli Waabayo. This work was followed up in 1989 with more intensive “emergency” excavations at the shelter in anticipation of the Somali Civil War that enveloped the country soon after. Following excavations, most of the materials from Guli Waabayo were exported to the U.S. with permission from the Somali Academy of the Arts and Sciences. Zooarchaeological data discussed in this paper derived from the site's faunal collections (Jones et al., 2018, 2021; Reid et al., 2019), currently curated at the University of Florida.

The BEAP team excavated 11 largely contiguous 1 × 1 m squares near the middle of the rock shelter (Fig. 5) (Jones et al., 2021; Reid et al., 2019). Excavation methods were consistent throughout the sequence. Unless a major sedimentary change was recognized, squares were excavated in arbitrary 5 cm levels. Nine of the shelter's 11 squares were

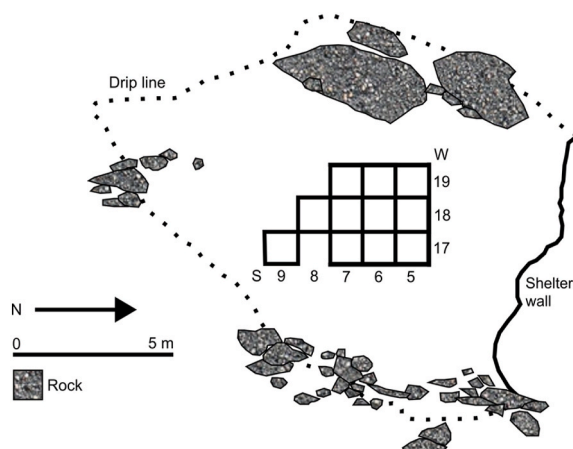


Fig. 5. Guli Waabayo site map showing the excavation grid plan for the 1989 excavations (after Jones et al., 2021).

dug to ~1.5 m below surface and two were excavated to ~2.5 m below surface. All excavated matrices were screened by level using 5 mm mesh.

### 3.1. The Guli Waabayo sequence

Although bedrock was never reached at Guli Waabayo, BEAP excavations revealed ~2.5 m of deposits containing up to eight different stratigraphic layers. Due to evidence of sloping stratigraphy and difficulties discerning subtle soil changes across the site's eleven excavation squares, Jones et al. (2021) consolidated the sequence into four main strata (Fig. 6).

The deepest, stratum 4, was composed of ~30 cm of undated, gravelly deposits bereft of archaeological material. This was capped by ~20 cm of undated, compact yellow-brown sands (stratum 3) containing very few faunal remains, but numerous examples of a “transitional”

Middle Stone Age (MSA)/Later Stone Age (LSA) industry characterized by Levallois and blade cores, bifacial and unifacial points, backed pieces, scrapers, and other retouched tools made of local quartz and thermally altered exotic cherts.

These deposits were overlain by ~1.2 m of grey-brown coarse sands (stratum 2) that preserved large amounts of animal bone and a distinctive LSA industry characterized by pressure-flaked unifacial, bifacial, and trifacial chert and quartz points, as well as backed pieces, scrapers, and rare burins. Clark (1954: 244–249) originally named this industry the “Doian”. However, Brandt (1986) later renamed it the “Eibian”, as it was identical to Graziosi's (1940) previously described Eibian industry at nearby Gogoshiis Qabe rock shelter. The Eibian deposits at Guli Waabayo were overlain by ~70 cm of yellow-brown sands (stratum 1) containing abundant fauna and a more informal, “expedient” LSA industry distinguished by small quartz bipolar cores and debitage, but few distinctive tools. Unnamed by Graziosi (1940) at Gogoshiis Qabe and Clark at Guli Waabayo (1954: 230–236), Brandt (1986) named this industry the “Bardaale”.

As geogenic and anthropogenic disturbances made it impossible to attribute the Guli Waabayo fauna to the four previously recognized sedimentary strata, Jones et al. (2021) decided to further consolidate the sequence into two lithostratigraphic units (LSUs). Bayesian modeling of dates from the site indicated that the LSUs were chronologically distinct (Jones et al., 2021). LSU 2 deposits (strata 2 and 3) dated to the mostly arid MIS 2, 29–14.7 ka, and were primarily associated with the distinctive Eibian industry. LSU 1 (stratum 1) dated to the second part of the African Humid Period, 11.7–6 ka, and was attributed to the Bardaale industry. This chronostratigraphic framework was used to analyze the faunal remains from Guli Waabayo. However, the long timespans of LSU 2 (~14,300 years) and LSU 1 (~5700 years) probably masked greater variability in hunting behaviors than recognized in this study.

The stratigraphy at Guli Waabayo provided no clear evidence for increasing site use or decreasing mobility through the sequence (as seen in site area, sediment volumes, or artifact densities). This analysis therefore emphasizes environmental factors, as well as evidence of

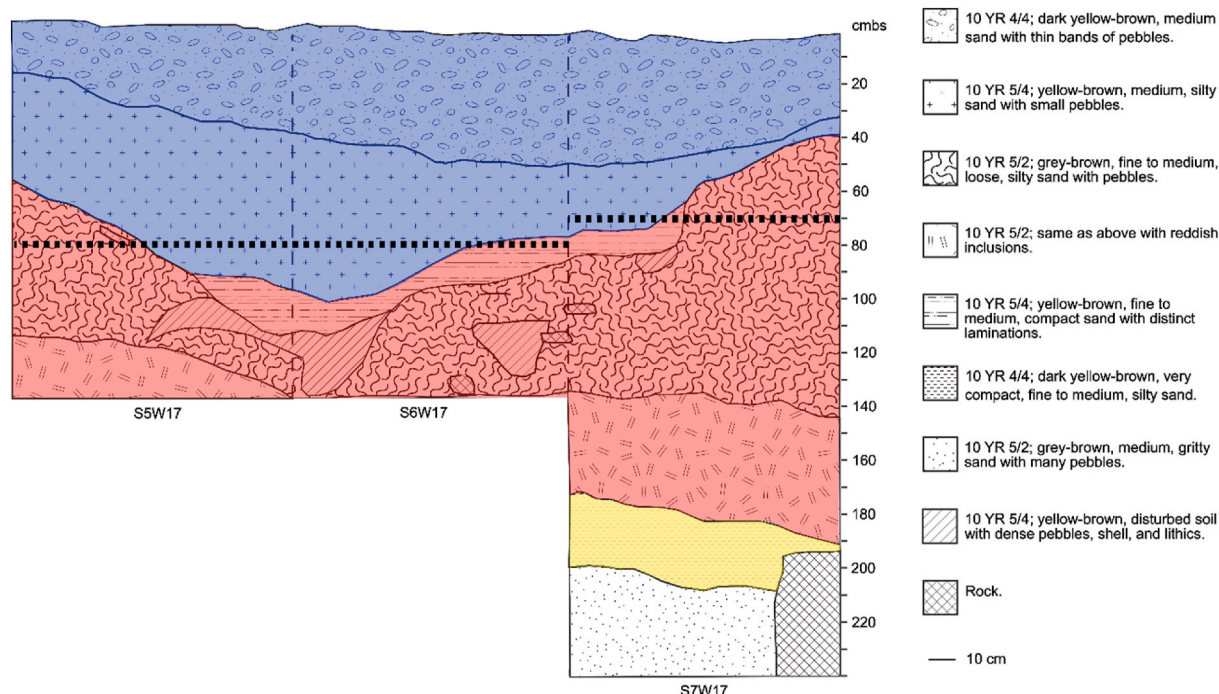


Fig. 6. East wall of the main trench at Guli Waabayo (digitized by R.E.B. Reid from BEAP profile drawings). Colors denote the three main strata associated with distinct lithic industries: yellow (stratum 3) = “transitional” MSA/LSA; red (stratum 2) = Eibian; blue (stratum 1) = Bardaale. The dotted lines denote the boundary between the two primary lithostratigraphic units (LSUs) defined by Jones et al. (2021): LSU 2 (~29–26 to ~15–11 cal ka; below), LSU 1 (~11–9 to ~7.5–6 cal ka; above). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



changing social and economic dynamics in the region (as opposed to demographic shifts), to interpret changing human relations with animals over time.

#### 4. Faunal analyses at Guli Waabayo

The large faunal assemblage from Guli Waabayo came from all 11 excavation squares within the shelter (Fig. 5). However, bones from a single square (S9W17) were excluded from more detailed analyses due to evidence of bioturbation, which made it impossible to confidently identify stratigraphic changes in the sequence (see Jones et al., 2021 for more information). The rest of the assemblage was divided by LSU and analyzed separately.

Faunal analyses were conducted by M. Jones in the Zooarchaeology Laboratory at Washington University in St. Louis and the Field Museum in Chicago using established zooarchaeological methods for eastern Africa (Brain, 1981; Gifford et al., 1980; Lesur et al., 2007; Prendergast, 2008). Identifiable specimens, preserving characteristic landmarks that allowed for identification to body part and classification to class or lower, were the focus of this study (Gifford and Crader, 1977). All mammal bones were initially sorted into five size classes (Table 1). Comparative materials from Washington University in St. Louis and the Field Museum, as well as identification manuals for African taxa (Gentry, 1978; Walker, 1985; Peters, 1988, 1989), aided further taxonomic classification. Size class estimates for specimens that could not be identified beyond Mammalia or Bovidae were made primarily on vertebrae, ribs, and long bone shafts using comparative skeletal materials of similar sized taxa. Cortical bone thickness was also used to estimate the size of indeterminate mammal bone fragments (following Pickering et al., 2003; Schmitt and Lupo, 1995).

The assemblage was quantified using Number of Identifiable Specimens (NISP) and Minimum Number of Individuals (MNI) after Klein and Cruz-Uribe (1984: 24–32) and Reitz and Wing (1999: 191–200). Following Cannon (2013) and Marshall and Pilgram (1993), NISP values were favored to account for high degrees of fragmentation among the assemblages. MNI values were used mainly for comparative purposes. Surface modifications, including evidence of burning, animal gnawing, and cut marks, were recorded for all identifiable specimens. Evaluations of preservation were conducted using bone weathering data (after Behrensmeyer, 1978) and bovid body part representation (after Thompson and Henshilwood, 2011). To investigate whether microbial/fungal damage disproportionately impacted less dense, cancellous bone portions (as discussed by Sharmin et al., 2003), differential preservation among bovid long bone ends and shafts was evaluated.

Faunal densities (NISP per cubic meter of excavated soil) were calculated and compared between LSUs to examine changes in the extent of animal-related activities practiced by people at the site through time (after Jones et al., 2018). Taxonomic frequencies of small (<20 kg) and large (>20 kg) animals—including all mammalian and non-mammalian remains—per LSU were calculated using the following formula (after Reitz and Wing, 1999: 200–202):  $X_n/Y_n = Z_{xn}$  where  $X_n$  = NISP or MNI of faunal materials attributed to subgroup X by LSU n;  $Y_n$  = NISP or MNI of all identifiable specimens by LSU n;  $Z_{xn}$  = relative frequency of subgroup X in LSU n. Small versus large taxonomic frequencies were also examined by 5 cm excavation level to test for changes

in LSA hunting strategies within each LSU. Levels 1–4 and 35–51 were omitted from this analysis because they contained very few bones. A weight limit of 20 kg was used to distinguish “small” animals typically transported whole from animals weighing over 20 kg that are often butchered before being moved (after Yellen, 1991b and Brain, 1981). However, Sinet-Mathiot et al. (2019) recently found considerable variability in the accuracy of mammalian size class estimations based on cortical bone thickness and fragment size at a paleolithic site in Italy. It was therefore possible that misidentification of mammal/bovid specimens to size classes that straddle the 20 kg boundary (1B and 2) could distort results at Guli Waabayo. To investigate the extent to which size class misidentifications potentially impacted our findings, small versus large game frequencies were calculated by LSU under two hypothetical “worst case” scenarios:

1. All indeterminate mammal and bovid bones assigned to size class 1B belong in size class 2.
2. All indeterminate mammal and bovid bones assigned to size class 2 belong in size class 1B.

Findings from these analyses were compared to our original taxonomic frequency values.

Following Faith and Du (2018), the unbiased Simpson Index was used to examine taxonomic diversity between LSUs because it accounts for differences in sample sizes more accurately than other methods. This index measures the likelihood that two randomly sampled specimens will belong to the same taxon, which acts as a proxy for taxonomic evenness within an assemblage. The equation for the unbiased Simpson Index ( $D'$ ) is as follows:

$$D' = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

In this formula,  $n_i$  equals the abundance of taxon  $i$  and  $N$  equals the total number of specimens in an assemblage. Richness (denoted by  $S$  in Results) is the total number of distinct taxa identified in an assemblage. Lower richness and evenness ( $1-D'$ ) values suggest a more specialized approach to hunting (Jones, 2004; Nagaoka, 2001). Conversely, greater richness and evenness indicate resource diversification and less focus on preferred prey species.

#### 5. Results

A total of 81,986 wild animal bones were recovered from Guli Waabayo rock shelter, including 7101 (8.7%) identifiable specimens. Mammals comprised over half of the identifiable assemblage, including both small (Table 2) and larger (Table 3) taxa. Reptiles were the second most represented taxonomic subgroup (Table 4). Turtles and tortoises were the most prevalent reptilian taxa identified, but over 80% of those were carapace or plastron fragments. The highly fragmentary nature of turtle and tortoise shell can inflate NISP measures in faunal studies (Steele and Klein, 2009), therefore all carapace and plastron fragments were excluded from secondary analyses at the site. Smaller proportions of amphibian, bird, and fish bones were also recovered from Guli Waabayo (Table 4). In general, animals weighing <20 kg dominated the faunal assemblages at the site.

Excluding those from S9W17 ( $N = 7968$ ) due to bioturbation, 74,018 bones could be attributed to LSU. LSU 2 preserved 55,844 specimens, including 4,066 identifiable bones. LSU 1 preserved 18,174 specimens, including 1,421 identifiable bones. Faunal density was greater in LSU 2 ( $5612.46/m^3$ ) than LSU 1 ( $2524.17/m^3$ ). Frequencies of small versus large game by LSU showed a high degree of small taxa in both LSUs (Fig. 7). Frequencies of small versus large game by 5 cm level also emphasized small game with little evidence of variability throughout the sequence (Fig. 8). Analysis of the potential effects of misidentifications among mammal/bovid size classes 1B and 2 supported the validity of these results, indicating no major differences in small

**Table 1**  
Mammalian size classes (after Jones et al., 2018).

Size class	Avg. weight
1a	<10 kg
1b	10–20 kg
2	20–60 kg
3	60–100 kg
4	100–500 kg
5	>500 kg

**Table 2**  
Small mammals (<20 kg), presented as NISP (MNI). SC = size class.

SC	Taxon	Common Name	LSU 2	LSU 1	S9W17	TOTAL
1A	Chiroptera	Bats	4 (1)	1 (1)	0 (–)	5 (2)
	Primates	Primates	0 (–)	1 (1)	0 (–)	1 (1)
		<10 kg				
	<i>Canis</i> spp.	Jackals	4 (1)	1 (1)	0 (–)	5 (2)
	cf. <i>Otocyon megalotis</i>	Bat-eared fox	3 (1)	0 (–)	0 (–)	3 (1)
	Canidae	Canids <10 kg	2 (–)	0 (–)	1 (1)	3 (1)
	cf. <i>Ictonyx striatus</i>	Striped polecat	1 (1)	1 (1)	0 (–)	2 (2)
	cf. <i>Genetta genetta</i>	Common genet	0 (–)	1 (1)	1 (1)	2 (2)
	Viverridae	Civets, genets	3 (1)	1 (–)	0 (–)	4 (1)
	cf. <i>Ichneumia albicauda</i>	White-tailed mongoose	4 (1)	0 (–)	0 (–)	4 (1)
	cf. <i>Herpestes ichneumon</i>	Egyptian mongoose	1 (1)	0 (–)	0 (–)	1 (1)
	cf. <i>Herpestes sanguineus</i>	Slender mongoose	2 (1)	0 (–)	0 (–)	2 (1)
	cf. <i>Mungos mungo</i>	Banded mongoose	1 (1)	0 (–)	0 (–)	1 (1)
	<i>Helogale</i> spp.	Dwarf mongooses	10 (2)	4 (1)	2 (1)	16 (4)
	Herpestidae	Mongoose	8 (–)	3 (1)	0 (–)	11 (1)
	cf. <i>Felis sylvestris</i>	Wildcat	1 (1)	0 (–)	0 (–)	1 (1)
	Carnivora	Carnivores <10 kg	10 (–)	6 (–)	3 (–)	19 (–)
	cf. <i>Procavia capensis</i>	Rock hyrax	199 (18)	36 (5)	18 (5)	253 (28)
	<i>Madoqua</i> spp.	Dik-dik	798 (22)	333 (19)	132 (6)	1263 (47)
	cf. <i>Heterocephalus glaber</i>	Naked mole-rat	2 (2)	1 (1)	0 (–)	3 (3)
	Gerbillinae	Gerbils	12 (2)	2 (1)	1 (1)	15 (4)
	Murinae	Rats and mice	0 (–)	1 (1)	1 (1)	2 (2)
	<i>Xerus</i> spp.	Ground squirrels	1 (1)	3 (2)	1 (1)	5 (4)
	Rodentia	Rodents	105 (–)	20 (–)	10 (–)	135 (–)
	<i>Lepus</i> spp.	Hares	169 (9)	21 (3)	19 (2)	209 (14)
	Mammalia	Mammals <10 kg	405 (–)	366 (–)	90 (–)	861 (–)
1B	cf. <i>Proteles cristatus</i>	Aardwolf	0 (–)	0 (–)	1 (1)	1 (1)
	Felidae	Cats 10–20 kg	3 (1)	3 (1)	0 (–)	6 (2)
	Carnivora	Carnivores 10–20 kg	10 (–)	5 (–)	2 (–)	17 (–)
	cf. <i>Ourebia ourebi</i>	Oribi	9 (2)	0 (–)	0 (–)	9 (2)
	cf. <i>Sylvicapra grimmia</i>	Bush duiker	2 (1)	0 (–)	2 (1)	4 (1)
	Bovidae	Bovids 10–20 kg	75 (1)	18 (2)	11 (–)	104 (3)
	cf. <i>Manis temminckii</i>	Ground pangolin	1 (1)	0 (–)	0 (–)	1 (1)
	cf. <i>Hystrix cristata</i>	Crested porcupine	4 (1)	1 (1)	0 (–)	5 (2)
	Mammalia	Mammals 10–20 kg	92 (–)	29 (–)	11 (–)	132 (–)
	Total		1941 (73)	857 (41)	306 (21)	3104 (135)

versus large game frequencies between our original results (Fig. 7) and the tested scenarios (Table 5).

Taxonomic frequencies within the small game category showed some variability through time (Fig. 9). Taxonomic richness and evenness values at the site were greater in LSU 2 than LSU 1 (Table 6). Taxonomic

indicators did not provide clear evidence of changing environmental conditions between LSU 2 and LSU 1 (Tables 2–4).

Most of the wild fauna from Guli Waabayo was well-preserved with little variation in bone weathering between LSUs (Fig. 10). Concretions, as seen in Fig. 11, were more common on bones from LSU 2 than LSU 1. Bovid body part representation showed similar patterns of survivorship between units (Table 7). Similar or higher frequencies of long bone ends compared to shafts among large and small bovids suggested that microbial/fungal factors did not significantly impact bone preservation (Table 8). Taphonomic data (weathering stage 4 and no evidence of mineralization) indicated that two domestic dromedary camel bones (metapodial and humerus fragments) associated with few other bones or artifacts in the uppermost levels at the site were almost certainly intrusive.

Evidence of butchery was noted primarily on larger faunal specimens at the site (Fig. 11). This was not particularly surprising, considering cutmarks are generally less common on small animal bones than larger specimens at archaeological sites (Masele and Willoughby 2021). Indications of burning were observed across taxonomic subgroups (Fig. 12). Rodent gnawing was observed primarily on smaller mammal bones, but carnivore gnawing was rare and identified only on larger specimens. This suggested that most of the wild fauna was deposited at the site by humans rather than other carnivores.

## 6. Discussion

The Guli Waabayo faunal assemblage is large, highly diverse, and dominated by mammals, birds, reptiles, and amphibians that weigh <20 kg. Jones et al. (2021) document repeated occupation of the rock shelter 26–6 ka. Our findings show a surprisingly heavy reliance on small game throughout this 20,000-year period, crosscutting regional climatic fluctuations and changing LSA lithic industries at the site.

Small, inselberg-centric taxa, including dik-dik, rock hyrax, and monitor lizard, comprise over 80% of the fauna associated with the more arid MIS 2, as well as the second half of the AHP. The taxonomic composition of small game, however, indicates a greater emphasis on mammals weighing <10 kg during the later occupations of the site. This coincides with diversity data that provides evidence for increasingly focused hunting practices that emphasize certain taxa, particularly dik-dik. Evidence of lower faunal discard in LSU 1 than LSU 2 also provides preliminary evidence of reduced or changing site use during the AHP compared to earlier times. The considerable sizes of the identifiable faunal samples from LSU 2 and LSU 1 and the lack of temporal variability in preservation suggest that these findings are robust. In particular, the large MIS 2 samples distinguish findings at Guli Waabayo from those at the Rifle Range Site. As a result, this study provides the first evidence of a prolonged reliance on small, localized prey by foragers over a ~20,000-year period spanning the Pleistocene/Holocene transition in a semi-arid region of eastern Africa, a pattern that is rare worldwide.

### 6.1. Small animals in MIS 2 and MIS 1 eastern Africa

Archaeologists have identified small animals at well-known LSA sites in eastern Africa outside of southern Somalia. However, taxa weighing <20 kg comprised only small percentages of the faunal assemblages from many (but not all) of these sites (Table 9). Marean's (1992a) study of multiple LSA rock shelter sites at the Lukenya Hill inselberg revealed large game hunting strategies that mostly ignored smaller, local species. At Enkapune Ya Muto rock shelter on the forest-grassland boundary of the Mau escarpment in the central Rift Valley of Kenya, Marean (1992b) showed that LSA hunters primarily focused on forest-dwelling ungulates such as bushbuck and bush duiker during the middle and later Holocene. Although small bovids (duikers) were emphasized, frequencies of animals that weighed <20 kg remained relatively low throughout the sequence overall. Large faunal assemblages were also recovered from

**Table 3**

Large mammals (&gt;20 kg), presented as NISP (MNI). SC = size class.

SC	Taxon	Common Name	LSU 2	LSU 1	S9W17	TOTAL
2	Primates	Primates 20–60 kg	2 (1)	0 (–)	0 (–)	2 (1)
	Felidae	Cats 20–60 kg	3 (1)	0 (–)	0 (–)	3 (1)
	Carnivora	Carnivores 20–60 kg	6 (–)	0 (–)	0 (–)	6 (–)
	cf. <i>Ammodorcas clarkei</i>	Clark's gazelle	2 (1)	0 (–)	0 (–)	2 (1)
	cf. <i>Gazella granti</i>	Grant's gazelle	3 (1)	0 (–)	1 (1)	4 (2)
	<i>Gazella</i> spp.	Gazelles	6 (–)	3 (1)	2 (–)	11 (1)
	cf. <i>Litocranius walleri</i>	Gerenuk	4 (–)	2 (1)	0 (–)	6 (1)
	Antilopini	True antelopes	14 (–)	5 (–)	2 (–)	21 (–)
	Bovidae	Bovids 20–60 kg	168 (–)	49 (–)	32 (–)	247 (–)
	Mammalia	Mammals 20–60 kg	65 (–)	28 (–)	26 (–)	119 (–)
3	cf. <i>Crocota crocuta</i>	Spotted hyena	0 (–)	1 (1)	1 (1)	2 (2)
	cf. <i>Panthera leo</i>	Lion	0 (–)	1 (1)	0 (–)	1 (1)
	<i>Phacochoerus</i> spp.	Warthogs	6 (1)	8 (1)	3 (1)	17 (3)
	<i>Potamochoerus</i> spp.	Bushpigs	7 (1)	2 (1)	3 (1)	12 (3)
	Suidae	Pigs	22 (–)	3 (–)	1 (–)	26 (–)
	cf. <i>Tragelaphus imberbis</i>	Lesser kudu	19 (2)	15 (1)	2 (1)	36 (4)
	Tragelaphini	Tragelaphines	0 (–)	1 (–)	0 (–)	1 (–)
	cf. <i>Oryx beisa</i>	East African oryx	1 (1)	1 (1)	0 (–)	2 (2)
	Bovidae	Bovids 60–100 kg	154 (–)	54 (–)	26 (–)	234 (–)
	cf. <i>Orycteropus afer</i>	Aardvark	7 (1)	4 (1)	1 (–)	12 (2)
	Mammalia	Mammals 60–100 kg	36 (–)	19 (–)	8 (–)	63 (–)
4	cf. <i>Equus grevyi</i>	Grevy's zebra	3 (1)	0 (–)	0 (–)	3 (1)
	<i>Equus</i> spp.	Asses, zebras	7 (–)	0 (–)	0 (–)	7 (–)
	cf. <i>Camelus dromedarius</i>	Dromedary camel	0 (–)	2 (1)	0 (–)	2 (1)
	cf. <i>Damaliscus lunatus jimela</i>	Topi	1 (1)	0 (–)	0 (–)	1 (1)
	cf. <i>Alcelaphus buselaphus</i>	Hartebeest	1 (1)	1 (1)	1 (1)	3 (3)
	Alcelaphinae	Alcelaphines	3 (1)	0 (–)	2 (–)	5 (1)
	cf. <i>Oryx dammah</i>	Scimitar-horned oryx	1 (1)	0 (–)	0 (–)	1 (1)
	Bovidae	Bovids 100–500 kg	34 (–)	19 (–)	7 (–)	60 (–)
	Mammalia	Mammals 100–500 kg	2 (–)	11 (–)	1 (–)	21 (–)
5	cf. <i>Diceros bicornis</i>	Black rhinoceros	0 (–)	2 (1)	0 (–)	2 (1)
	cf. <i>Giraffa camelopardalis</i>	Giraffe	4 (1)	1 (1)	1 (1)	6 (3)
	Bovidae	Bovids >500 kg	2 (1)	3 (1)	1 (1)	6 (3)
	Mammalia	Mammals >500 kg	1 (–)	0 (–)	0 (–)	1 (–)
n/a	<i>Oryx</i> spp.	Oryx	1 (–)	0 (–)	1 (1)	2 (1)
	Hippotraginae	Hippotragines	3 (–)	1 (–)	0 (–)	4 (–)
	Bovidae UD	Bovids, undetermined	1 (–)	0 (–)	0 (–)	1 (–)
	Artiodactyla	Even-toed ungulates	8 (–)	2 (–)	1 (–)	11 (–)
	Total		602 (17)	235 (14)	121 (9)	958 (41)

long MIS 2/1 sequences at rock shelter sites in Tanzania, including Nasera (Tryon and Faith, 2016), Mumba (Prendergast et al., 2007), and Kisele II (Marean and Gifford-Gonzalez, 1991; Tryon et al., 2018). However, taxonomic information from these sites was either limited or unavailable for comparison at the time of this study. North of these sites, Lesur et al. (2016) also reported evidence of primarily large game hunting at lakeshore LSA sites in the Zwai-Shalla Basin of the Ethiopian Rift Valley during the AHP.

A preference for large animals among LSA hunters at many inland sites contrasted with faunal data from MIS 2/1 sites along the eastern African coast and islands. At Panga ya Saidi cave in humid coastal Kenya, small game consistently accounted for over half of all fauna between ~25.3 and 7.6 ka (Roberts et al., 2020). Prendergast et al. (2016: S1 Table) documented evidence of an even greater reliance on small game among LSA foragers at Kuumbi Cave on Zanzibar Island throughout MIS 2 and the AHP. In both cases, the prevalence of small animal bones was associated with hunting among relatively stable wooded environments.

Although the forests of coastal Kenya and Zanzibar differ significantly from the semi-arid plains and inselbergs of southern Somalia, an emphasis on small game hunting in these areas provided the closest faunal analog to findings from the Rifle Range Site. However, whereas small animals remained important throughout MIS 2 and the AHP at Panga ya Saidi and Kuumbi Cave, Jones et al. (2018) argued that hunters at the Rifle Range Site of Buur Hakaba in inter-riverine southern Somalia targeted a greater proportion of small game during the AHP than the drier MIS 2. The authors suggested that this apparent transition from larger to smaller animals was linked to climatic amelioration and an

increased emphasis on the abundant and centralized resources of the inter-riverine inselbergs following the Pleistocene/Holocene transition. Unfortunately, the small size of the site's MIS 2 faunal assemblage constrained this argument.

Large faunal samples from both MIS 2 and MIS 1 (the AHP) at Guli Waabayo provide strong evidence for consistent small animal hunting in southern Somalia. These findings bolster arguments regarding the AHP at the Rifle Range Site made by Jones et al. (2018), but warrant reconsideration of long-term, diachronic interpretations at the site. Evidence of a continued reliance on small, inselberg taxa throughout Guli Waabayo's 20,000-year sequence shows that changing climatic, social, and economic factors did not significantly impact LSA hunting strategies. Instead, findings from this study suggest that the unique environmental context of Buur Heybe encouraged long-term subsistence stability, with only minor changes in the types of small animals hunted, over time. This pattern calls into question the extent and amplitude of eastern African MIS 2/1 climatic fluctuations and offers new perspectives on prior models of changing LSA land and resource use in eastern Africa.

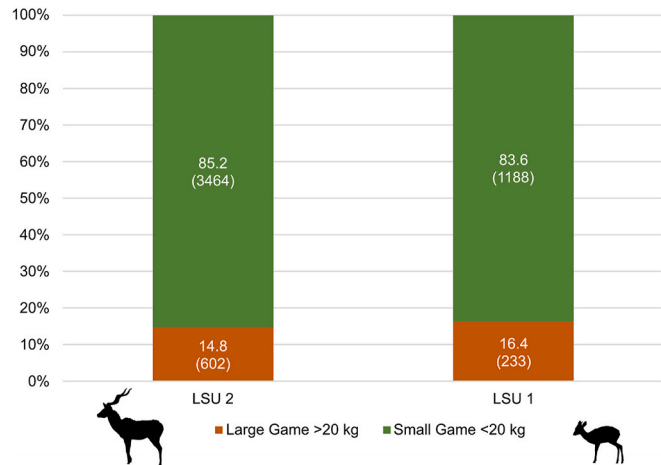
## 6.2. Why hunt small animals in semi-arid southern Somalia?

Archaeologists working in a variety of global settings have argued that reliance on smaller, lower ranked game hunting by MIS 2/1 foragers was often used as a means for dealing with resource strain from rising human populations, sedentism, and environmental degradation (Badenhorst and Driver, 2009; Jerardino, 2010, 2012; Schmitt et al., 2002; Stiner et al., 2000; Stutz et al., 2009; Zhang et al., 2013).

**Table 4**

Birds, reptiles, amphibians, and fish, presented as NISP (MNI).

Taxon	Common name	LSU 2	LSU 1	S9W17	TOTAL
Accipitridae	Eagles, hawks, kites	4 (1)	0 (–)	0 (–)	4 (1)
Galliformes	Landfowl	27 (4)	8 (1)	6 (2)	41 (7)
Aves	Birds	65 (–)	20 (–)	13 (–)	98 (–)
Testudinidae	Tortoises	4 (1)	0 (–)	0 (–)	4 (1)
Pelomedusidae	Side-necked turtles	18 (1)	10 (1)	0 (–)	28 (2)
Testudines	Tortoises, turtles	105 (–)	23 (–)	28 (2)	156 (2)
Testudines (shell)	Tortoises, turtles	646 (–)	77 (–)	119 (–)	842 (–)
Varanus spp.	Monitor lizards	158 (4)	70 (5)	10 (1)	238 (10)
Cordylidae/Gerrhosauridae	Girdle-tailed and plated lizards	58 (6)	19 (3)	9 (2)	86 (11)
Lacertilia	Lizards	378 (–)	36 (–)	194 (–)	608 (–)
Boidae	Boas	48 (1)	10 (1)	5 (1)	63 (3)
Serpentes	Snakes	140 (2)	45 (2)	21 (–)	206 (4)
Squamata	Lizards, snakes, worm lizards	5 (–)	2 (–)	0 (–)	7 (–)
cf. <i>Pyxicephalus adspersus</i>	African bullfrog	28 (6)	2 (1)	1 (1)	31 (8)
Anura	Frogs, toads	87 (–)	5 (2)	18 (–)	110 (2)
Reptilia/Amphibia	Reptiles, amphibians	392 (–)	78 (–)	37 (–)	507 (–)
Euselachii	Sharks	1 (1)	0 (–)	0 (–)	1 (1)
Siluriformes	Catfishes	3 (1)	2 (2)	0 (–)	5 (3)
Gnathostomata	Bony fishes	2 (–)	1 (1)	0 (–)	3 (1)
Total		2169 (28)	408 (17)	461 (9)	3038 (54)

**Fig. 7.** Frequencies of small versus large taxa at Guli Waabayo by LSU, presented as % (NISP).

Researchers also observed similar patterns among recent African hunter-gatherer groups. In arid and semi-arid habitats, Hawkes et al. (1991) and Yellen (1991a) argued that the incorporation of a diverse range of smaller prey by Hadza and San foragers was more efficient and less risky than focusing solely on large mammals. Kent (1993) and others (Lee and Yellen, 1976) also linked a trend toward small game hunting to decreasing large mammal populations and increasingly dense, sedentary lifeways among some San groups.

From these perspectives, evidence of small game hunting at Guli Waabayo should increase during periods when large game resources were reduced due to aridity or overhunting and decrease with higher rainfall or population mobility. Steiner et al. (2022), however, recently

argued that prey diversification associated with mostly smaller animals at the Ohalo II site in the southern Levant was linked to resource abundance during the Last Glacial Maximum. This suggested that evidence of foragers targeting a diverse range of smaller taxa at Guli Waabayo could also align with climatic amelioration and increased environmental productivity in the region (as discussed at the Rifle Range Site). Our findings, however, show that LSA hunters at Guli Waabayo maintained a focus on small game throughout MIS 2 and MIS 1.

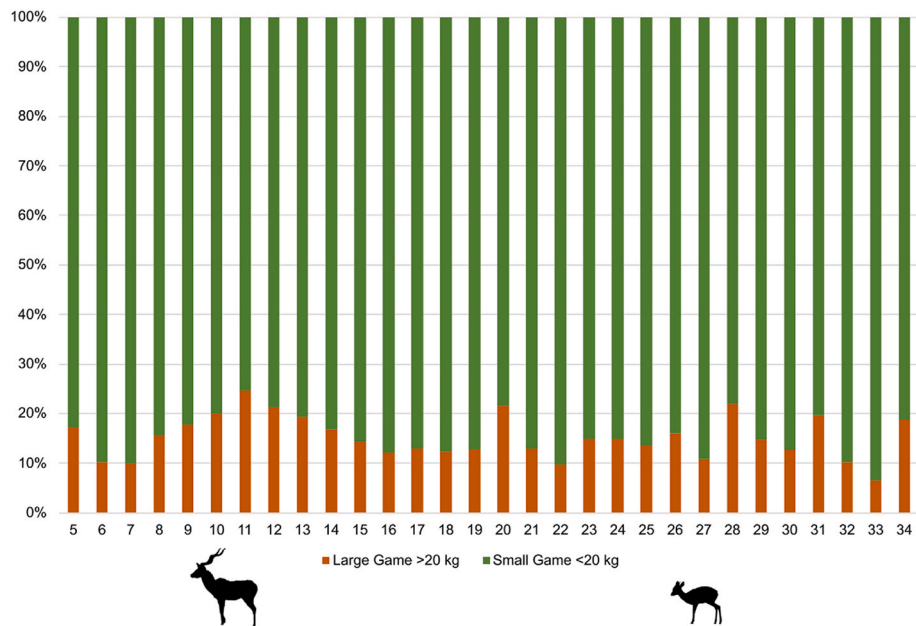
Explanations for this pattern remain uncertain. Demographic/population-based arguments for why people hunted small game cannot be adequately tested given the lack of evidence for changes in site area or deposition, as well as the sparseness of excavated sites in the region. However, the productive habitats of Buur Heybe and archaeological evidence for changing social and economic systems in the region provide interesting insights into other factors that could have influenced hunting strategies at Guli Waabayo for 20,000-years.

Like arguments linking persistent small game hunting and forest stability at Panga ya Saidi (Roberts et al., 2020) and Kuumbi Cave (Prendergast et al., 2016), it is possible that LSA hunting strategies at Guli Waabayo remained unchanged because the relative abundance and diversity of local inselberg resources did not fluctuate significantly during the site's use. Jones et al. (2021) and Reid et al. (2019) suggested that climatic changes during the AHP were less pronounced in southern Somalia than other parts of eastern Africa, limiting the scale of environmental reorganization in the region. This was supported by a lack of evidence for significant environmental differences among the MIS 2 and AHP faunal assemblages from Guli Waabayo. When rainfall was low across eastern Africa, as throughout most of MIS 2, the density of large animals in the semi-arid plains surrounding Buur Heybe were likely low and unpredictable. Therefore, Late Pleistocene Eibian foragers at Guli Waabayo could have maximized caloric gain and reduced risk by targeting the small mammals, birds, reptiles, and amphibians local to Buur Heybe. However, if overall rainfall did not greatly increase during the AHP, then it is possible that large animal stocks remained much the same in inter-riverine Somalia. As a result, Holocene Bardaale hunters at Guli Waabayo would have had little incentive to leave the inselberg, at least not for everyday food. A cache of lesser kudu horn cores associated with human burials at Gogoshiis Qabe reported by Brandt (1988), however, indicated that people at least periodically hunted larger game for use in feasts and/or ceremonial activities during the AHP. This suggested new social and economic systems were developing in the region at the time.

Based on the burials and grave goods at Gogoshiis Qabe, Brandt (1988, after Dyson-Hudson and Smith, 1978) argued that ideas of territoriality centered on the dense plant and animal resources at Buur Heybe emerged in inter-riverine Somalia during the AHP. Ambrose (1986) made similar arguments for early and middle Holocene Eburran hunter-gatherers in the forest/grassland ecotones of Kenya's central Rift Valley. Evidence of changing lithic industries at Guli Waabayo—from pressure flaked Eibian tools to more expedient Bardaale debitage—could have also signaled the arrival of new groups (rather than stylistic shifts) in the area, thereby contributing to growing ideas of territoriality at the time. Human osteological data from the site will examine this possibility. From a faunal perspective, territoriality resulting in an increased emphasis on inselberg environments should have led to more small, localized game hunting at the site during the AHP compared to MIS 2. The large samples from both MIS 2 and the AHP at Guli Waabayo provide clarity on this issue.

Although our findings suggested little change in LSA hunters' overall reliance on inselberg taxa over time, increased small mammal bones (compared to other small taxa) in the upper levels at the site provided preliminary evidence for changing group dynamics during the AHP. Jones et al. (2018) proposed that nets and snares may have been used by Holocene hunters at the Rifle Range Site to capture certain small mammal taxa (e.g., dik-dik). A less generalized approach to hunting in later occupations that focused on mammals weighing <10 kg at Guli

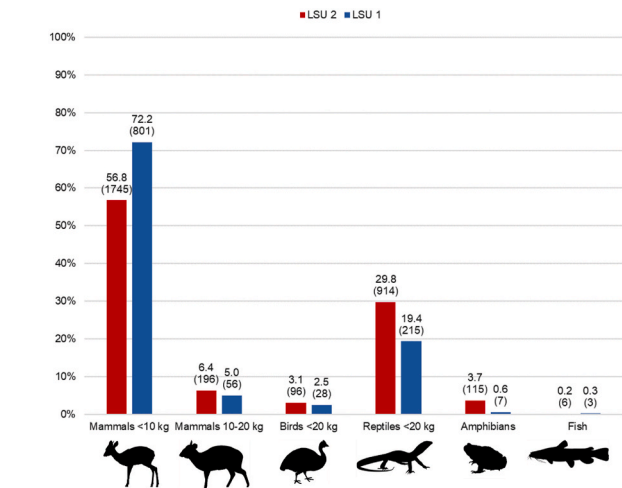




**Fig. 8.** Frequencies of small versus large taxa at Guli Waabayo by 5 cm excavation level, presented as % (NISP). Levels 1–4 and 35–51 were omitted because they included very few faunal remains.

**Table 5**  
Potential small versus large game frequencies at Guli Waabayo if mammalian and bovid size class 1B and 2 specimens were misidentified. Scenario 1 = All indeterminate mammal and bovid bones assigned to size class 1B belong in size class 2; Scenario 2 = All indeterminate mammal and bovid bones assigned to size class 2 belong in size class 1B.

		LSU 2	LSU 1
Scenario 1	Small game <20 kg	81.1% (3297)	80.3% (1141)
	Large game >20 kg	18.9% (769)	19.7% (280)
Scenario 2	Small game <20 kg	90.9% (3697)	89.0% (1265)
	Large game >20 kg	9.1% (369)	11.0% (156)

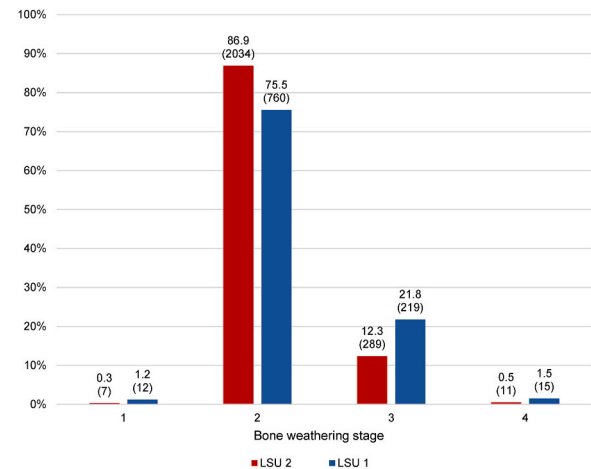


**Fig. 9.** Frequencies of small taxa at Guli Waabayo by LSU, presented as % (NISP).

Waabayo supported this idea. Scholars in central Africa (Lupo and Schmitt, 2005), North America (Steward, 1938), and Australia (Satterthwait, 1987) have associated such technologies (particularly nets) with communal hunting strategies, food surpluses, and changing political dynamics among forager groups. If LSA hunters at Buur Heybe and

**Table 6**  
Unbiased Simpson Indices at Guli Waabayo calculated using NISP.  $S$  = taxonomic richness;  $1-D'$  = taxonomic evenness.

	LSU 2	LSU 1
$S$	48	35
$1-D'$	0.78	0.69



**Fig. 10.** Bone weathering stages (after Behrensmeyer, 1978) of all mammal specimens (excluding teeth) at Guli Waabayo, presented as % (NISP).

Buur Hakaba used nets to hunt dik-dik, then similar social and economic changes may have occurred in southern Somalia during the AHP. Preliminary evidence from Guli Waabayo also suggested that LSA foragers altered their land use patterns along with new hunting methods during later occupations at the site. Whereas MIS 2 Eibian groups emphasized a more diverse range of small taxa at Buur Heybe, taxonomic and faunal density data showed that AHP Bardaale hunters may have used the site less frequently and for more specific purposes compared to earlier periods. If Holocene hunters emphasized Buur Heybe primarily for dik-dik hunting at the time, then they may have also



Fig. 11. Dik-dik mandible (left) from LSU 2 and aardvark medial cuneiform with cut marks (right) from LSU 1 at Guli Waabayo (photos by M. Jones).

Table 7

Bovid body part representation at Guli Waabayo by LSU and size class (SC), following Thompson and Henshilwood (2011). Results presented as NISP.

Element	SC 1A	SC 1B	SC 2	SC 3	SC 4	SC 5	Total
LSU 1							
Tooth	20	1	23	19	5	1	69
Cranial	11	1		1	2		15
Mandible	15			1	2		18
Atlas/Axis	2						2
Pelvis	10	1	1				12
Scapula	27						27
Humerus	35		2	1			38
Radius/Ulna	42	1	3				46
Femur	22	4	3				29
Tibia/Fibula	9	2	1		1		13
Patella/Sesamoid	3		4	4	6		17
Carpal/Tarsal	30	1	4	8	2		45
Metapodial	38	2	8	12	1		61
Phalanx	58	4	20	15	2		99
LSU 2							
Tooth	51	9	38	46	3	3	150
Cranial	48	3	2	2	1	1	57
Mandible	65	4	4	2			75
Atlas/Axis	9	2	1	1			13
Pelvis	20	1	2				23
Scapula	28			2			30
Humerus	48	3		1			52
Radius/Ulna	73	8	10	2			93
Femur	44	6	2	2			54
Tibia/Fibula	30	3	3	1			37
Patella/Sesamoid	4	1	9	23	13		50
Carpal/Tarsal	86	8	22	11	7		134
Metapodial	139	6	19	28	8		200
Phalanx	150	25	84	47	7	1	314

Table 8

Small and large bovid long bone portion frequencies at Guli Waabayo, presented as % (NISP).

	Proximal	Shaft	Distal
Bovids <20 kg	34.6% (212)	27.1% (166)	38.3% (235)
Bovids >20 kg	20.2% (21)	16.3% (17)	63.5% (66)

used other parts of the landscape for different subsistence-related activities. A more detailed analysis of the large dik-dik assemblages from Guli Waabayo, as well as ongoing lithic analyses, will help elucidate the specific types of activities practiced at the rock shelter over time. Ultimately, additional surveys in inter-riverine southern Somalia would also provide critical information for understanding the different ways LSA foragers used the landscape and its resources throughout MIS 2 and the AHP.

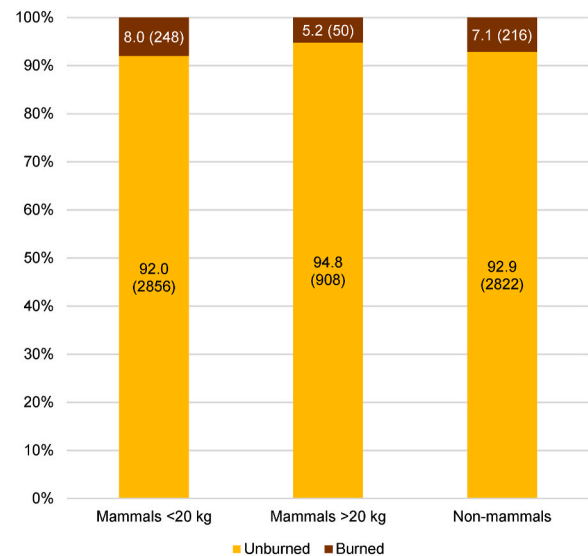


Fig. 12. Frequencies of burned bones at Guli Waabayo by taxonomic subgroup, presented as % (NISP).

## 7. Conclusions

The fauna from Guli Waabayo is one of the largest and most well-dated assemblages in eastern Africa. Due to ongoing conflict, it also represents one of only a few available datasets for examining forager behavior during MIS 2/1 in a semi-arid eastern African context. Analyses of the site's large faunal assemblages therefore signify a crucial step in reconstructing humanity's deep history in a particularly interesting and understudied world region. Findings from this study provide the first evidence of small animal hunting in a semi-arid eastern African context spanning a 20,000-year period marked by climatic variability and cultural change (as expressed in lithics and human burials, but not subsistence). Similar studies in Eurasia and North America mostly emphasize smaller, lower-ranked game hunting in response to environmental and/or human-induced resource pressures. Evidence of long-term small game hunting at Guli Waabayo, however, crosscuts major climatic fluctuations and is not associated with evidence of major demographic changes in the region. The fauna from Guli Waabayo therefore augments global understandings of the ways forager hunting strategies in risky environments related to climatic and human transformations in the past, raising interesting questions regarding changing hunter-gatherer sociality and landscape use in the arid tropics.

**Table 9**

Eastern African sites with analyzed MIS 2/1 faunal assemblages, showing frequencies of small (<20 kg) versus large (>20 kg) game by NISP.

Site	Age Range (ka)	% <20 kg	% >20 kg	Reference
Guli Waabayo	11.7–6	83.6 (1188)	16.4 (233)	This study
Guli Waabayo	29–14.7	85.4 (3464)	14.8 (602)	This study
Rifle Range Site	<12	69.5 (476)	30.5 (209)	Jones et al. (2018)
Rifle Range Site	20.4	27.5 (11)	68.2 (30)	Jones et al. (2018)
B1s1, Zwai-Shalla	13.5–13.2	15.5 (336)	84.5 (1791)	Lesur et al. (2016)
B1s4, Zwai-Shalla	14–13.8	15.4 (2)	84.6 (11)	Lesur et al. (2016)
GvJm19, Lukenya Hill	14–4	12.1 (47)	87.9 (334)	Marean (1992a)
GvJm46, Lukenya Hill	21–18	1.9 (8)	98.1 (403)	Marean (1992a)
GvJm22, Lukenya Hill	26–15	2.1 (56)	97.9 (2640)	Marean (1992a); Tryon et al., (2018)
GvJm62, Lukenya Hill	40–12	26.8 (26)	73.2 (71)	Marean (1992a)
Enkapune ya Muto	6.4–2.4	27.2 (5384)	72.8 (14,437)	Marean (1992b)
Nasera	8	0.0 (0)	100.0 (13)	Tryon and Faith (2016)
Nasera	37–16	0.5 (1)	99.5 (214)	Tryon and Faith (2016)
Panga ya Saidi	7.7–7.6	54.5 (24)	45.5 (20)	Roberts et al. (2020)
Panga ya Saidi	25.3–14.2	54.5 (242)	45.5 (202)	Roberts et al. (2020)
Kuumbi Cave	13–11.3	90.4 (1064)	9.6 (113)	Prendergast et al. (2016)
Kuumbi Cave	20–18.5	84.0 (2535)	16.0 (483)	Prendergast et al. (2016)

## Data availability

Additional data from this research is available from the authors upon request.

## CRediT authorship contribution statement

**Mica B. Jones:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Steven A. Brandt:** Data curation, Investigation, Project administration, Supervision, Validation, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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