Zooarchaeological reconstruction of newly excavated Middle Pleistocene deposits from Elandsfontein, South Africa.

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Zooarchaeological Reconstruction of Newly Excavated, Middle Pleistocene Deposits from Elandsfontein, South Africa.

Highlights

- First zooarchaeological account of systematically excavated faunal material from Elandsfontein, South Africa (ca. 1.0 – 0.6 Ma).
- Frequencies of hominin-induced butchery are higher than reported for previously described surface collections.
- Demonstrates butchery of megafauna on at least two occasions.
- Varying degrees of hominin and carnivore activity across the paleolandscape.

Abstract

The current study provides the first zooarchaeological account of systematically excavated faunal material from Elandsfontein, South Africa (ca. 1.0 – 0.6 Ma). Archaeological assemblages of this age typically lack well-preserved faunal remains recovered in primary association with artifacts, and thus studies have primarily focused on lithic technology. The sizeable faunal sample from Elandsfontein, South Africa is a rare exception and has dramatically influenced the way that we interpret early hominin foraging behavior during this time. Surface collections, starting in the 1950s, recovered ~13,000 mammalian fossils and more than 160 Acheulean artifacts. The Elandsfontein faunal assemblage was interpreted as having accumulated through natural mortality and subsequent scavenging by carnivores and hominins, with hominins playing a very minimal role in carcass modification. Low frequencies of stone tool cutmarks were taken as evidence that Acheulean hominins had limited ability to obtain large carcasses. However, this interpretation contrasts with a growing body of evidence suggesting that many Acheulean hominins across sub-Saharan Africa not only had access to large mammal carcasses but were often the primary agents of accumulation and modification. The majority of the original Elandsfontein faunal material was collected from deflation surfaces and lacks sufficient contextual information. We conducted a detailed zooarchaeological analysis of faunal remains from four recent excavations within the Elandsfontein dune field. Our results differ from those based on surface collections and suggest multiple agents of bone accumulation with varying degrees of hominin and carnivore activity across the paleolandscape. Frequencies of hominin-induced butchery are higher (up to 3.6% NISP) than reported for previously collected samples (<1% of limb surfaces) and demonstrate butchery of megafauna on at least two occasions. Our findings indicate that earlier zooarchaeological studies at Elandsfontein underestimate the degree of hominin contribution to the fossil assemblage and do not take into account the complicated taphonomic history across the paleolandscape. The results of this analysis are congruent with recent studies suggesting that Acheulean hominins and their Oldowan producing predecessors had regular access to large carcasses and that megafauna were an essential component of the diet for early *Homo*.

Keywords: Hominin foraging behavior; Tooth mark; Cutmark; Percussion mark; Skeletal part profiles; Paleolandscape

Introduction

The Elandsfontein assemblage provides a rare glimpse into hominin foraging behavior during a critical and under-investigated time in human evolution (ca. 1.0 – 0.6 Ma). Climatic changes coincide with the extinction of *Homo erectus* in Africa and Europe and the appearance of behaviorally and anatomically derived Middle Pleistocene hominins across the Old World (Berger and Jansen, 1994; Blome et al., 2012; Head and Gibbard, 2005). The development of the Acheulean tool complex (~1.76 Ma-100 ka) is often attributed to the appearance of these derived African hominins with increased intellectual ability, larger absolute brain size, and larger body size. Biological changes are suggested to have been fueled by major behavioral and dietary shifts such as increased consumption of animal tissue and increased predatory behavior (Aiello and Wheeler, 1995; Klein, 2009; Milton, 1987; O'Conell et al., 1999; Pante, 2010; Ruff and Walker, 1993; Shipman and Walker, 1989). Unfortunately, our understanding of Acheulean hominin foraging behavior is limited by a lack of well-preserved faunal remains in association with evidence of hominin behavior (e.g., artifacts). Despite the abundance of Early-Middle

Pleistocene hominin localities across sub-Saharan Africa, many of these assemblages represent individual scatters of artifacts or isolated fossil finds and thus have not been the subject of intense study. (e.g., Beaumont 1982; Beyen et al., 2013; Butzer, 1974; Chavaillon et al. 1974; Clark 1987; Cruz-Uribe et al. 2003; de la Torre et al., 2003; Deino & McBrearty, 2002; Gibbon et al., 2009; Gowlett & Crompton 1994; Harris and Isaac 1997; Howell, 1961; Kuman and Clark, 2000; Lepre et al., 2011; Potts et al., 2004; Quade et al., 2004; Shackley, 1980; Schick & Clark, 2003;). Our current understanding of landscape use in early *Homo* derives mainly from a relatively limited number of localities in East Africa [e.g., Olorgesailie, Olduvai Bed I and II, Koobi Fora, (Blumenschine and Peters, 1998; Bunn, 1994; Peters and Blumenschine, 1995; Potts et al., 1999; Rogers et al. 1994; Sikes, 1994)]. Elandsfontein provides a rare opportunity to investigate Acheulean hominin foraging behavior in South Africa on a landscape scale (Braun et al., 2013a; 2013b).

Elandsfontein lies within the Cape Floral Kingdom (CFK) and Winter Rainfall Zone (WRZ). This unique setting provides an opportunity to expand our comprehension of Acheulean hominin interactions with their environments. Conditions were likely more difficult for hominins in southern Africa than elsewhere on the continent. Dust, pollen, and leaf wax records have been linked with intensified upwelling of cold bottom waters in the Benguela Current System (Dupont et al., 2005; 2011; 2013; Etourneau et al., 2009; Marlow et al., 2000). This climatic event resulted in regional aridity and growth of the endemic Cape flora. However, stable isotopic analysis of micromammal and macromammal teeth suggests that Elandsfontein may have been spared from regional aridification by ancient spring activity (Lehmann et al., 2016; Patterson et al., 2016).

The Elandsfontein fossil and artifact collections have been subject to a long history of research. Initial survey and surface collections occurred between the 1950's and 1990's (Avery, 1989; Drennan, 1953; Klein, 1978; Singer, 1956; Singer and Crawford, 1958; Singer and Heltne, 1966). Collection efforts focused primarily on well-preserved, easily identifiable specimens (Braun et al., 2013a; 2013b; Klein, 1988; Klein and Cruz-Uribe, 1991; Klein et al., 2007). In the mid-1960's, a series of excavations were undertaken in the southern part of the dune field, though only one (Cutting 10) has been fully described (Deacon, 1998; Singer and Wymer, 1968). In total, over 13,000 mammalian fossils were collected along with >160 Acheulean bifaces, thousands of flake tools, and flaking debris. The most notable discovery was a hominin calvaria that is variably classified as *Homo rhodesiensis*, ''archaic'' *H. sapiens*, or *H. heidelbergensis* (Drennan, 1953; Rightmire, 1998, 200; Singer, 1954), and is referred to as the "Saldanha skull" (Drennan 1953, 1955; Singer 1954, 1958). The fossil and artifact collections from these initial reconnaissance efforts are collectively referred to as "Elandsfontein Main" (EFTM) (Klein et al., 2007). Despite the long history of research at Elandsfontein, many studies have focused on materials collected from deflated surface horizons which have no spatial or temporal provenience.

Taphonomic and zooarchaeological interpretations of the EFTM fauna have had an important influence on our perception of Acheulean hominin foraging behavior in Africa (Klein, 1988; Klein and Cruz-Uribe, 1991; Klein et al., 2007; Milo, 1994). Low frequencies of stone tool cutmarks [<1% of limb surfaces (Milo, 1994)] were interpreted as evidence that hominins had little impact on the mammalian community and limited ability to obtain large carcasses (Klein 1988). This view of hominin foraging ability contrasts with a growing body of evidence suggesting that hominins at many Oldowan and Acheulean sites had primary access to carcasses and often consumed very large ungulates, including megafauna (e.g. Díez et al., 1999; Domínguez-Rodrigo and Barba, 2007; Domínguez-Rodrigo *et al*., 2002; 2009b; 2014b; Egeland and Domínguez-Rodrigo, 2008; Fernández- Jalvo *et al*., 1999; Goren-Inbar *et al*., 1992, 1994, 2000; Monohan, 1996; Pante, 2010, 2013; Pickering *et al.,* 2004a; 2004b; Pobiner et al., 2008; Rabinovich & Biton, 2011; Rabinovich *et al*., 2008; 2012; Saladie *et al*., 2014).

In 2008, the West Coast Research Project (WCRP) began systematic excavations throughout the Elandsfontein dune field to better understand the relationship between early human behavior and paleoenvironmental context. Excavations took place in bays or natural deflation hollows across an area of nearly 4km^2 (Fig. 1a). These excavations exposed a large number of vertebrate fossils (*n* =~20,000) in primary association with artifacts (*n* =~3,800) and provided a high-resolution stratigraphic framework that allowed for the distinction between deflation deposits and those in primary context. Geological analysis reveals that fossils at Elandsfontein are preserved in two distinct stratigraphic horizons (Fig. 1b). The majority of the fauna and all of the lithic material derive from a nodular layer in the Upper Pedogenic Sands. The older Carbonate Quartz Sands contain vertebrate and invertebrate fossils, but they are not abundant and are not associated with any artifacts. It is most likely that the original EFTM faunal sample conflates fossils from both the Upper Pedogenic Sands and Carbonate Quartz Sands (Braun et al., 2013a; 2013b).

The current zooarchaeological study focuses on excavations from four bays: Bay 0710, Bay 0209, Bay 0110, and Bay 0313 (Fig. 1a). These bays span the distance of the dune field research area and are considered representative of the entire buried land surface. All fossils in this study were recovered *in situ*, are thought to be in primary context, and are stratigraphically associated with the artifact-bearing horizon in the Upper Pedogenic Sands. All of the fossils from the Upper

Pedogenic fossil horizon come from a similar aeolian depositional context suggesting that they were deposited at the same time or at several temporally contiguous points in time (Braun et al., 2013b). The main objectives of this study are to 1) determine the primary agents of fossil accumulation and modification, 2) establish the role that hominins played in the modification of carcasses, and 3) determine whether the activities of different bone-modifying agents varied across the paleolandscape.

Many recent zooarchaeological studies make inferences about hominin and carnivore activity based on comparisons with controlled experiments (e.g. Binford *et al*., 1988; Blumenschine, 1988, 1995; Bunn, 2001; Capaldo, 1997, 1998; Domínguez-Rodrigo, 1997a, b, 1999, 2001, 2002; Domínguez-Rodrigo and Barba, 2006; Lupo and O'Connell, 2002; Marean and Spencer, 1991; Marean *et al*., 1992; Organista *et al*., 2016; Parkinson, 2013; Parkinson *et al*., 2014, 2015; Selvaggio, 1994, 1998). Such studies have provided crucial data on the relationship between bone modification patterns and timing of access to carcasses. Nonetheless, it is unlikely that this small number of actualistic studies represents the full range of variation expected across hominin and carnivore feeding scenarios. The Elandsfontein fossil assemblage is highly fragmentary and cortical surfaces are poorly preserved. Because of the limitations of the fossil sample, our study describes assemblage characteristics that are mostly qualitative rather than attempting to present a quantitative comparison of inconsistent data. The lack of statistical comparisons precludes us from determining which bone-modifying agents had primary access to carcasses, though we show evidence of large mammal butchery at considerably higher frequencies than previously reported for the EFTM surface collected material and demonstrate evidence for butchery of at least two megafaunal species.

Materials and methods

Fossils were collected by the WCRP between 2008 and 2014 (see Braun et al., 2013a; 2013b). Only materials that were excavated from the Upper Pedogenic fossil and artifact horizon were included in the following analyses. The faunal sample consisted of all macromammal fossils that were greater than two cm in length and/or identifiable to skeletal element, including long bone shaft fragment (LBSF) (*n* = 3,919). The fossil sample was collected from Bay 0209 (*n* = 1,546), Bay 0110 (*n* = 758), Bay 0710 (*n* = 937), and Bay 0313 (*n* = 678) and included only fossils recovered *in situ* (Fig. 1a, b). Concentrations of fossils and artifacts (per cm^3) were calculated for each excavation, and fossil size distribution was considered to assess post-depositional transport and/or destruction (Pobiner et al., 2008). All identifiable bones and teeth (*n* = 1,591), were assigned to taxon, size class, skeletal element, bone portion, and side, whenever possible with the assistance of comparative osteological collections at the Iziko South African Museum and University of Cape Town, (Bunn, 1986; Marean, 1991).

Measures of skeletal abundance include NISP (number of identifiable specimens), MNE (minimum number of elements), and MNI (minimum number of individuals) (Lyman 1994). MNE was calculated by examining individual bone specimens and considering taxonomic family, mammal size class, individual size, age, morphology, and overlap of homologous parts. MNE data were used to calculate MNI for each taxon. Skeletal part profiles were constructed to investigate bone survivorship and transport and are expressed as %MAU [(minimum animal units) (Binford, 1984)]. Limb bones were separated into three categories: Proximal (humerus and femur), intermediate (radius and tibia), and distal (metacarpals and metatarsals) after Domínguez-Rodrigo (1997a, b).

Fossils were coded for weathering stage to estimate the amount of time that bones were exposed on the land surface before burial. In the current analysis, we refer to three weathering phases; fresh, slightly weathered, and weathered. These phases are based on weathering stages defined by Behrensmeyer (1978). Fresh corresponds to Stage 0 (0-1 years), slightly weathered correspond to Stages 1 (0-3 years) and 2 (2-6 years), and weathered corresponds to Stage 3 (4-15 years) or above.

We examined fossils with both dry (mineralized) and green (fresh) breakage. Bone breakage patterns were determined using the method described by Villa and Mahieu (1991). Curved or spiral breaks typically occur on green bone and can often be attributed to hominin and/or carnivore consumption. Transverse breaks usually occur on dry bone and are more likely to be the result of post-depositional factors. Fossils with dry breakage are typically removed from zooarchaeological samples as they can have unpredictable effects on damage frequencies. Removal of bones with dry breakage was not possible in the current study as almost all of the fossils at Elandsfontein demonstrate at least some evidence of dry breakage. As an alternative, we implemented a size (2 cm or above) and cortical surface readability (50% or above) threshold.

A readability score was implemented using the method defined by Ferraro (2007). The score indicates the percentage of cortical surface that is in adequate condition to preserve surface damages (e.g., tooth marks, cutmarks). Bone surfaces were considered readable if the cortical surface was intact and displayed minimal surface abrasion and weathering (Stage 2 or below as defined by Behrensmeyer, 1978). The following analyses include only those fossils in which 50% or more of the cortical surface was readable (*n* = 874).

Bone surfaces were examined using a 10x hand lens and digital microscope with variable magnification (1-500x). Fossils were inspected for stone tool cutmarks, hammerstone percussion marks, carnivore tooth marks, rodent gnawing, root etching, trampling marks, and sedimentary abrasion. Cutmarks were defined as linear marks displaying V-shaped cross-sections and internal micro-striations (Bunn, 1981,1983; Cook, 1986; Lyman, 1987; Potts and Shipman, 1981; Shipman, 1983; Shipman and Rose, 1983a, b, 1984; Walker and Long, 1977). Trampling and sedimentary abrasion marks were differentiated from cutmarks by the presence of sinuous trajectories and discontinuous/irregularly trending micro-striations (Domínguez-Rodrigo et al., 2009a). Percussion marks refer to pits and notches. Pits are often closely associated with striae that result from slippage of the stone tool (Blumenschine and Selvaggio, 1988; Pickering et al., 2004 b). Percussion notches are defined as semicircular to arcuate indentations on fracture edges with corresponding negative flake scars (Capaldo and Blumenschine, 2002). Tooth pits refer to circular depressions that commonly show crushing of the cortical surface (Binford, 1981; Blumenschine, 1995) as opposed to punctures in which the entire thickness of the compact bone had been broken through (Binford, 1981; Maguire et al., 1980). Tooth scores were defined as u-shaped marks with a length measuring three or more times its breadth (Selvaggio; 1994). Rodent gnaw marks were described as multiple parallel grooves with relatively broad, flat bases (Brain, 1981; Bunn, 1981; Cook, 1986; Dixon, 1984; Johnson, 1983,1985; Shipman and Rose, 1983a).

Chi-square tests were conducted to test whether variation between bays was statistically significant. We examined variation in weathering, taxonomic composition, ungulate size class, limb elements representation, and bone surface modification. Chi-squared tests require that no cells in the contingency table have an expected value <1 and that no more than 20% of the cells have a value <5. Our data did not meet all of these criteria, and as an alternative, significance of association was determined using a Monte-Carlo permutation test with 9999 replicates.

Results

The concentrations of fossils and artifacts varied considerably between bays with both being exceptionally high at Bay 0209 (Table 1, Fig. 2). The majority of the fossils at Elandsfontein were heavily fragmented (Fig. 3). Most fossils examined from Bay 0209, Bay 0110 and Bay 0710 ranged in size from 2.0 to 2.9 cm (20-35% NISP). At Bay 0313 fossils were less fragmented with 15% NISP between 3.0-3.9 cm and another 15% NISP between 5.0 and 5.9 cm (Fig. 3). In all bays, 86.2% to 94.13% of specimens demonstrate dry breakage. Green breakage is recorded on 6.5% to 1.92% of specimens (Table 2).

All four bays contained a mix of small (size 1-2), medium (size 3-4), and large (size 5-6) fauna [(Fig. 6) (Bunn, 1986)]. Medium-sized ungulates were most frequent, representing between 56.7% and 63.9% MNI per excavation. Fossil size class distribution at Bay 0313 differed slightly from the other bays as it was the only excavation in which the frequency of small taxa (22.7%) exceeded the frequency of large taxa (18.2%). However, this variation was not statistically significant (Table 5).

Six hundred and sixty-six large mammal fossils were identified to taxonomic family (Table 3, Fig. 5). Bovids dominate both the recently excavated material and the original EFTM faunal sample. Of the excavated samples, Bay 0209 had the highest overall MNI ($n = 52$) and was the only sample to contain suid and giraffid fossils. In contrast, Bay 0313 had the lowest MNI ($n = 27$) but exhibited the highest frequency of carnivores (19% MNI) including hyaenids, canids, and viverrids, and was the only primate bearing excavation (*Theropithecus oswaldi*). The ratio of ungulates and carnivores varied significantly between bays (Table 5). The EFTM faunal sample contains a greater diversity of taxa than the recently excavated material and includes several taxa, such as pangolin (*Phataginus* sp.) and dirk-toothed cat (*Megantereon whitei*), which have not been recovered *in situ* and were thus not included here. Hippopotamids were not recovered in the four excavations described in the current study but were included in the taxonomic analysis as they have been retrieved *in situ* in other excavations (Bay 0909) (Fig. 5).

Bovid skeletal part profiles revealed an elevated frequency of high-density elements across all bays. Overall, the frequencies of axial elements were relatively low compared to appendicular elements (Fig. 7). The frequencies of proximal, intermediate, and distal limb elements varied between bays (Fig. 8). Bay 0209, Bay 0110, and Bay 0710 all exhibited relatively high frequencies of distal elements, followed respectively by intermediate and proximal elements. In contrast, Bay 0313 showed relatively high frequencies of proximal elements and an even number of intermediate and distal elements though variation between bays was not statistically significant (Fig. 8, Table 5).

Weathering stages were low (Fig. 4). The vast majority of fossils displayed fresh or slightly weathered surfaces (98-100% NISP) indicating burial in less than six years. Weathering stages were lowest at Bay 0313 with 82% of the fossils displaying no signs of weathering (fresh). Variation in weathering between bays was statistically significant (Table 5).

Cortical surface readability at Elandsfontein was also relatively low, making bone surface damage challenging to recognize. In general, there was a positive correlation between surface readability and surface damage frequencies (Table 4, Fig. 9). Consequently, analysis of bone surface damage was restricted to fossils with 50% or higher surface readability. The majority of fossils from the excavations had a readability score between 0% and 25% and thus could not be incorporated into the analysis of surface damage patterns.

All fossils greater than 2 cm with surface readability of 50% or above were examined for bone surface modification (*n* = 874). Bone surface damage includes hominin produced stone tool cutmarks and hammerstone percussion marks, carnivore tooth marks, and porcupine gnaw marks (Fig. 10 a-i). Damage frequencies varied significantly between bays and differed considerably from frequencies reported for the original EFTM faunal sample (Fig. 11). We subsequently combined zooarchaeological data from all four excavations and recalculated damage frequencies to see whether the combined frequencies more closely resembled those reported for the EFTM faunal collection (Fig. 11). The combined damage frequencies were remarkably similar to frequencies reported by Milo (1994). Nonetheless, hominin damage frequencies remained slightly higher in the excavated WCRP material.

Discussion

Previous analyses of surface collected fossils at Elandsfontein (EFTM) have been critical for assessing Acheulean hominin foraging behavior. Nevertheless, we demonstrate that such studies can be improved upon by incorporating higher resolution contextual information. The EFTM faunal sample showed carnivore tooth marks on 1.6% of "wildebeest-sized" bones and 1.4% of "eland-sized" bones. The reported frequencies for stone tool marks were only 0.7% and 0.2%, respectively (Milo, 1994). These frequencies were interpreted as evidence that hominins played little role in bone modification and that bone-artifact association was primarily the result of natural mortality in an area that attracted both hominins and other mammals. In turn, it was predicted that hominins at Elandsfontein rarely fed on large mammals despite their abundance in the EFTM fossil assemblage (Klein, 2009).

Results of the current zooarchaeological study (WCRP) differ from previous faunal studies (EFTM) based on surface collected material (Klein and Cruz-Uribe, 1991; Milo, 1994). We demonstrate cutmarks on limb bones of extinct buffalo (*Syncerus antiquus*) and rhinoceros (*Diceros bicornis*), indicating that hominins at least occasionally butchered megafauna. Also, evidence of hominin-induced bone damage is considerably more abundant in Bay 0209 (3.6% NISP) than previously recognized in the EFTM faunal sample (Milo, 1994). In part, damage frequencies were lower in the original EFTM faunal collection because the sample included specimens with low cortical surface readability which tends to deflate damage frequencies.

Various organisms, including carnivores, porcupines, and hominins, contributed to bone surface modification at Elandsfontein and appear to have concentrated their activities in different parts of the landscape. Bay 0209 and Bay 0313 reveal significantly higher frequencies of hominin and/or carnivore damage compared with Bay 0110 and Bay 0710. The former probably signify areas that were more frequently visited by carnivores and hominins while Bay 0110 and Bay 0710 more likely represent background scatter. When we combine data from all bays and analyze them as a single sample, there is a marked similarity in damage frequencies compared to those reported for the original EFTM faunal sample. This similarity highlights the fact that the EFTM sample represents an amalgamation of sites with different levels of historical site integrity and resolution (sensu Binford 1981) and lacks the necessary contextual information to parse out this complicated taphonomic history.

Overall, carnivore and hominin damage frequencies at Elandsfontein are low compared with experimental butchery and carnivore feeding models (e.g. Binford *et al*., 1988;

Blumenschine, 1988, 1995; Bunn, 2001; Capaldo, 1997, 1998; Domínguez-Rodrigo, 1997a,b, 1999, 2001, 2002; Domínguez-Rodrigo and Barba, 2006; Lupo and O'Connell, 2002; Marean and Spencer, 1991; Marean *et al*., 1992; Organista *et al*., 2016; Parkinson, 2013; Parkinson *et al*., 2014, 2015; Selvaggio, 1994, 1998). It is likely that a percentage of bone surface damage at Elandsfontein has been obliterated by taphonomic processes. The fragmentary nature of the excavated fossil material and elevated frequency of high-density elements indicates *in situ* bone breakage. Also, cortical surface preservation is weak and has likely suffered from sedimentary abrasion due to aeolian deposition, chemical processes due to soil activity, and sediment compaction. This phenomenon is observable in Figures 10e and 10f. Both specimens display cutmarks on abraded cortical surfaces and we can infer that if these marks were not as pronounced, they would likely have gone undetected. Together, these factors result in a loss of behavioral information, and thus all calculations of bone surface damage are assumed to be underestimated.

Nevertheless, frequencies of hominin butchery at Bay 0209 fall within the range reported for some African and Middle Eastern Early Stone Age localities where hominins are thought to be the primary agents of carcass accumulation (Blumenschine, 1995; Bunn and Kroll, 1986, Domínguez-Rodrigo and Barba, 2006; Egeland and Domínguez-Rodrigo, 2008; Ferraro et al., 2013; Monahan, 1996; Pobiner et al., 2008; Rabinovich et al., 2012)]. It is unclear whether hominins were the primary agents of carcass modification at Bay 0209, but it appears that butchery activity occurred more frequently in this part of the landscape compared to Bay 0110, Bay 0710, and Bay 0313. Bay 0209 also has elevated concentrations of fossils and artifacts. Artifact concentrations at Elandsfontein have been demonstrated to correlate positively with $\delta 13^{C}$ values in *Bathyergus suillus* tooth enamel across different bays, suggesting that intensity of hominin activity may be associated with the presence of C_4 vegetation and freshwater availability (Patterson et al., 2016).

Carnivore and porcupine damage frequencies are highest at Bay 0313, indicating that both agents played an important role in modifying and perhaps transporting bones at this site. While the incidence of porcupine damage (11.3%) exceeds that of carnivores (5.4%), it is far below the 60% minimum seen in modern porcupine lairs (Brain, 1981; Maguire et al., 1980) and thus porcupines are not thought to be the primary agents of bone modification in this bay. Instead, it seems likely that Bay 0313 was predominantly accumulated by carnivore activity. We know from modern and prehistoric hyena assemblages that it is common to find high frequencies of non-hyeanid carnivore remains in hyena dens. In such assemblages, taxonomic MNI is typically about 20% carnivore fossils and 80% ungulate fossils. In hominin accumulations, the frequency of carnivore fossils is generally about 10% MNI (Cruz-Uribe, 1991). At Bay 0313, 19% of the large mammal MNI consists of carnivore fossils and the diversity of carnivore taxa approaches that of known prehistoric hyena accumulations in South Africa such as Swartklip 1, Equus Cave, Sea Harvest, Elandsfontein bone circle, Deelpan, and Ysterfontein [ranging from 24-42% (Cruz-Uribe, 1991; Klein, 1983; Northey, 1979; Scott and Klein, 1981)].

Overall, weathering stages were quite low but demonstrated some variation between bays. The vast majority of fossil surfaces were fresh or slightly weathered indicating that bones were buried in less than six years across the landscape (Behrensmeyer, 1978). Burial appears to have occurred more rapidly at Bay 0313, predominantly less than one year, with 82% of the fossils displaying no signs of weathering. This variation was found to be significant and demonstrates a different depositional environment at Bay 0313 compared to Bay 0209, Bay 0110, and Bay 0710.

Bay 0313 also contains a higher frequency proximal limb elements, particularly distal humeri, than samples from the other three bays. Because limb bones decrease in nutritional value from proximal to distal elements, disparity in limb element abundance between bays might reflect preferential transport of high utility elements to Bay 0313 by carnivores (Domínguez-Rodrigo, 1997a). If carnivores were preferentially transporting smaller, more easily portable carcasses, it would also account for the higher frequency of small taxa at Bay 0313. Both findings are consistent with Bay 0313 representing a carnivore den site though neither variation in limb element abundance nor variation in animal size class between bays was statistically significant. Alternatively, distal limb elements yield higher structural densities and thus higher frequencies at Bay 0209, Bay 0110, and Bay 0710 might reflect variation in bone preservation. However, the latter scenario is unlikely given the similarity in fossil size distribution and relative amount of axial to appendicular elements among bays.

The heavily fragmented nature of the Elandsfontein fossils and poor surface preservation limits the ability to make statistical comparisons with published experimental data, and thus we cannot determine whether hominins at Elandsfontein regularly had early access to fleshed carcasses. Nonetheless, the majority of stone tool cutmarks at Elandsfontein, including cutmarks on megafauna, occur on limb shafts. Domínguez-Rodrigo & Barba (2007) have demonstrated that when flesh specializing carnivores have first access to meaty limb elements, limb shafts are typically devoid of adhering tissue and leave little for hominins to scavenge. Since hominins rarely leave cutmarks on shafts when scavenging from carnivores, this pattern suggests that hominins at Elandsfontein had early access to large packets of muscle tissue on at least some occasions (Bunn, 2001; Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997a, b, 1999, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering *et al*., 2004b). However, it is important to keep in mind that attrition and epiphyseal deletion may have erased evidence for cutmarking on less dense bone portions.

Conclusions

Elandsfontein is one of the few African Acheulean localities where systematic taphonomic and zooarchaeological investigation have been undertaken. The current study reveals a more complicated history of faunal accumulation and bone surface modification than had been recognized by the previously reported EFTM faunal sample (Milo 1994). Hominins, carnivores, and porcupines all played a significant part in site formation and subsequent taphonomic alteration of bone assemblages. The frequency of activity by different bone-modifying agents varied across the mid-Pleistocene landscape. Bay 0209 preserves the highest concentration of hominin damage, suggesting that hominin butchery was more common in this part of the landscape. However, carnivores also repeatedly modified bones at Bay 0209 and we cannot determine the primary agents of bone accumulation in this bay. Carnivores appear to be the primary agents of bone accumulation at Bay 0313, and this site likely represents a carnivore den. Bay 0110 and Bay 0710 consist of low frequencies of all damage types and probably represent natural background scatter. Damage frequencies at all bays are assumed to be underestimates given the fragmentary nature of the fossils and poor condition of cortical surfaces. Overall, higher frequencies of hominin-induced bone damage in the excavated sample indicate that hominins at Elandsfontein had more frequent access to large mammal carcasses than suggested by previous studies and were at least occasionally butchering very large animals (>150kg). These results are consistent with a growing number of zooarchaeological studies indicating that Acheulean hominins and their Oldowan producing predecessors frequently had early access to large carcasses and had become more successful at competing with large carnivore for access to meat resources (Monahan 1996; Rogers et al. 1994).

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Figure captions

Figure 1a-b. a) Sitemap with location of study bays highlighted in red. b) Composite section of the Elandsfontein stratigraphy (after Braun et al., 2013b).

Figure 2. Concentration of *in situ* fossils and artifacts per excavation

Figure 3. Size distribution of all fossils >2 cm.

Figure 4. Degree of bone surface weathering per excavation. Weathering stages were assigned following Behrensmeyer, 1978. Fresh surface = Stage 0; Slightly weathered = Stage 1-2; Weathered = Stage 3 or above.

Figure 5. Distribution of large mammal taxa in each excavation and the original EFTM faunal collection (*Klein at al., 2007).

Figure 6. Distribution of ungulate fossils by size class. Size classes were assigned following Bunn, 1986.

Figure 7. Bovid skeletal elements stratified by %MAU (minimum animal units). MAU is calculated by standardizing MNE by the number of times that each element occurs in a complete skeleton.

Figure 8. Bovid limb bones stratified by element category. Proximal includes the humerus and femur, intermediate includes the radius and tibia, and distal includes the metacarpal and metatarsal. Element categories were assigned following Domínguez-Rodrigo, 1997.

Figure 9. Cortical surface readability and frequencies of bone surface modification. Readability scores were assigned following Ferraro, 2007.

Figure 10 a-i. Examples of bone surface damage observed in this study. a) Unidentified long bone shaft fragment with carnivore induced notch, b) Unidentified long bone shaft fragment with carnivore induced tooth pit, c) Small bovid calcaneum with carnivore induced tooth puncture and score, d) Unidentified long bone shaft fragment with carnivore produced tooth score (and several small tooth pits), e) Complete *Pelorovis* metacarpal with stone tool cutmarks, f) Rhinocerotidae distal humerus with stone tool cutmarks, g) Unidentified long bone shaft fragment with hammerstone induced percussion notch, h) Unidentified long bone shaft fragment with hammerstone induced percussion pit, i) Bovid innominate with porcupine gnaw marks.

Figure 11. Frequencies of cortical surface damage for each excavation, all excavations combined, and the original EFTM faunal collection (*Milo, 1994). The sample includes all identifiable specimens (including long bone shaft fragments-LBSF) greater than 2 cm with 50% or higher cortical surface readability.

Table 1. Volume and number of fossils and artifacts per excavation.

Excavation	**Volume excavated (cm^3)**	***In situ* fossil**	***In situ* artifacts**
Bay 0209	29,144	3,937	1,105
Bay 0110	16,104	644	160
Bay 0710	16,504	1,189	111
Bay 0313	11,104	280	27

Table 2. Numbers of specimens (>2 cm) with dry (mineralized)and green (fresh) fractures.

Excavation	**Dry break**	**Green break**	**Indeterminate**	**Both**	**None**
Bay 0209	1,306	37	82	26	95
Bay 0110	705	12	18	8	15
Bay 0710	869	5	40	13	10
Bay 0313	611	30	13	14	10

Table 3. NISP (number of identifiable specimens), MNE (minimum number of elements), and MNI (minimum number of individuals) for each by large mammal taxon per excavation.

Excavation	Taxon		NISP	MNE	MNI
Bay 0209	Bovidae	Alcelaphini	6	6	2
		Antilopini	1	1	1
		Bovini	3	3	3
		Hippotragini	1	1	1
		Tragelaphini	2	2	1
		Reduncini	1	1	1
		Bovid indet. Size 1-2	16	15	4
		Bovid indet. Size 3-4	41	41	8
		Bovid indet. Size 5-6	6	4	1
	Equidae		20	18	5
	Giraffidae		1	1	1
	Suidae		3	3	3
	Rhinocerotidae		13	13	3
	Elephantidae		1	1	1
	Ungulate indet.	Ungulate size 1-2	11	10	2
		Ungulate size 3-4	48	41	8
		Ungulate size 5-6	36	30	4
	Carnivora	Viverridae	1	1	1

		Canidae	2	2	1
		Felidae	1	1	1
	Total		**214**	**195**	**52**
Bay 0110	Bovidae	Alcelaphini	1	1	1
		Bovini	2	2	1
		Hippotragini	1	1	1
		Tragelaphini	3	3	1
		Bovid indet. Size 1-2	6	6	1
		Bovid indet. Size 3-4	57	55	11
		Bovid indet. Size 5-6	11	11	3
	Equidae		12	12	4
	Rhinocerotidae		13	13	2
	Elephantidae		1	1	1
	Ungulate indet.	Ungulate size 1-2	4	4	2
		Ungulate size 3-4	50	47	8
		Ungulate size 5-6	25	24	3
	Total		**186**	**180**	**39**
Bay 0710	Bovidae	Alcelaphini	7	7	1
		Antilopini	2	2	1
		Bovini	1	1	1
		Hippotragini	1	1	1

		Tragelaphini	4	4	2
		Reduncini	1	1	1
		Bovid indet. Size 1-2	5	5	3
		Bovid indet. Size 3-4	58	54	10
		Bovid indet. Size 5-6	9	9	2
	Equidae		7	7	2
	Rhinocerotidae		19	15	2
	Elephantidae		1	1	1
	Ungulate indet.	Ungulate size 1-2	4	4	1
		Ungulate size 3-4	61	59	4
		Ungulate size 5-6	8	8	4
	Carnivora	Carnivore indet.	1	1	1
	Total		**189**	**179**	**37**
Bay 0313	Bovidae	Alcelaphini	1	1	1
		Bovini	8	8	2
		Neotragini	1	1	1
		Bovid indet. Size 1-2	6	3	2
		Bovid indet. Size 3-4	22	22	6
		Bovid indet. Size 5-6	3	2	1
	Equidae		4	4	2
	Rhinocerotidae		4	4	1
	Ungulate indet.	Ungulate size 1-2	8	7	2

	Ungulate size 3-4	9	9	3
	Ungulate size 5-6	1	1	1
Carnivora	Viverridae	4	4	1
	Canidae	1	1	1
	Hyaenidae	3	3	2
Cercopithecidae	*Theropithecus*	2	1	1
Total		**77**	**71**	**27**

Table 4. Cortical surface readability score and number of cutmarks, percussion marks, and tooth marks per excavation. Sample includes all fossils greater than 2 cm and/or identifiable to skeletal element.

Readability	Bay 0209		Bay 0110		Bay 0710		Bay 0313	
	n (%)	#CM/PM/TM	n (%)	#CM/PM/TM	n (%)	#CM/PM/TM	n (%)	#CM/PM/TM
0-25%	1175 (76.0)	0/0/0	487 (64.2)	0/0/0	618 (66.0)	1/0/0	470 (69.3)	0/0/0
26-50%	93 (6.0)	2/0/1	79 (10.4)	0/0/0	83 (8.9)	0/0/0	40 (5.9)	0/0/1
51-75%	122 (7.9)	5/0/3	91 (12.0)	2/0/0	94 (10.0)	0/1/0	71 (10.5)	0/0/2
76-99%	147 (9.5)	3/2/4	99 (13.1)	0/0/0	140 (15.0)	0/0/1	91 (13.4)	1/1/7
100%	9 (0.6)	0/0/0	2 (0.3)	0/0/0	2 (0.2)	0/0/0	6 (0.9)	0/0/0
Total	1,546	10/2/8	758	2/0/0	937	1/1/1	678	1/1/10

Table 5. Results of chi-square analyses between all bays (Bay 0209, Bay 0110. Bay 0710, Bay 0313). Weathering (Stages 0-3 after Behrensmeyer, 1978), Taxon MNI (Ungulate, Carnivore), Ungulate size class (Small 1-2, Medium 3-4, Large 5-6 after Bunn, 1986), Bovid limb elements (Proximal, Intermediate, Distal), Bone surface modification (Cutmarks, Percussion marks, Tooth marks).

	chi-square	d.f.	p-value	Monte Carlo p
Weathering (NISP)	176.73	9	0.0000	0.0001
Taxon (MNI)	8.120	3	0.0436	0.0302
Ungulate size class (MNI)	3.04	6	0.8036	0.819
Bovid limb element (MNE)	7.02	6	0.3188	0.3215
Bone surface modification	11.87	6	0.0649	0.0462