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Taphonomic and zooarchaeological analysis of fauna from the Howiesons Poort and post-Howiesons Poort at Klasies River main site: Examining links between the environment and subsistence behaviour in Marine Isotope Stages 4 and 3

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ABSTRACT

Marine Isotope Stages (MIS) 4 and 3 were significant periods encompassing some 50,000 years, including at least two techno-cultural entities: the Howiesons Poort (HP) and post-HP. Exploring subsistence and environmental changes during these periods may help us understand broader aspects of behavioural and occupational patterns over MIS 4 and 3. In this paper, we report on taphonomic analyses of a sample of early HP, late HP and post-HP fauna from Klasies River main site cave 1A. We use these and other faunal data to examine the links between subsistence behaviour and the environment during the HP and post-HP. The results of our analyses indicate that percussion marks are abundant in the HP, with percussion mark frequencies more prevalent in the later HP than the early HP indicating that humans were the primary accumulators of fauna in the HP. Other taphonomic data such as fracture patterns, burning and trampling marks also suggests that human activity was more prevalent in the HP than the post-HP. In contrast, in the post-HP, the prevalence of zoogenic marks on small mammal remains, and comparisons to actualistic assemblages indicate that carnivores probably contributed significantly to the post-HP assemblage. In all the samples investigated, crania dominate skeletal-part profiles. This could be a result of taphonomic bias, or it could indicate that foraging likely occurred relatively close to the site. Analyses of carcass-part utility show that marrow-extraction may have been a key subsistence strategy in the HP. In the post-HP, bone density-mediated attrition had a significant effect on fauna making it challenging to ascertain subsistence patterns, but preliminary analysis may also suggest marrow extraction in combination with other strategies.

Post-depositional taphonomic marks such as manganese staining suggest that post-HP and late HP deposits were significantly more affected by moisture than the early HP deposits. Previous investigations of large mammal data point to more closed environments in the early HP, while our data indicate that the environment in the late HP and post-HP was largely similar. In comparing our data to previously analysed micromammal proxy data, we show that major environmental changes at KRM occurred after the shift to post-HP lithic technology. However, the taphonomic data suggests a close relationship between changing subsistence strategies and the MIS4/3 transition.

1. Introduction

The later Middle Stone Age (MSA) period in southern Africa, between c. 71,000 and 29,000 years ago (ka) (Marine Isotope Stages [MIS] 4-3), saw a flourish of complex behaviours in MIS 4 and its waning in MIS 3 (Mackay, 2011; Wurz, 2013; Wadley, 2015; McBrearty and Brooks, 2000). The Still Bay and Howiesons Poort (HP) technocomplexes occur partly during MIS 4 and are frequently associated with an increase in innovative behaviours. These include the increased use of fine-grained raw materials, ochre and lithic heat treatment,

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engravings, marine shell beads, carnivore skinning and a variety of bone tools (Wurz, 2013; Mackay et al., 2014; Wadley, 2015; d'Errico and Backwell, 2016; Bradfield, 2021; Val et al., 2020; Wadley, 2021; Dapschauskas et al., 2022; Lombard et al., 2022). Such innovations have deep roots and are not only associated with the HP and Still Bay technocomplexes (Wurz, 2024), but they seem to be more visible during these periods. With regard to subsistence patterns, smaller fauna often dominate MIS 4 assemblages (Clark, 2011; Clark and Kandel, 2013; Dusseldorp and Reynard, 2022). A combination of hunting methods also appears in the archaeological record at this time, with hypotheses for the use of javelins, bow-hunting and, possibly, trapping being proposed (Wadley, 2010; Bradfield et al., 2020; Lombard, 2021; Dusseldorp and Reynard, 2022).

By contrast, in the post-Howiesons Poort (post-HP) – dated to MIS 3 – we see less coherent lithic technology and an increased diversity in lithic patterns, with fewer items such as beads and engraved ostrich eggshell (OES) (Wurz, 2013; Wadley, 2021; Bader et al., 2022; Blackwood and Wilkins, 2022). At many sites there appears to be a return to the dominance of larger fauna during MIS 3, as in MIS 5 (Clark and Kandel, 2013). This may suggest shifts in subsistence behaviour and hunting methods when, possibly, hand-held thrusting or stabbing spear weapons again become more commonplace (Lombard, 2021; Dusseldorp and Reynard, 2022). There is no loss of complexity in behaviour though, as attested by, for example, the recovery of bedding topped with aromatic leaves that occur at Sibudu (Sibhudu) Cave and Border Cave (Wadley et al., 2011; Sievers et al., 2022) and various types of bone tools from the post-HP layers at Sibudu Cave (Bader et al., 2022). This fluorescence of complexity in the HP and its lesser visibility in the post-HP has been linked to population dynamics with coalescence of groups during the HP and fragmentation of populations during MIS 3 (Mackay et al., 2014). Others have hypothesised that the HP industry's disappearance may be associated with changes in mobility strategies and resource distribution (Dusseldorp, 2014; de la Peña and Wadley, 2017), occupational intensity (Jacobs and Roberts, 2009; Reynard et al., 2016a) or environmental and subsistence change relating to the transition from MIS 4 to 3 (Parkington et al., 2005; Cochrane, 2008; McCall and Thomas, 2012).

MIS 4 (c. 71-57 ka) and MIS 3 (c. 57-29 ka) are marked by different climatic regimes, with the generally cooler, glacial MIS 4 followed by an interstadial MIS 3; still cool, but with warmer periods. MIS 4 and 3 are associated with shorter-term climatic oscillations (Simon et al., 2015; Braun et al., 2019), with both associated with lower sea stands (Fisher et al., 2010; Cawthra et al., 2020). The MIS 4/3 transition corresponds to changes in climate and rainfall regimes. In the southern Cape, MIS 4 is often associated with colder wetter conditions influenced by the northward shift in the westerlies (Van Zinderen Bakker, 1976, 1983; Chase and Meadows, 2007; Chase, 2010). It is also posited that the wetter conditions may coincide with increased summer rainfall associated with the southward shift of the Intertropical Convergence Zone (Braun et al., 2019). An analysis of leaf wax data from the southern Cape wetland, Vankersvelsvlei, indicate relatively drier conditions during early MIS 3. During MIS 4, relatively more vegetation using C4 and or CAM photosynthetic pathways compared to MIS 3 occur (Strobel et al., 2022). One suggestion is that more stratiform winter rain is linked to the MIS 4/3 transition (Braun et al., 2019, p. 281).

Areas of the South African coast show persistent occupations in spite of climatic fluctuations during the Late Pleistocene and have been modelled as possible refugia due to geographical diversity, temperate environment, and availability of ecotonal areas (Marean, 2010; Blinkhorn et al., 2022). It has been suggested that occupation hiatuses occur in the southern Cape in MIS 3, possibly due to hyper-arid conditions (Deacon and Thackeray, 1984; Mitchell, 2008; Steele and Klein, 2009). Thus understanding the environmental conditions during these periods is important for exploring the ecological conditions that framed human development. Ideally, palaeoenvironmental reconstruction should be based on specific local proxies, but these are frequently in short supply (Stratford et al., 2021). The period from MIS 4 to 3 encompasses over 50, 000 years. We therefore focus on three particular phases within this period – the early, late and post-HP – as a means of exploring environmental and behavioural trends over this timeframe.

Klasies River main site (KRM) has an extensive archaeological sequence spanning over 70, 000 years. Archaeological sites in the southern Cape such as Klipdrift Shelter, Pinnacle Point 5/6 and Die Kelders may be associated with the early and late HP, and the MIS 4/3 transition. KRM's sequence in its Upper Member captures the full sequences of HP to post-HP dating from prior to c. 65 to 50 ka (Table 1). Here we discuss trends for a pre-65 ka period (the early HP), the late HP dating to c. 65ka, and the post-HP, occurring at the MIS 4/3 transition, between c. 59 and 50 ka (Table 1). The abundance of faunal remains at Klasies makes this an important database in exploring environmental change during this period. Archaeo-faunas are unique in that a single dataset can be used to explore subsistence behaviour, palaeoenvironments and site formation process. The faunal remains from Klasies can thus be used to understand how these processes are linked and to what extent they document change during MIS 4 and 3.

The aim of this paper is to report on the taphonomic analyses of the HP and post-HP fauna at Klasies River, and to use these data to explore links between subsistence behaviour and environmental change from MIS 4 to 3. Taphonomic analyses of faunal remains are a critical means of identifying and understanding subsistence patterns, and are particularly valuable because, with it, we are able to investigate precise diachronic changes at a site. Bone surface modification affects all faunal specimens, not just identified ones. Given that non-identified remains constitute most fauna, larger samples can be employed as taphonomic datasets to explore layer-specific changes at KRM.

This study is important for two key reasons. Firstly, few taphonomic analyses have been conducted on the HP and post-HP fauna from KRM, and taphonomy is critical for contexualising environmental analyses (Lyman, 1994; Fernández-Jalvo et al., 2011). In addition, fauna from the post-HP in southern Africa is generally under-studied. Secondly, a question we hope to address is if any shifts in subsistence patterns are evident from the HP to the post-HP, and, if so, whether these could be associated with environmental change. KRM has a substantial HP and post-HP sequence likely covering tens of thousands of years so examining trends from the early HP to the post-HP is an important means of understanding environmental and behavioural change from MIS 4 to 3. This is especially pertinent given that these periods are so closely aligned to the HP and post-HP, respectively, at KRM. We use the abundance of site-specific archaeological data from KRM and the number of regional palaeoenvironmental proxies available to test links between environmental trends and subsistence strategies from MIS 4 to 3. Given that technological and environmental changes are evident between MIS 4 and 3, our expectations are that subsistence patterns will change over these periods.

2. Regional environment

KRM is part of the Eastern Fynbos Biome of the Greater Cape Floristic Region (GCFR). Currently, the natural vegetation surrounding KRM is dominated by *fynbos* (shrubs) with *strandveld* and *renosterveld* also occurring (Bergh et al., 2014). In addition, valleys and ravines near the site contain Southern Afrotemperate Forest vegetation (Mucina and Rutherford, 2011). The site is within the aseasonal (year-round) rainfall zone of the southern Cape coast with most precipitation in the form of stratiform rain. The current mean annual precipitation (MAP) for the region surrounding KRM is relatively high at an estimated 1000 mm/year (Van Wijk et al., 2017). Historic records show that smaller bovids such as grey rhebok (*Pelea capreolus*), Cape grysbok (*Raphicerus melanotis*) and steenbok (*R. campestris*) were common fauna but larger ungulates such as hippo (*Hippopotamus amphibius*), zebra (Equus quagga) and hartebeest (*Alcelaphus buselaphus*) were also present (Skead, 2007). It is likely that larger fauna would have been more common during the Late Pleistocene in the GCFR and the area

Table 1
HP and post-HP dates.

Deposits	Location (Cave)		Square and unit (Deacon)	Age (ka)	Method	References
Post-HP SW layer 1–9/Deacon E50 layer TSG – YS3	1A		E50 BS layer	59.3 ± 2.8	OSL single grain	Jacobs and Roberts (2017)
			E50 BSS3	57 ± 4	TL	(Tribolo et al., 2013)
			Above HP (E50 YS3)	43.4 ± 3.0	OSL/IRSL	Feathers (2002)
HP (Upper) SW layer 10–13, Deacon E50 layer CP5 – CP19	1A			63.2 ± 2.7	OSL single grain	Jacobs and Roberts (2017)
			E50 YS4	54 ± 7	TL	Tribolo et al. (2013)
			E50 CP7	53 ± 6	TL	Tribolo et al. (2013)
			E50 CP8	52 ± 6	TL	Tribolo et al. (2013)
			E50 CP18	50 ± 5	TL	Tribolo et al. (2013)
				55 ± 8	TL	Tribolo et al. (2013)
HP (Mid-upper) SW layer 14–15, Deacon H51 layer YS1 – CP2	1A		SW layer14	65.6 ± 5.3	U – series	Vogel (2001)
			SW layer 15	46.7 ± 3.3	OSL/IRSL	Feathers (2002)
	2			52.4 ± 4.0	OSL/IRSL	Feathers (2002)
HP (Mid) SW layer 16–18 Deacon H51 layer CP3 – CP12			H51 CP3	55 ± 5	TL	Tribolo et al. (2013)
			H51 CP4C	55 ± 5	TL	Tribolo et al. (2013)
				58 ± 7	TL	Tribolo et al. (2013)
			H51 CP6	52 ± 4	TL	Tribolo et al. (2013)
			H51 CP7	54 ± 6	TL	Tribolo et al. (2013)
			H51 CP7 AF2	48 ± 4	TL	Tribolo et al. (2013)
				52 ± 8	TL	Tribolo et al. (2013)
			H51 CP10	56 ± 7	TL	Tribolo et al. (2013)
	2			63.3 ± 2.9	OSL single grain	(Jacobs and Roberts,2017)
		Sieving platform		66.9 ± 3.3	OSL single grain	Jacobs and Roberts (2017)
HP (Lower) SW layer 19 - 21 Deacon J51 layer CP1 – YS5	1A		J51 CP4	No date		
			J51 YS5	No date		
Pre-HP SW layer 22 Deacon Rockfall Member	1A			71.8 ± 4.7	OSL single grain	Jacobs and Roberts (2017)
				77.4 ± 7.0	U – series	Vogel (2001)
				80.6 ± 17.6	OSL/IRSL (weighted average)	Feathers (2002)
	2	Sieving platform		69.9 ± 6.2	OSL single grain	Jacobs and Roberts (2017)

surrounding KRM (Klein, 1976; Faith, 2011).

Local and regional proxies show significant differences between the MIS 4 and 3 environments near KRM. Iron/Potassium (Fe/K) ratios from marine sediment cores off the south-eastern Cape coast indicate an increase in humidity at c. 60 ka in this region (Ziegler et al., 2013). Thereafter, aridity and humidity fluctuate significantly throughout MIS 3 in the southern Cape (Ziegler et al., 2013; Simon et al., 2015; Charidemou, 2018; Braun et al., 2024). Planktonic foraminiferal data from these cores show warmer conditions in MIS 3 than in MIS 4, although decreasing $\delta^{18}O$ values indicate gradual cooling towards the onset of MIS 2 (Ziegler et al., 2013). Speleothem data from Bloukrantz Cave near Klipdrift Shelter indicate drier condition in this region during MIS 3 after c. 48 ka (Maccali et al., 2023). Chase and colleagues' (Chase and Meadows, 2007; Chase, 2010) argument that conditions during MIS 4 were likely more humid is supported by data from marine core CD154-17-17K showing wetter conditions in the Eastern Cape between 65 and 60 ka (Simon et al., 2015; Ziegler et al., 2013). However, other research suggest that this period may have been dryer (Deacon, 1989). For example, a spike in *Stoebe* type pollen at c. 67 ka around Vankervelsvlei indicates drought stress (Quick et al., 2016), and Avery's (1983) analyses of micrommamals points to dryer conditions then.

3. Site background

KRM is located on a cliffed section of the Tsitsikamma mountain range on the southern Cape coast, in the Eastern Cape (Fig. 1). It consists of a group of coastal caves and overhangs which are overlaid by a fossil dune (Geelhoutboom Dune), described as cross-bedded sands, resting on the edge of a coastal platform (Singer and Wymer, 1982; Deacon and Geleijnse, 1988). KRM contains a well-stratified, 21-m sequence of deposits which includes caves 1 and 2, and their associated overhangs (caves 1A and 1B) (Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Wurz et al., 2018).

John Wymer first excavated the main site in 1967 and 1968 (Singer and Wymer, 1982). These excavations were extensive and removed most of the deposits in cave 1 and cave 1A, and in limited areas in caves 1B and 2 (Fig. 2). The analyses of the excavated material from these excavations provided the first interpretations of the stratigraphy and dating of the deposits. Hilary Deacon led a phase of fieldwork at KRM from 1984 to 1995, which involved detailed excavation methods that provided valuable information on the site's stratigraphy (Deacon and Geleijnse, 1988). During this phase, caves 1, 1A, 1B and 2 were excavated, with material screened through 3 mm and 2 mm mesh (Deacon and Geleijnse, 1988). The layers were categorised into units based on their sedimentary properties and processes and each unit was assigned a name based on these properties (Deacon and Geleijnse, 1988). These include Carbonised Parting (CP), Shell (S), Shell Midden (SM), Ash Feature (AF), and various types of sand units usually with an identifier based on colour, such as Yellow Sand (YS) and Brown Sand (BS) (Deacon and Geleijnse, 1988). Units with similar characteristics were grouped to form members, such as Light Brown Sand (LBS) at the base of the site, associated with the MSA I, the MSA II Shell and Sand (SAS), the Rock Fall (RF) and the Upper Member in which the HP and post-HP deposits occur (Fig. 3) (Deacon and Geleijnse, 1988).

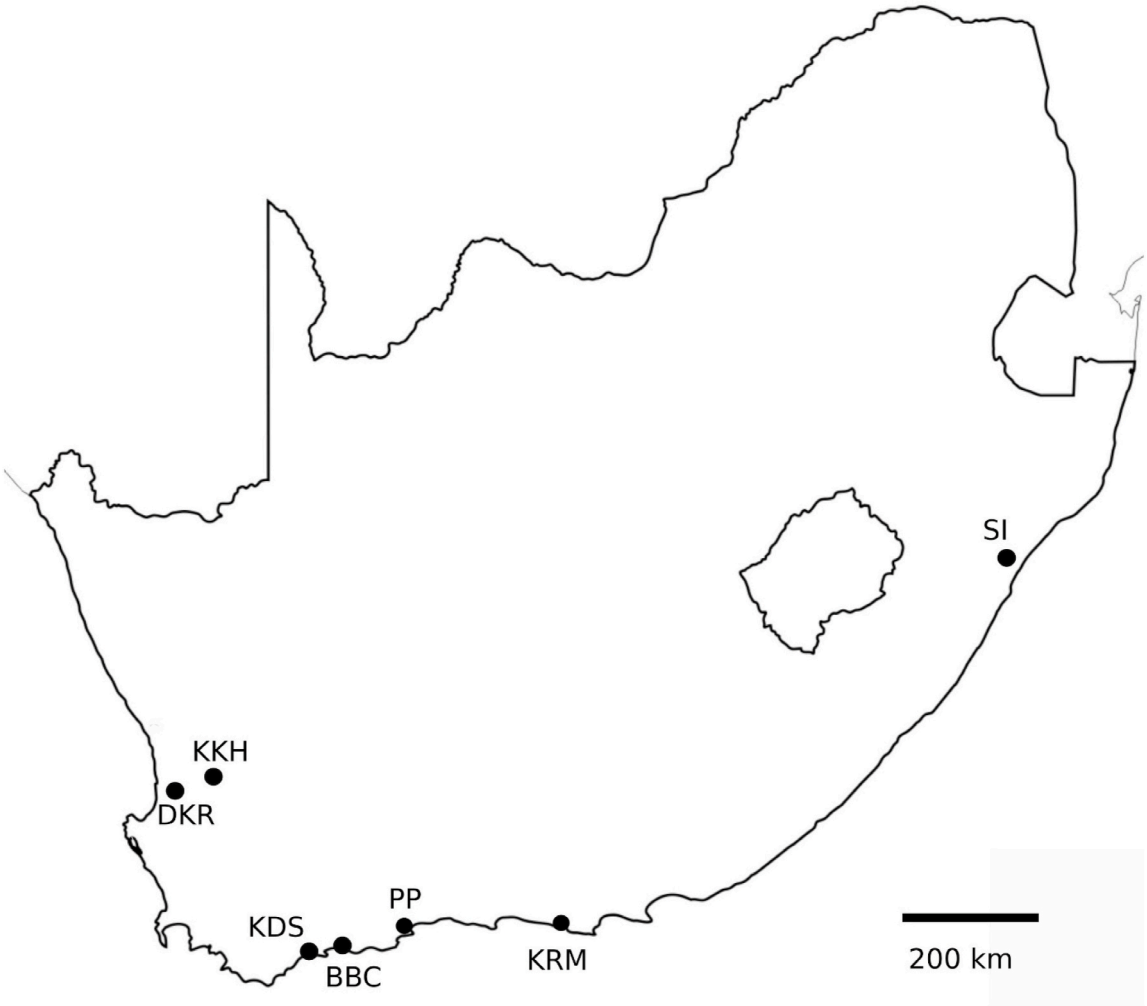


Fig. 1. Klasies River main site (KRM) and other sites mentioned. BBC=Blombos Cave, DKR = Diepkloof rockshelter, KDS=Klipdrift Shelter, KKH = Klein Kliphuis rockshelter, PP=Pinnacle Point, SI=Sibudu (Sibhudu).

3.1. Howiesons Poort and post-Howiesons Poort stratigraphy

The HP is found in caves 1A and 2, and the post-HP (or MSA III) deposits overlie the HP in cave 1A. The HP and post-HP from caves 1A originate from Wymer's initial and upper cuttings (Singer and Wymer, 1982) and Deacon's Upper Member (Deacon and Geleijnse, 1988). The Upper Member is characterised by carbon partings interspersed with sand units that exhibit numerous ash features. The carbon partings and ash units are associated with higher occupational density, and the sandy units with lower occupational intensity probably reflecting occasional site visits (Deacon and Geleijnse, 1988; Reynard, 2022a). These deposits in cave 1A correspond to Singer and Wymer's (hereafter, S–W) layers 10 to 21 (HP) and 1 to 9 (post-HP) (Singer and Wymer, 1982). The HP deposits in cave 1A are subdivided into three phases based on observable lithic technology changes, namely the Lower HP (square J51), Middle HP (square H51), and Upper HP (square E50), a subunit which also contains post-HP deposits (Fig. 3) (Deacon and Geleijnse, 1988; Wurz, 2000; Villa et al., 2010).

The HP and post-HP sequence has been dated through thermoluminescence (TL), optical stimulated luminescence (OSL) and uranium-series methods (Table 1) bracketing the layers underlying the lower HP as younger than 80-70 ka, and the middle to upper HP to between 67 and 48 ka (Table 1). The post-HP is associated with the transition to MIS 3, and dates to between 57 and 59 ka, although Feathers (2002) date of c. 43 ka provides a different interpretation. Feathers (2002) did note that his relatively younger assays for the HP and post-HP may be due to the complex post-depositional environment.

3.2. Technology

The three phases of the HP and the post-HP show changes in technology through the sequence. Backed pieces are the most common retouched artefact type in the HP, with more than 90% of backed tools made on complete blades (Wurz, 2002; Villa et al., 2010). Blades are generally a little larger in the lower HP than in the middle phase, and somewhat thicker and wider in the upper HP. Flake production becomes more prominent from the middle phase of the HP into the post-HP (Villa et al., 2010). In terms of raw material, the lowermost HP phase is dominated by quartzite, the middle phase by increased amounts of quartz and silcrete, whereas the upper HP again show relatively more quartzite (Wurz, 2000; Villa et al., 2010). In the post-HP, blade production continued but using a different technology, similar to that used in the MSA II or Mossel Bay period at the site (Wurz, 2002). No backed artefacts occur in the post-HP, instead it is associated with the typical toolkit of the MSA consisting of scrapers, notches and denticulates and a low percentage of unifacial points. Quartzite makes up more than 80% of the raw material.

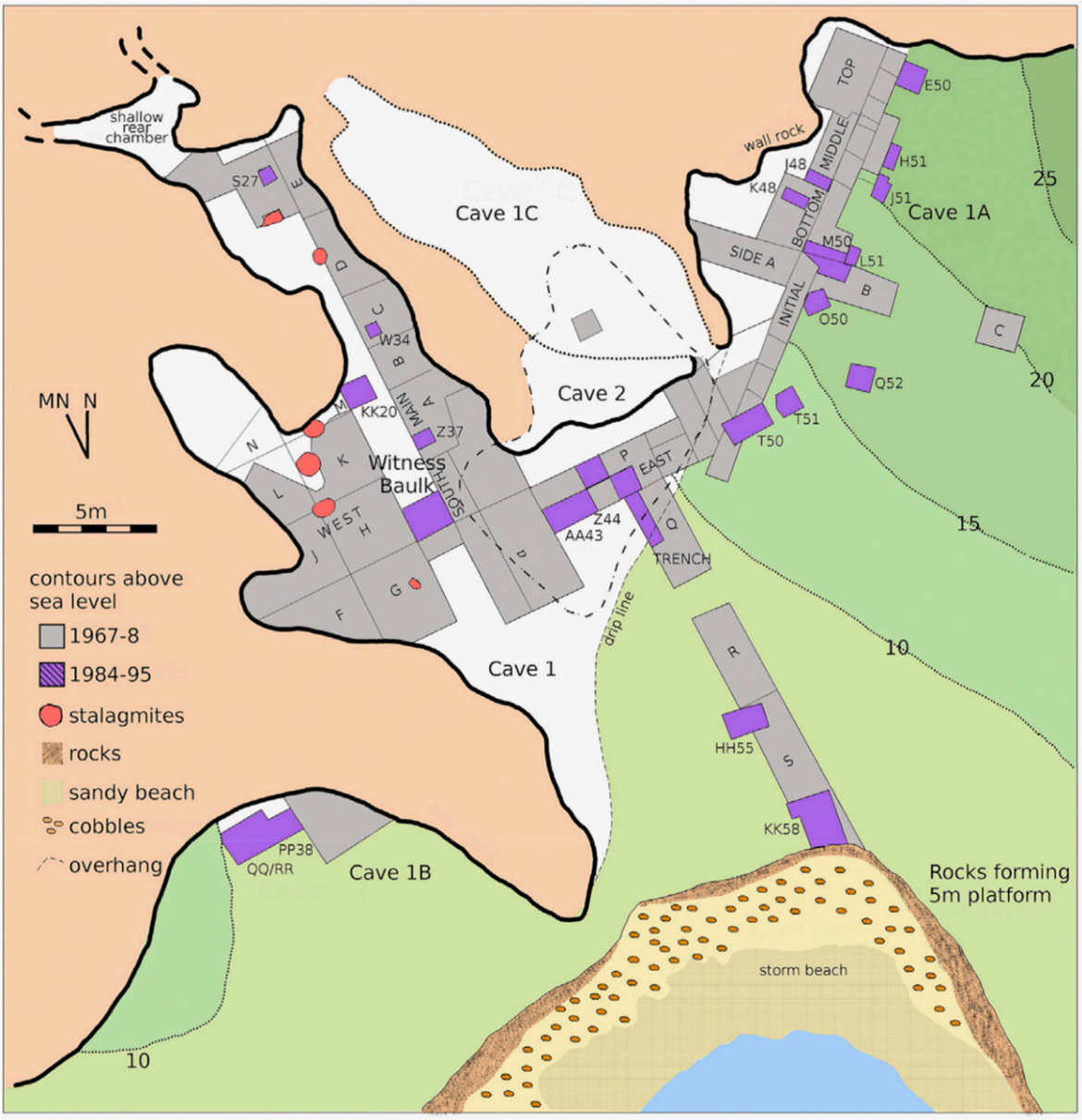


Fig. 2. Site map of Klasies River.

3.3. Faunal remains

An abundance of fauna was recovered from both the S–W and Deacon excavations. Klein (1976) analysed the S–W material in his seminal report showing that a range of mammals occurred at the site. While analyses of the faunal assemblage have expanded our understanding of subsistence behaviour in the southern Cape (Klein, 1976, 1978; Singer and Wymer, 1982; Milo, 1998), it led to various controversies in the discourse surrounding 'modern' human behaviour. In his analysis of fauna from the S–W excavations, Binford (1984) argued that large mammals at KRM were accumulated through obligate scavenging by hominins, with little evidence of systematic hunting. However, Milo's (1998) microscopic analysis of the same remains showed that humans were, in fact, the primary accumulator. Other controversies include the debate around the excavation methods used to recover the fauna (Turner, 1989; Marean and Kim, 1998). The fauna from the S–W excavation were "preliminary sorted in the field, and all bones which were not regarded as taxonomically identifiable were discarded." (Klein, 1976, p. 76). This led some questioning its utility as a dataset for subsistence analyses (Turner, 1989; Bartram and Marean, 1999; Marean et al., 2004). All faunal remains assessed in our study were recovered from the Deacon excavations and not sorted in the field. The fauna was identified to taxa by Van Pletzen and Brink for a Masters project (Van Pletzen, 2000; Van Pletzen-Vos et al., 2019).

A key discussion surrounding the S–W sample was the 'Klasies Pattern' or the head-and-foot dominated skeletal profile prevalent in the S–W sample. A detailed discussion on the Klasies Pattern is in Bartram and Marean (1999) and Van Pletzen-Vos et al. (2019). Suffice it to say that it was initially argued that this head-and-foot pattern occurred because of the 'schlepp effect' – the idea that carcasses were dragged back to the campsite with their skulls and feet intact (Perkins and Daly, 1968; Klein, 1976). Later, it was suggested that the cause may relate to transport decisions (Klein, 1989; Klein et al., 1999), but other arguments posited that the pattern was likely a result of sampling bias and intense fragmentation of long bones (Turner, 1989; Bartram and Marean, 1999; Marean et al., 2004; Pickering et al., 2003). Van Pletzen-Vos et al. (2019) noted that the Klasies Pattern was evident in the S–W sample, and not in the Deacon assemblage, suggesting that sampling bias may

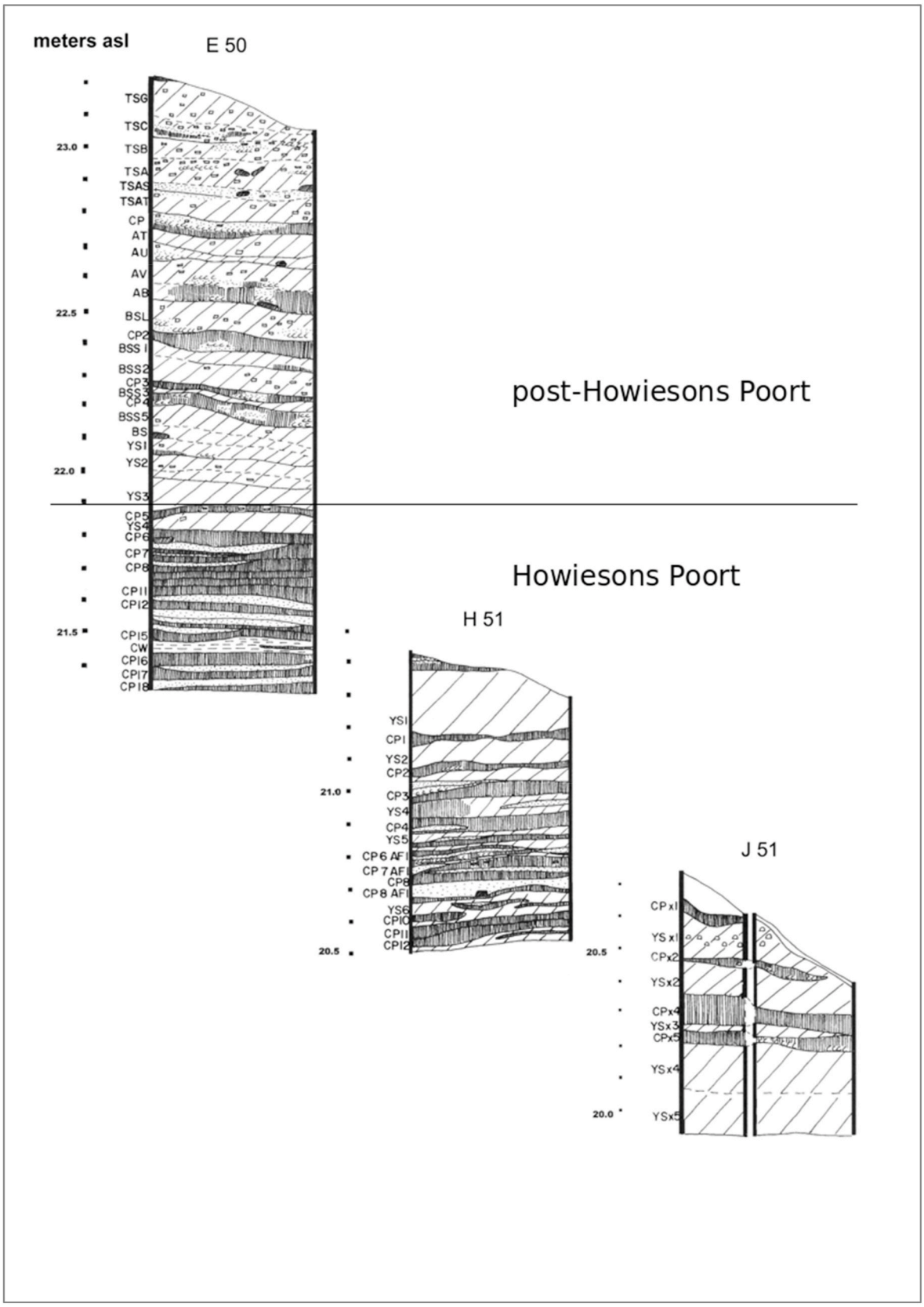


Fig. 3. Howiesons Poort and post-Howiesons Poort stratigraphy in the Upper Member.

have played a role.

Recent taphonomic analyses of fauna from the HP and post-HP layers suggest that occupational patterns differ between these periods (Achieng, 2019; Pearson, 2021). While there is little evidence of declining foraging efficiency or subsistence intensification during the HP, high frequencies of trampling marks and burnt bone suggest that the HP at KRM was an intensely occupied period (Reynard, 2022a). In contrast, the abundance of zoogenic marks in the post-HP indicates lower human occupational intensity during this phase. Given the relative similarity between taxa in the HP and post-HP samples in both the Singer and Wymer, and Deacon assemblages, we expect there to be no specific differences in species proportions between those periods in our sample. Likewise, the taphonomic analyses reported in Reynard (2022a) show little difference in the assemblages. Our taphonomic study includes the same dataset used in Reynard (2022a) but expands on it to include a more detailed assessment of the fauna.

4. Materials and methods

The fauna analysed in this study is from Deacon's 1984 to 1995 cave 1A excavations of the Upper Member. Analyses focused on all piece plotted specimens and remains larger than 2 cm recovered from coarse fraction from selected HP and post-HP layers (Table 2). In total, 5480 remains were analysed from fifteen layers. Of these, 1098 specimens are from seven post-HP layers in square E50, 2686 specimens are from four upper HP layers from square E50 and, and 1696 specimens are from two layers in the lower HP layers from square J51 (Table 2).

4.1. Taphonomic analyses

Three sets of data are included in the taphonomic analyses: post-HP, Late HP and Early HP samples. The Late and Early HP samples are sometimes combined and referred to as the HP or total HP. All three datasets are sometimes referred to collectively as from the Upper Member. The samples reported here include all specimens identified to element, unidentified specimens > 2 cm and unidentified long bone fragments. Only specimens with 'good' cortical surface preservation (i.e., >60% of the cortical surface visible) were assessed, with 2305 specimens analysed from the HP, and 1070 from the post-HP. Specimens were analysed noting element, skeletal portion, side, fracture patterns and surface modification. Bone surface modifications (BSM) were observed using an Olympus SZ60 low magnification binocular light microscope (10-40× magnification) under oblique, unidirectional lighting following standard criteria (Behrensmeyer, 1978; Blumenschine and Selvaggio, 1988; Fisher, 1995; Blumenschine et al., 1996; Reynard, 2014). Percentages of BSM pertain to the specific frequencies of a particular sample (e.g., Late HP or post-HP). Fracture patterns are based on long bone fracture outlines. While the analysis of long bone breakage has an deep history in archaeology (see Lyman, 2023), we follow previous studies of southern Cape sites (e.g., Marean et al., 2000; Thompson, 2010; Faith, 2013; Reynard et al., 2016a) by using Villa and Mahieu (1991) based on criteria of Johnson (1985).

To examine skeletal-part distributions, the skeleton is divided into four anatomical units: the head (skull and mandible), forelimb (humerus and radius), hindlimb (femur and tibia) and the distal limbs (metacarpal, metatarsal or metapodium). These units consist of high-survival elements (Marean and Cleghorn, 2003). High-survival elements are high-ranked skeletal-parts composed of very dense bone which are less susceptible to bone density-mediated attrition (Marean, 1991; Lam et al., 1999). We use the number of identified specimens (NISP) per skeletal element. Skeletal-part profiles comprise the NISP for each element (e.g., femora and tibiae) that make up the four anatomical units (cf. Van Pletzen-Vos et al., 2019). Given the small samples used to examine skeletal-part profiles, the advantage of using high survival elements is that there is no need to normalise the NISP of these elements by dividing them by two. Because skull bones and long bones are paired (cf. Clark, 2011), raw NISP values can be used (the exception is metapodia, which are divided by two).

To investigate the distribution of anthropogenic marks, we use the frequency of specimens with cut and/or percussion marks (i.e., the NISP frequency method). Abe et al. (2002) has noted that fragmentation can affect assessments of cut marks since an increase in fragmentation may lower BSM frequencies. However, the NISP frequency method has become the standard in southern African taphonomic analyses (e.g., Marean et al., 2000; Faith, 2013; cf. Thompson et al., 2017) so we follow that protocol. All identified elements were examined for anthropogenic marks to explore butchery and marrow-extraction patterns.

Table 2
Units and layers analysed in this study. Left to right = bottom to top layers.

Technocomplex		Layers	Unit
Post-Howiesons Poort		CP4, BSS3, CP3, BSS2, BSS2 (AF1), BSS1, CP2	E50
Howiesons Poort	Late HP	CP9, CP6, YS4, CP5	E50
	Early HP	YSX5, CPX4	J51

4.2. Taxonomic data

Three lists of taxa identified from KRM are referred to in this paper. The Klein (1976) analysis was conducted on fauna from the S–W excavations. Despite issues surrounding the sampling techniques, it contains the largest sample of identified fauna from KRM and is here referred to as the K sample. Van Pletzen-Vos and James Brink analysed faunal remains from the Deacon excavations (Van Pletzen, 2000; Van Pletzen-Vos et al., 2019) which we call the V sample. Identified taxa from our study is referred to as the 'taphonomic sample'.

Taxa in the taphonomic sample were identified using the Ditsong National Museum of Natural History in Pretoria. All fauna reported from KRM are hereafter referred to by their common names. For binomial names, readers are referred to Table 9. Only mammals the size of, or larger than, the Cape dune molerat were analysed. NISP was used to quantify specimens. Standard references were used in the analysis of the faunal remains (Klein and Cruz-Uribe, 1984; Reitz and Wing, 2008), and data were catalogued following Driver (2005). Bovidae (bovids) not assigned to a Linnaean Family were categorised to size classes originally based on Brain (1974) and Klein (1976). Cranial, rib, vertebral and other indeterminate mammal remains that could only be identified to element were grouped into 'small', 'medium' or 'large' indeterminate mammal size classes. Small mammal is comparable to size 1 bovids, medium mammals to size 2 and 3 bovids, and large mammals to size 4 and 5 bovids. Given the small sample sizes, we use small, medium and large mammal size categories in our assessment of faunal remains unless noted otherwise. Statistical tests were conducted using PAST (PAST® free software; Hammer and Harper, 2001).

5. Results

5.1. Taphonomic history

5.1.1. Fragmentation

As with many MSA faunal assemblages, fragmentation is relatively intense in both the HP and post-HP samples. Fragment size is often used as a proxy for fragmentation. Noting that only specimens larger than 2 cm were assessed, an independent *t*-test shows that the average length of analysed specimens from the HP (21.7 mm) is significantly shorter than those from the post-HP (27.4 mm) [$t(5478) = -5.137$; $p < 0.0001$].

To explore subsistence strategies, it is critical to identify whether bone attritional processes may have impacted the abundance of skeletal elements recovered in the assemblages (Lyman, 1994). Skeletal-part abundance was correlated with bone density values from Lam et al.

(1999). In this instance, skeletal-part abundance was based on normed NISP. Normed NISP (nNISP) is the NISP of a given element divided by the number of times that element occurs in a complete skeleton (Faith, 2007). We limited bone density-mediated attrition analyses to medium and large mammal remains because these are more likely to be affected by human transport decisions. We distinguish between all elements and high survival elements given that the latter (e.g., humeri, femora and tibiae) are less likely to be affected by density-mediated attrition (Lyman, 1994; Marean and Cleghorn, 2003). In both the medium mammal and large mammal samples from the HP, there is no significant correlation between bone density and element abundance (both in the 'all elements' and 'high survival' samples) (Table 3). Because the post-HP large mammal sample was particularly small, the medium and large mammals were combined. Spearman's rho analyses indicate that the medium-large mammal samples were indeed significantly affected by bone attrition in the post-HP. Here, the 'all element' sample reflects a relatively moderate correlation coefficient ($r_s = 0.45$), while the high survival sample shows a strong coefficient ($r_s = 0.78$).

5.1.2. Long bone fracture patterns

Spiral fractures dominate both the HP and post-HP (Table 4), but are substantially more common in the HP (n = 135; 68.2%). Medium mammal long bones are particularly likely to exhibit spiral fractures (n = 83; 75.5%). Transverse fractures are often associated with burning, and the HP contains more burnt bones than the post-HP (Reynard, 2022a). Despite this, there is no significant difference between the number of bones with transverse fractures between the HP and post-HP ($\chi^2 = 2.734$; df = 1; p = 0.098). Similarly, there is little significant difference between the types of breaks in the HP and post-HP.

5.1.3. Bone surface modification

Burnt bone is common throughout the sequence but especially prevalent in the HP (Table 5). Severely burnt bone – specimens burnt black, grey or white – are prevalent in the Late HP (n = 564; 58.6%) and relatively rare in the post-HP (n = 101; 9.4%).

Comparing anthropogenic to zoogenic marks is often used to assess who the primary bone accumulators were (Blumenschine, 1988; Thompson et al., 2017). In the HP, percussion marks (n = 251; 11%) are more common than tooth marks (n = 152; 6.6%) (Table 6). Much of this is driven by the high frequency of percussion marks in the Late HP sample (n = 204; 21.2%) while, in the Early HP, tooth marks (n = 99; 7.4%) are more abundant than percussion marks (n = 47; 3.5%). In the post-HP, tooth marks (n = 334; 31.2%) are significantly more prevalent than percussion marks (n = 147; 13.7%) ($\chi^2 = 93.779$; df = 1; p < 0.001). Gastric acid-etched bone is also significantly more common in the post-HP (n = 229; 21.4%) than in the HP (n = 118; 5.1%) ($\chi^2 = 210.034$; df = 1; p < 0.001).

If anthropogenic and zoogenic marks are assessed per layer, we see that cut marks are relatively stable, occurring on under 7% of specimens throughout the Upper Member sequence (Fig. 4). Percussion marks are notably more frequent in the HP, decreasing substantially in the post-HP. Conversely, tooth marks and gastric acid etching occur more frequently in the post-HP.

Table 3
Spearmans' rank-order correlation between bone density based on Lam et al. (1999) and skeletal-element abundance (based on normed NISP) of medium and large mammal elements. 'High survival' elements consist of skulls and long bones. Significant values emboldened.

Sample	r_s	*p*-value
HP medium mammal (all elements)	0.128	0.479
HP medium mammal (high survival only)	0.24	0.355
HP large mammal (all elements)	0.422	0.117
HP large mammal (high survival only)	0.598	0.156
Post-HP medium-large mammal (all elements)	**0.448**	**0.015**
Post-HP medium-large mammal (high survival only)	**0.774**	**0.002**

Table 4
Long bone fracture patterns. Percentages in brackets.

	Sample	N	Spiral	Transverse	Irregular	Eroded
HP	Small	18	9 (50)	2 (11.1)	3 (16.7)	3 (16.7)
	Medium	110	83 (75.5)	14 (12.7)	10 (9.1)	3 (2.7)
	Large	70	43 61.4)	10 (14.3)	9 (12.9)	3 (4.3)
	Total	198	135 (68.2)	26 (13.1)	22 (11.1)	9 (4.6)
Post-HP	Small	66	16 (24.2)	2 (3.0)	9 (13.6)	7 (10.6)
	Medium	76	44 (57.9)	5 (6.6)	16 (21.1)	5 (6.6)
	Large	36	24 (66.7)	7 (19.4)	1 (2.8)	3 (8.3)
	Total	178	84 (47.2)	14 (7.9)	26 (14.6)	15 (8.4)

Table 5
Burnt bone patterns. Percentages in brackets.

Sample	N	Brown	Localised	Black	Grey	White	Total
Post-HP	1070	63 (5.9)	191 (17.9)	64 (6.0)	30 (2.8)	7 (0.7)	355 (33.2)
Late HP	963	209 (21.7)	69 (7.2)	267 (27.7)	254 (26.4)	43 (4.5)	842 (87.4)
Early HP	1342	3 (0.2)	65 (4.8)	53 (3.9)	85 (6.3)	18 (1.3)	224 (16.7)
Total HP	2305	212 (9.2)	134 (5.8)	320 (13.9)	339 (14.7)	61 (2.7)	1066 (46.3)

Table 6
Anthropogenic and zoogenic bone surface modification. Percentages in brackets.

Sample	N	CM	PM	TM	GE
Post-HP	1070	88 (8.2)	147 (13.7)	334 (31.2)	229 (21.4)
Later HP	963	35 (3.6)	204 (21.2)	53 (5.5)	11 (1.1)
Earlier HP	1342	23 (1.7)	47 (3.5)	99 (7.4)	107 (8.0)
Total HP	2305	58 (2.5)	251 (11.0)	152 (6.6)	118 (5.1)

CM = cut marks, PM = percussion marks, TM = tooth marks, GE = gastric acid etching.

Manganese staining is by far the most common BSM in the post-HP (n = 950; 88.8%) and Late HP sample (n = 818; 84.9%) (Table 7). Despite its abundance, manganese stains usually occur as small spots on bone specimens. Weathering was also prevalent, but all cases were categorised as mild (stage 1). Mild weathering was evident on over half the HP (n = 1185; 51.4%) and post-HP specimens (n = 618; 57.8%).

5.2. Skeletal-part profiles

The sample of elements recovered from the assemblages is small. Of the 2305 specimens taphonomically analysed in the HP, 308 (13.4%) were identified to element, with 307 (13.3%) classified as unidentified long bone fragments. In the HP, vertebrae are the most abundant remains (NISP = 58) with rib fragments also common (NISP = 53). Given these small samples, we must be cautious in interpreting skeletal-part profiles and element patterns.

Fisher's exact test indicate a significant differences between skulls and post-cranial long bones in small and medium mammals in the HP (p < 0.05), with no significant difference between medium and large mammals (p > 0.05). This is probably because skull remains dominate medium and large mammal samples and are rare among small mammals (Fig. 5). In the post-HP, of the 1070 specimens taphonomically analysed, 271 were identified to element (25.3%), with 47 (4.4%) categorised as unidentified long bone fragments. Here, ribs (NISP = 59) and phalanges (NISP = 47) are the most abundant elements.

As in the HP, skull remains are also appear proportionally more abundant in medium and large mammals in the post-HP (Fig. 6). Fisher's exact test indicate a significant difference between skulls and the post-cranial bones between small and medium mammals (p < 0.05). Small mammals generally have a relatively more equitable distribution than

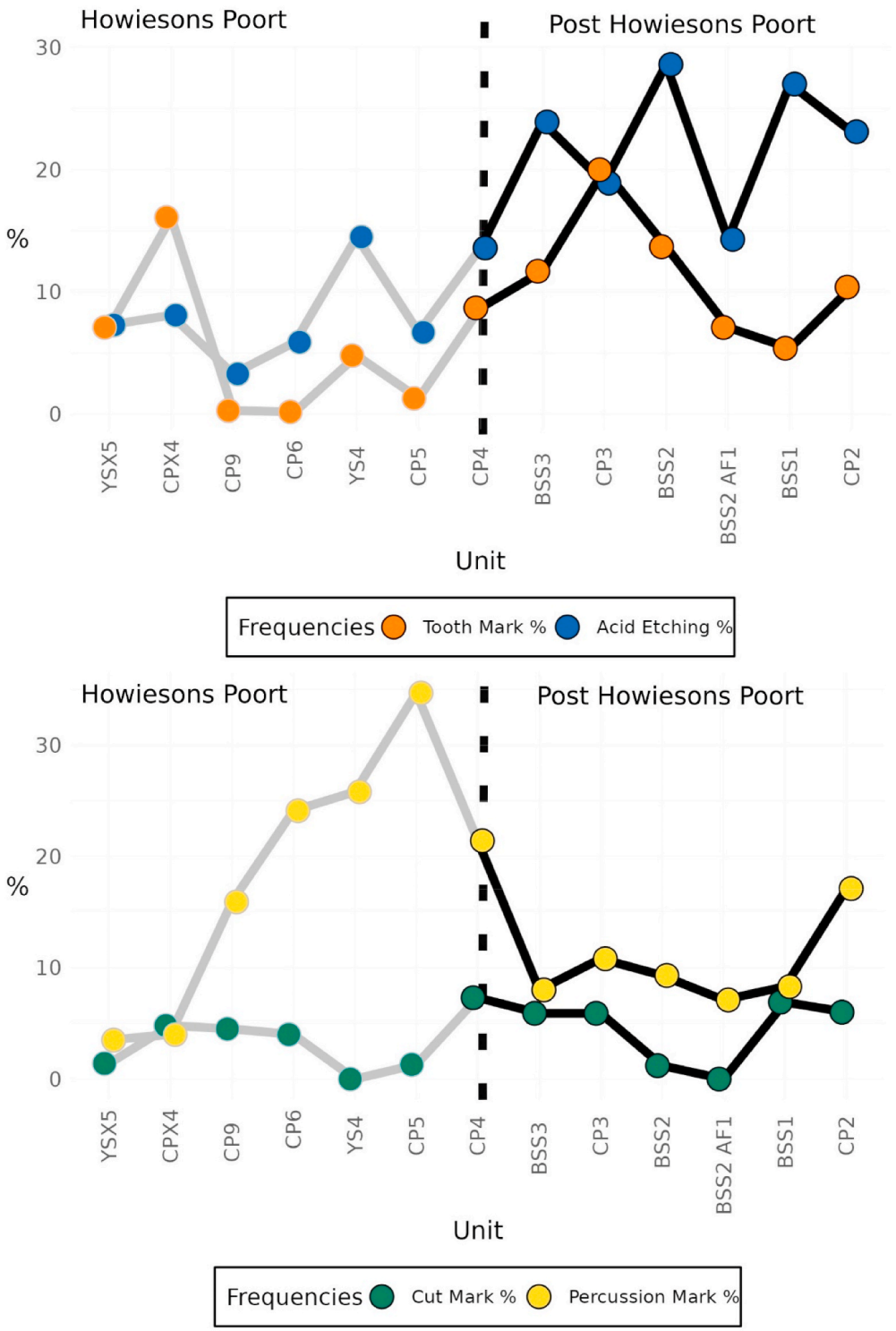


Fig. 4. Frequencies of zoogenic (top) and anthropogenic marks (bottom) per layer through the Howiesons Poort (HP) and post-HP. Grey line represents HP, black line represents post-HP. Dotted line shows HP/post-HP transition.

larger mammals.

5.2.1. Butchery marks on elements

Cut marks are quite rare in both assemblages. In the HP, they occur over a range of elements and are often associated with distal limb joints (Fig. 7). In the post-HP, they occur in low frequencies throughout the carcass. Cut marks in the post-HP sample occur mostly on distal limb elements and metapodial shafts. In the Late HP, cut marks occur mostly on axial elements, mainly on rib fragments, and in low frequencies. Cut marks in the Early HP occur mostly on unidentified long bone fragments, with some on phalanges and sesamoids of small bovids. Percussion marks are more common, in both frequency and element distribution, than cut marks. In both the HP and post-HP, they appear more often on long bones, especially metapodia.

5.3. Utility indices

Originally derived by Binford (1978), utility indices are often viewed

Table 7
Natural and diagenetic modification. Percentages in brackets.

Sample	N	Polish	Tramp	Weath	Mang	RE	GM
Post-HP	1070	406 (37.9)	47 (4.3)	618 (57.8)	950 (88.8)	94 (8.8)	4 (0.4)
Later HP	963	814 (84.5)	286 (29.7)	558 (57.9)	818 (84.9)	116 (12.0)	0 (0.0)
Earlier HP	1342	119 (8.9)	125 (9.3)	627 (46.7)	45 (3.4)	285 (21.2)	11 (0.8)
Total HP	2305	933 (40.5)	411 (17.8)	1185 (51.4)	863 (37.4)	401 (17.4)	11 (0.5)

Tramp = trampling marks, Weath = weathering, Mang = manganese staining, RE = rootlet etching, GM = gnaw marks.

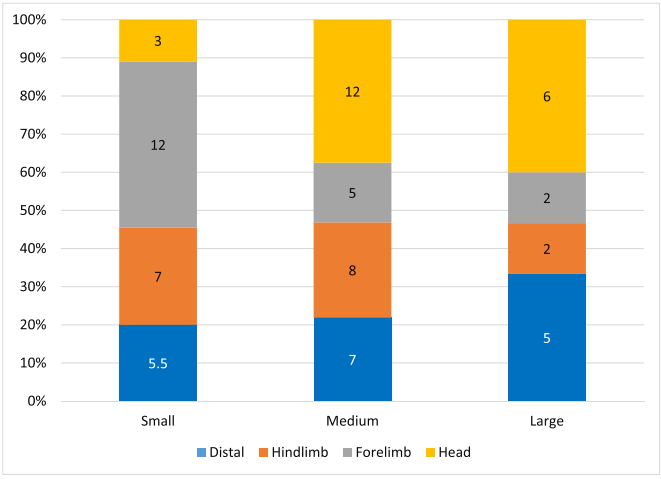


Fig. 5. Skeletal-part profile in the Howiesons Poort. NISP in columns.

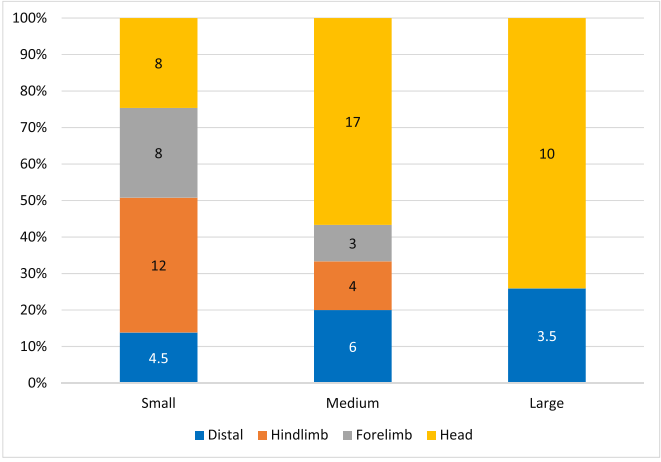


Fig. 6. Skeletal-part profiles in the post-Howiesons Poort. NISP in columns.

as a useful means of examining transport and processing decisions (Marean and Frey, 1997). As with all other analyses based on small sample sizes, utility indices must be taken with caution. This is especially the case since most of the indices in our analyses are based on North American ungulates – caribou (*Rangifer tarandus*) and bison (*Bison bison*). Furthermore, analyses of carcass-part utility are affected by various factors such as element identifiability and small samples sizes (see Lyman, 1992; Speth, 2022 for a discussion of issues around utility indices). Despite these challengers, a key reason analyses of carcass-part utility are still in use is because they encompass well-defined economic variables where the value of skeletal-parts are rank in terms of meat, grease, fat and/or overall nutritional utility (Metcalfe and Jones, 1988; Emerson, 1990; Morin and Ready, 2013). We restrict our analyses of carcass utility to medium and large mammals under the assumption that small mammals would have been brought back whole to the site. Because there was no significant correlation between skeletal-part abundance and density-mediated attrition in the HP sample, utility analyses were conducted on these fauna. The significant correlation between skeletal-part abundance and bone density in the post-HP sample means that analyses of carcass-part utility from this sample are problematic. However, to gain some insight into subsistence behaviour in the post-HP, these were conducted anyway.

Table 8 shows the results of the analyses on all elements and for high-survival elements (following Marean and Cleghorn, 2003). Skeletal abundance (nNISP) was compared to flesh weights for impala and wildebeest (Blumeschine and Caro, 1986). We also used utility data from caribou and bison because a range of economic indices (food, meat, marrow and meat-drying) could be derived from these species. Given their similar sizes, medium mammal data was compared to caribou and large mammal data to bison. The exception is the post-HP sample, where medium and large mammal data were combined. Because of that, we compared carcass-part utility to wildebeest for flesh weight, and both caribou and bison for other indices in this sample. In the HP samples, there is a significant relationship (and strong correlation coefficient) between medium mammal skeletal abundance and marrow utility (UMI). There is also a significant association (and a strong correlation) between large mammal skeletal abundance and UMI. Interesting, the post-HP dataset shows a significant (and moderate) correlation between nNISP and UMI, and a significant (moderate) inverse correlation between skeletal abundance and the meat-drying index (MDI). However, the significant correlation between skeletal abundance and bone density in the post-HP samples (Table 3) means that other factor besides economic utility may be at play.

5.4. Taxa

Table 9 reports specimens identified to taxa in our taphonomic sample. These taxa were identified from the Late HP and post-HP samples. The identified sample is small so ungulate diversity indices could not be assessed. In both the HP and post-HP, grazers are prevalent. Hartebeest (NISP = 10) is the most abundant species in the HP. This is likely related to the relatively high number of size 3 bovid and indeterminate medium mammal remains here. Long-horned buffalo are also quite common (NISP = 5). In the post-HP, in terms of identified species, hyrax dominate the sample (NISP = 39) with Cape fur seal (NISP = 12) and African buffalo (NISP = 9) also common. Generally, the post-HP samples have more non-ruminant species such as hyrax, carnivores and seal, with relatively fewer identified bovids. However, a relatively large percentage of the sample consist of size 1 bovid remains (NISP = 62; 20% of identified remains) suggesting the presence of small bovids such as the Cape grysbok/steenbok (cf. Reynard and Wurz, 2020).

6. Discussion

Our small sample size limits the extent to which we can make nuanced inferences about subsistence behaviour through the sequence. Indeed, care must be taken to not to over-estimate any possible trends in anthropogenic marks or skeletal-part patterns. Furthermore, we only have samples from the Early and Late HP, with no taphonomic data from the middle HP. Thus, we lack a clear understanding of how subsistence patterns in the Early and Late HP link. Despite that, our data does display patterns through the sequence we have, and these may give us some insight into subsistence behaviour in MIS 4 to 3 at KRM. In this section, we first discuss bone preservation and the accumulation agents, and then consider subsistence patterns and how these relate to the palaeoenvironment.

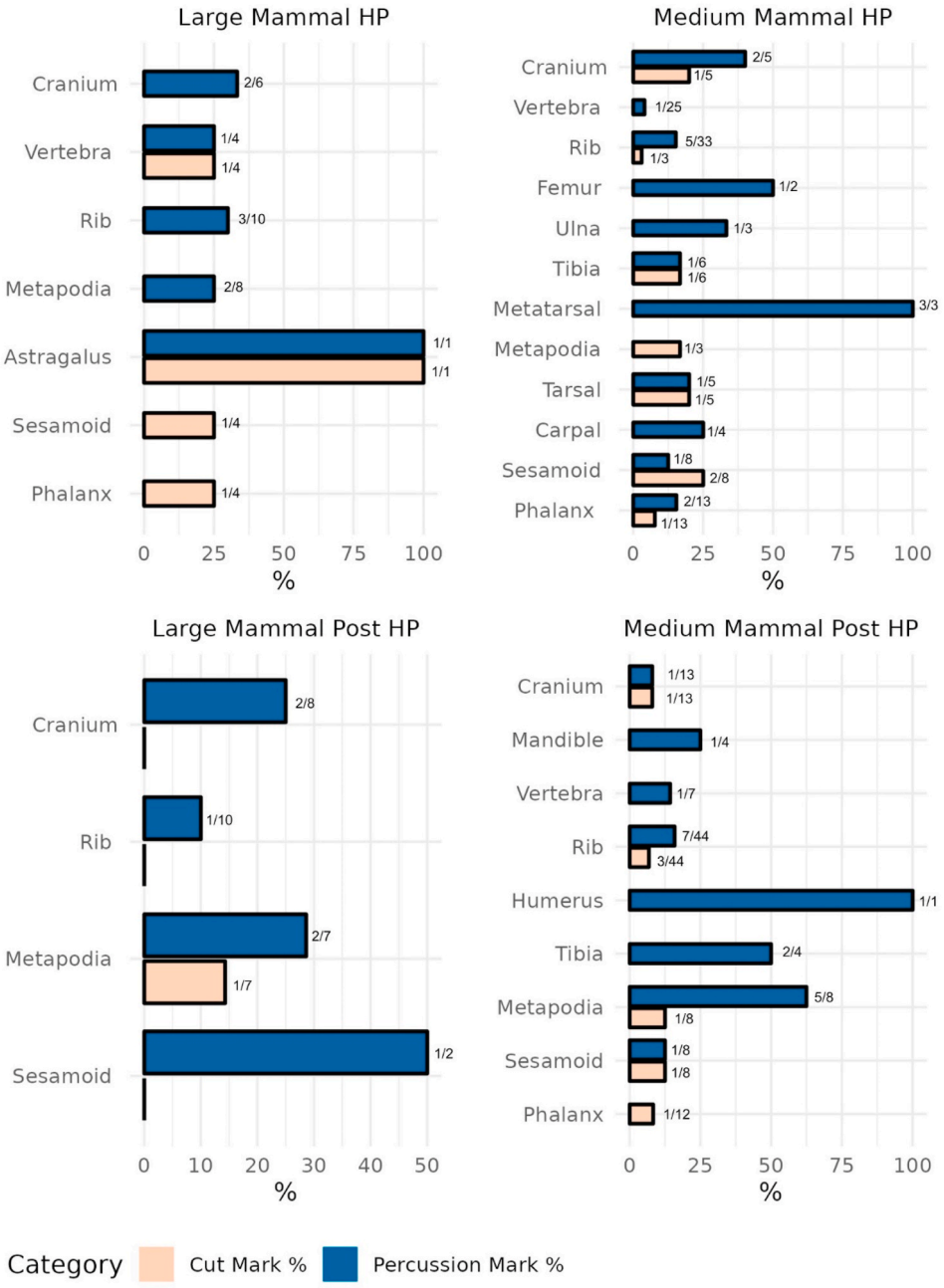


Fig. 7. Anthropogenic mark frequencies on large and medium-sized mammal skeletal elements in the Howiesons Poort (HP) and post-HP. NISP per specimen beside rows.

6.1. *Differential bone preservation*

An interesting question our analyses raise is why skeletal abundance is not correlated with bone density in the HP. Fauna from both the HP and post-HP are extremely fragmented. Juvenile and immature specimens are more susceptible to density-mediated attrition but this was probably not the case in the Upper Member. In both the HP and post-HP samples, juveniles are not common, with 16.7% (n = 39) of the HP sample categorised as juvenile, and no juveniles recovered from the post-HP (Reynard, 2022a). The Upper Member at KRM was probably an open or partially-covered overhang which means the faunal material would have been exposed to the elements and susceptible to natural attritional process such as leaching and weathering. In the post-HP, a significant association exists between bone density and element abundance (Table 3). Carnivore ravaging of bone assemblages has a strong mediating influence on element survivability (Brain, 1967, 1969, 1981; Marean et al., 1992). Thus, given the abundant evidence of carnivore ravaging in the post-HP sample (Table 6), it is possible that carnivores, scavengers and raptors may have had a significant influence on bone density-mediated attrition in the post-HP. Given the intensive fragmentation, density-mediated attrition should also be apparent in the HP. In fact, fragmentation appears more intensive in the HP with higher frequencies of transverse fractures (Table 4), more burnt bone (Table 5), and significantly smaller fragment sizes here than in the post-HP. Smaller sample sizes can sometimes result in a lack of statistical power and Type II errors. However, in the even smaller post-HP assemblage, we *do* see a correlation between bone density and skeletal abundance, so why would this be the case?

A few key reasons may account for the lack of evidence of density-mediated attrition in the HP. Firstly, fragmentation itself may be to

Table 8
Spearmans' rank-order correlation between Unit Flesh Weight (UFW[a]), Standardised Food Utility Indices (SFUI), Meat Utility Indices (MUI), Unsaturated Marrow Indices (UMI), Meat Drying Indices (MDI) and skeletal abundance (nNISP) for all elements (All) and high-survival elements (HS). Ungulate reference data from Metcalfe and Jones (1988), Emerson (1990), Friesen (2001) and Morin and Ready (2013).

Site	Size class	Sample	UFW[a]		SFUI		MUI		Ref
			r_s	*p*-value	r_s	*p*-value	r_s	*p*-value	data
HP	Medium	All	0.218	0.638	0.171	0.510	0.110	0.747	Caribou
		HS	–	–	0.184	0.611	0.322	0.398	
	Large	All	0.638	0.173	0.174	0.654	−0.069	0.850	Bison
		HS	0.105	0.895	0.707	0.182	0.353	0.559	
post-HP	Medium-large	All	0.479	0.192	−0.374	0.209	−0.328	0.389	Caribou
		HS	0.200	0.800	−0.270	0.558	0.198	0.670	
		All			0.330	0.295	0.307	0.266	Bison
		HS			0.051	0.935	−0.359	0.553	
				UMI		**MDI**			
				r_s	*p*-value	r_s	*p*-value		
HP	Medium	All		0.687	0.014	−0.047	0.879		Caribou
		HS		**0.853**	**0.031**	0.265	0.526		
	Large	All		**0.896**	**0.006**	−0.853	0.002		Bison
		HS		0.707	0.182	0.707	0.182		
post-HP	Medium-large	All		**0.623**	**0.041**	−0.304	0.337		Caribou
		HS		0.564	0.322	−0.396	0.379		
		All		0.381	0.352	**−0.516**	**0.049**		Bison
		HS		0.051	0.934	0.205	0.741		

[a] UFW are percentages of total flesh weight. Medium mammals based on impala data, Large mammals based on wildebeest data and Medium-large data based on wildebeest data from Blumenschine and Caro (1986).

blame. Because epiphyses are less dense than the cortical shaft bone, fragmentation increases the likelihood that diagnostic regions on epiphyses are destroyed (Lyman, 1984). Indeed, because carnivores generally ravage long bone epiphyses, they are particularly impactful destructive agents (Marean et al., 1992). Highly fragmented assemblages may therefore affect element survivability, resulting in Type I and II errors when skeletal abundance and bone density values are correlated (Lyman, 1994). Secondly, burning, particularly in the Late HP, may have influenced differential survivability of bone. Burning weakens bone making it more brittle and susceptible to breakage and fragmentation (Shipman et al., 1984; Stiner et al., 1995). This would especially be the case if meat-bearing elements were discarded into hearths (Costamagno et al., 2005). Another reason may be related to grease-rendering processes where the destruction of selected elements for grease and fat may impact skeletal-part profiles (Costamagno, 2013). While there is no direct evidence for this, the fact that marrow-extraction appears to be a key strategy in the HP means that grease and fat may have been important commodities at this time (Speth, 2022; Speth and Spielmann, 1983).

6.2. *Who were the bone accumulators?*

One of the most notable difference between the HP and post-HP is the contrast between zoogenic and anthropogenic mark frequencies. In particular, percussion marks are significantly more common than zoogenic marks in the HP than the post-HP and *vice versa* (Fig. 4). In fact, the post-HP has the highest frequency of zoogenically modified bone than any other phase at KRM (Reynard, 2022a). If we consider the effects of density mediated attrition, and only examine high-density, long bone mid-shafts (Thompson et al., 2017), we see the same trends in size classes. Fig. 8 shows percussion and tooth mark frequencies on long bone mid-shafts for mammal size classes using data from Reynard (2022a). Here, we see that small mammal remains from the post-HP were particularly affected by zoogenic modification. The abundance of zoogenic marks is probably related to lower human occupational intensity. With less intense human occupations, animals are more likely to dominate cave sites, which is often reflected in an abundance of gastric acid-etched and tooth-marked bone in archaeo-faunas (Brain, 1981). This may be the case in the post-HP (Reynard, 2022a).

Singer and Wymer (1982, p. 21) note that the deposits from the post-HP layers mostly consist of 'sandy scree' which is often associated with geogenic sediment and less intense human habitation (Haaland et al., 2021). Deacon and Geleijnse (1988) also highlight the relative increase in 'Yellow Sand' units in the post-HP. The decrease in spiral fractures during the post-HP (47.2%) compared to the HP (68.2%) also suggest a different taphonomic history between these periods (Table 4). Furthermore, in both the V and taphonomic samples, common carnivore and raptor prey such as hyrax and size 1 bovids are abundant in the post-HP. All this, and the high frequencies of zoogenic marks, indicates that carnivores were a significant accumulator of bone in the post-HP.

The HP samples show a different pattern. Here, zoogenic marks are generally not common (Fig. 9). Percussion mark frequencies, on the other hand, are relatively abundant in the HP. Along with high frequencies of burnt bone (Table 5), these data suggest that human activities in the HP were prevalent then and that people were likely the dominant bone accumulators at this time. Reynard (2022a) showed that the HP was a more intensely occupied period than the post-HP with abundant evidence of human activity, burning and the highest frequency of trampled bone than in any other phases at KRM.

Small mammal skeletal-parts are generally more equitably distributed than larger mammals in both the HP and post-HP samples, which raises important questions as to why this is so. It is possible that this may be a result of differential bone preservation. In highly-fragmented faunal assemblages, smaller mammal long bones may be more likely to be identified to element because they would more likely to resist fragmentation (Johnson, 1985) – possibly because they have a proportionally larger cross-sectional area relative to their size compared to larger long bones (Currey, 2003). Indeed, analyses of the cortical thickness of unidentified long bone fragments at Blombos Cave suggests that more large and medium-sized animals are present in the Still Bay than was identified to species (Reynard et al., 2014). Thus, this type of preservation issue would result in biased skeletal-part profiles in small-sized assemblages.

If these differences do represent accumulation events, then it suggests non-human accumulation. Raptors are often responsible for small fauna accumulations in rockshelters, so it would be reasonable to expect that they contributed to the assemblage (Cruz-Uribe and Klein, 1998; Badenhorst et al., 2014). Actualistic surveys of eagle nest assemblages show that crania (maxilla) and mandibles dominate both hyrax and bovid skeletal profiles (up to 94% of the %MAU for hyrax [Armstrong

Table 9
Numbers of identified specimens (NISP) in the Late Howiesons Poort (HP) and post-HP taphonomic samples.

Order	Taxa	Common Name	Late HP		post-HP	
			NISP	% NISP	NISP	% NISP
Rodentia	*Bathyergus suillus*	Cape dune mole rat			1	0.3
Hyracoidea	*Hystrix africaeaustralis*	Porcupine	1	0.8		
	Procavia capensis	Hyrax			39	12.5
Carnivora	*Arctocephalus pusillus*	Cape fur seal	4	3.2	12	3.9
	Carnivore: canid	Carnivore			2	0.6
	Carnivore: felid				4	1.3
	Carnivore: indet.		1	0.8	8	2.6
Ruminantia	*Equus* spp.	Zebra/ quagga			1	0.3
	Tragelaphus oryx	Eland	3	2.4		
	Syncerus afer[a]	African buffalo			9	2.9
	Syncerus antiquus	Long-horned buffalo	5	4.0		
	Alcelaphinae spp.	Hartebeest/ wildebeest/ bontebok	10	8.1		
	Megalotragus spp.	Giant hartebeest	1	0.8		
	Connochaetes spp.	Wildebeest			2	0.6
	Antidorcas sp.	Springbok	1	0.8		
Bovidae: indet	BOV I	Bovid	8	6.5	62	19.9
	BOV II		7	5.6	20	6.4
	BOV II/III				3	1.0
	BOV III		16	12.9	34	10.9
	BOV III/IV		4	3.2	3	1.0
	BOV IV		11	8.9	10	3.2
	BOV IV/V		4	3.2	3	1.0
Mammal: Indet	Small	Mammal	4	3.2	15	4.8
	Medium		29	23.4	66	21.2
	Large		15	12.1	17	5.5
Total			**124**	100	**311**	100

[a] Given the racial offensiveness of the original species name *Syncerus caffer*, we follow recent recommendations on ethical scientific naming by Smith and Figueiredo (2021) by removing the *c* and the second *f*.

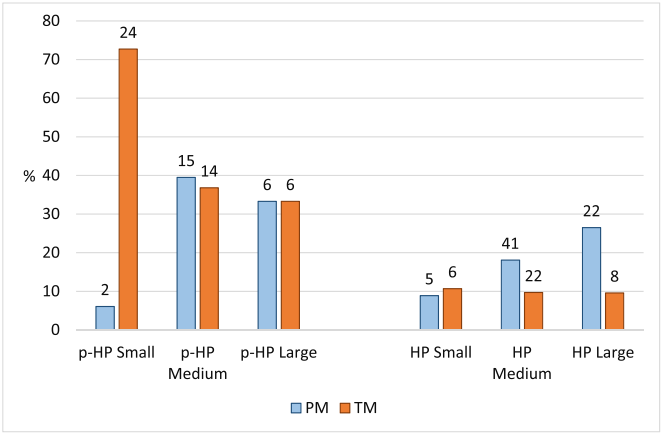


Fig. 8. Percussion mark (PM) and tooth mark (TM) frequencies on small, medium and large mammal long bone mid-shafts in the Howiesons Poort (HP) and post-Howiesons Poort (p-HP) layers at Klasies River. Data from Reynard (2022a).

and Avery, 2014]), with fore- and hindlimbs relatively evenly distributed (Cruz-Uribe and Klein, 1998; Armstrong and Avery, 2014). Given the general scarceness of crania in the Upper Member samples, raptors were probably not a significant contributor to the assemblages. In her survey of bone scatter in the Amboseli National Park in southern Kenya, Behrensmeyer (1983) documented the skeletal-part profiles of various types of bone assemblages. Fig. 10 shows three types she documented that we compared with our small mammal profiles. The 'Dispersed' bone assemblage represents passive accumulation of background 'bone scatter' across the landscape. It represents incremental natural deaths and is the most equitable skeletal distribution (Lyman, 1994, p. 190). The 'Predation patch' assemblage is a multiple predator-accumulated collection of bones confined to a specific geographical location over time. Here, skulls are rare, and axial remains common. In the hyena den, skulls are also rare and fore- and hindlimbs are common. The post-HP sample is most similar to that of the dispersed assemblage and the hyena den. This supports other lines of evidence indicating the significant contribution of carnivores to the post-HP assemblage. In contrast, the HP profile differs from all other non-human accumulated, actualistic assemblages – which likely reflects the effect of human agency. Furthermore, the relatively high frequency of burnt and butchered small mammal bone (Reynard, 2022a) supports the notion that people were the dominant bone accumulator for small mammals in the HP.

Carnivore/ungulate ratios are sometimes used to distinguish carnivore-dominated accumulations from anthropogenic ones, where higher ratios imply more carnivore contribution (e.g., Brain, 1981; Grayson and Delpech, 2003). Calculating this ratio from the K sample, Thackeray (1990) noted ratios for the Upper Member of 9.38 (post-HP), 3.85 (Late HP), 4.76 (Mid-HP) and 9.09 (Early HP). Here, we see that the post-HP and Early HP likely had greater carnivore contributions that the other periods. Thackeray (1990) has further argued that leopards would have been significant contributors to the assemblage; a reasonable suggestion given that an almost complete leopard skeleton was recovered in Cave 1 during the S–W excavations (Singer and Wymer, 1982).

6.3. *Transport decisions and processing strategies*

Understanding the dispersal and distribution of large mammal skeletal-part profiles is a useful means of inferring subsistence strategies. Studies of modern foragers show that the skulls of larger ungulates are more likely to be abandoned as foraging distances increase (O'Connell et al., 1988; Schoville and Otárola-Castillo, 2014). Similarly, the proportion of crania to mandibles may also be linked to transport distances with the lighter, marrow-containing mandible more likely to be brought back to the home-base than bulkier crania (Speth and Clark, 2006; Clark, 2011).

Skull bones dominate the HP and post-HP larger mammal skeletal profiles. Again, there may be taphonomic reasons for this. Crania in highly fragmented assemblages may be over-represented because they are relatively easy to identify and so could dominate even normalised element abundance metrics (Reynard et al., 2016b). However, given the fragmented nature of the entire KRM assemblage, by this logic, crania should dominate all layers of the site. In the deeper MSA II Lower layers, cranial elements are quite rare in the large mammal samples (Reynard, 2022a). In the highly fragmented HP assemblage from Sibudu, skull remains are also not common for large bovids (Clark, 2017) and large mammal crania are quite rare in the c. 77 ka Still Bay layers at Blombos Cave (Reynard and Henshilwood, 2019). If the abundance of cranial remains in the Upper Member is not a product of taphonomic or identifiability bias, it may suggest that larger herbivores were hunted relatively close to the site. This is supported by crania/mandible ratios which show that, in the HP, crania of larger mammals (size 3 and above) (NISP = 7) are more common than mandibles (NISP = 2). Similarly, in the post-HP large mammal crania (NISP = 8) are also more common than mandibles (NISP = 4).

Cut mark data is slim and, given the small sample sizes (of both

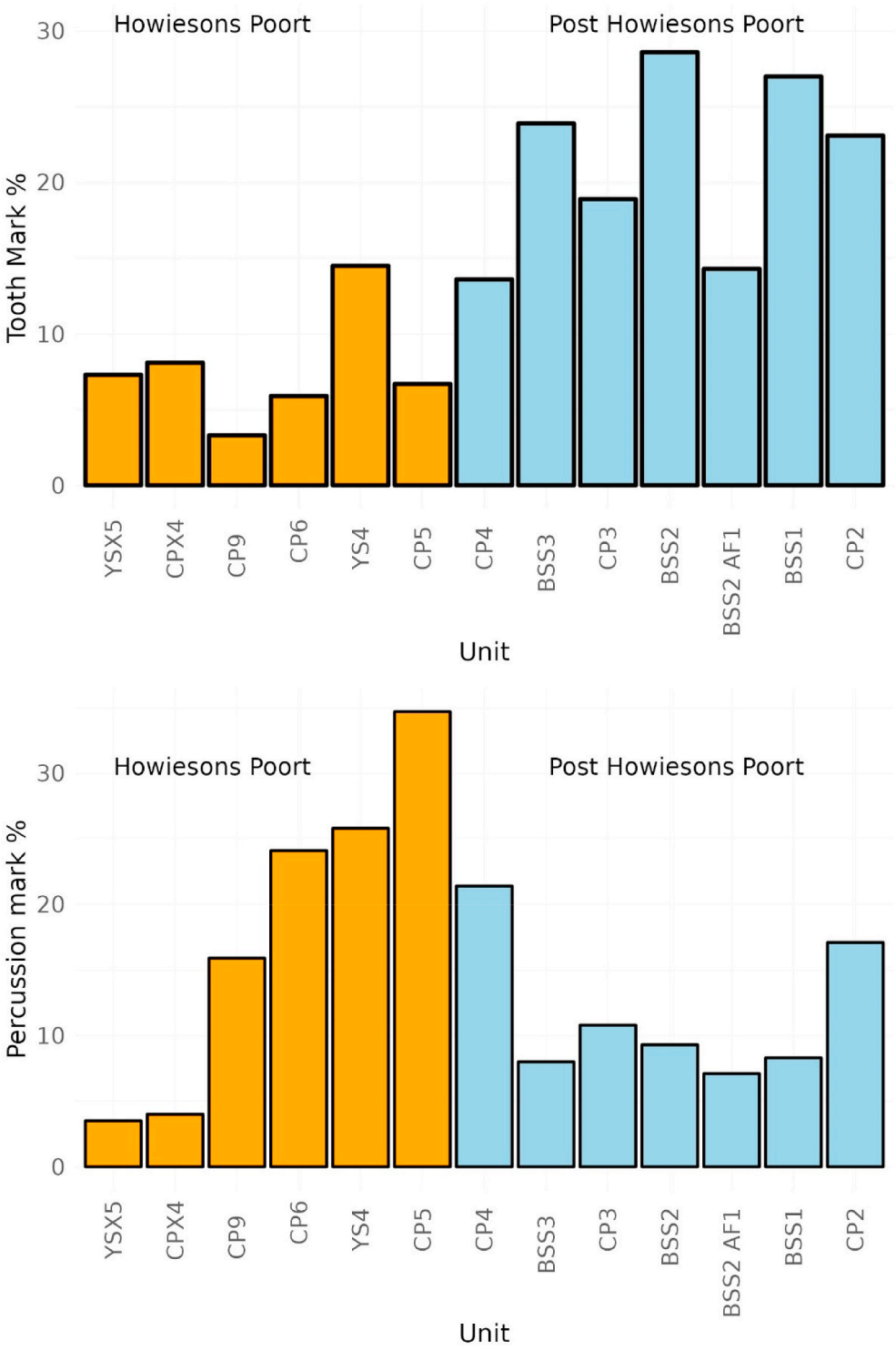
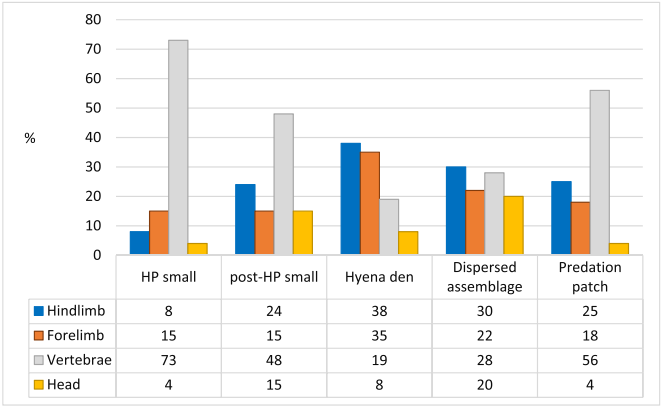


Fig. 9. Percussion marks and tooth mark frequencies per layer through the Howiesons Poort (HP) and post-HP sequence.

marks and elements), we must again emphasise caution in over-analysing any trends in the anthropogenic data. That said, cut mark frequencies may point to some specific processing activities in the Upper Member. In the Early HP, the fact that most cut marks are on unidentified long bone mid-shaft fragments may imply that filleting was common (Dominguez-Rodrigo, 1999). Cut marks are centred on axial remains in the Late HP pointing to disarticulation activities. In the post-HP, the relative prevalence of slice and scrape marks from a variety of mammal and bovid sizes on mostly distal limb long bone elements, may be indicative of filleting and skinning activities at the site (Binford, 1981; Dominguez-Rodrigo, 1999; Val and Mallye, 2011). In their experimental study using reindeer, Galan and Dominguez-Rodrigo (2013) show that skinning marks are common on the proximal portions of metapodia. Of the five cut-marked metapodia in the medium mammal post-HP sample, three of those are on proximal ends (Fig. 7). On the whole, however, cut marks on long bones in the post-HP are relatively evenly distributed between mid-shafts (n = 8; 11.4%) and epiphyses (n = 3; 9.6%).

As noted earlier, grease and fat may have been a key resource focus in the HP. Utility indices show an emphasis on marrow-extraction in the



	HP small	post-HP small	Hyena den	Dispersed assemblage	Predation patch
Hindlimb	8	24	38	30	25
Forelimb	15	15	35	22	18
Vertebrae	73	48	19	28	56
Head	4	15	8	20	4

Fig. 10. Skeletal-part frequencies for various types of bone accumulations. Hyena den, Dispersed assemblage & Predation patch data from Behrensmeyer (1983.

HP (Table 8), and frequencies of percussion marks increase significantly at this time (Table 6; Fig. 9). Fat was a limited resource in the Late Pleistocene but is a rich source of caloric energy (Speth and Spielmann, 1983). Long bone marrow would have been particularly desirable as a crucial and reliable source of fat (Bar-Oz and Munro, 2007). Based on ethnographic evidence, marrow-fat could also have been used to water-proof skins (Binford, 1978), as an aid to tanning (Leighton, 1995), and as fuel (Théry-Parisot et al., 2005). Combustion features and hearths dominate the HP, which could also be linked to the use of fat as fuel. However, recognising whether bone was used as fuel is challenging and other evidence of the use of bone fat as fuel (e.g., high frequencies of calcined bone) is lacking in our samples (Table 5; Costamagno, 2013). It should also be noted that high frequencies of burnt bone may also be associated with site maintenance activities such as the intentional discard of bone into hearths (Cain, 2005; Clark and Ligouis, 2010).

Experimental studies by Blasco et al. (2019) suggest that metapodia may have been significant sources of marrow-fat, and that these elements were likely used to store bone marrow for delayed consumption at the Middle Palaeolithic site of Qesem Cave in the Levant. Blumenschine and Madrigal (1993, p. 559) note that, while metacarpals are often the lowest ranked marrow bone, they may have been used as important sources of energy as stress increases in response to seasonal changes in forage quality and/or reproductive states. Incidentally, almost half (n = 31/63) of all long bones in the HP are metapodia, and they are more prevalent in larger, more marrow-bearing mammals (Fig. 5). They are also generally the most percussion-marked element (Fig. 7), so it is reasonable to suggest that, as at Qesem Cave, they might have been used as fat-storage instruments in the HP. However, Blasco et al. (2019) show that cut marks are relatively common on metapodia undergoing processing for marrow storage, while in our samples, these marks are rare. Furthermore, even in fragmented assemblages metapodia are easy to identify, so the abundance of metapodia in both the HP and post-HP samples may be related to identifiability bias.

6.4. *Palaeoenvironmental conditions*

We turn now to environmental conditions at KRM, and how data from the site can be used to infer the prevailing palaeoenvironment. Local marine data show significant environmental shifts from MIS 4 to 3. Cawthra et al. (2018) record stillstand to transgressive conditions for offshore deposits at 18 km east of Mossel Bay at 57.9 ka, which could mark the transition from MIS 4 to 3. Differences between shellfish taxonomy in the HP and post-HP assemblages also suggest changes in shore habitat in the MIS 4 and 3 (Langejans et al., 2017). In both the HP and post-HP, sea surface temperature (SST) may have been variable (Ziegler et al., 2013) but remained within the Algoa range, and more sandy substrates in an estuarine environment are indicated (Langejans et al., 2017). The alikreukel (*Turbo sarmarticus*) opercula in the HP are similar in size to the earliest MSA I layers at the site, with the post-HP opercula the largest of the opercula found in the sequence, and SSTs lower than in the HP phase (Langejans et al., 2017).

6.4.1. *Taphonomy and the palaeoenvironment*

The taphonomic conditions of the fauna may infer site formation processes and may be linked to prevailing environmental conditions at KRM. Darker, black or dark-grey layers are common in HP deposits and often represent combustion events (Goldberg et al., 2009). The stratigraphy in the Upper Member generally alternates between the lighter 'Yellow Sand' (YS) and darker 'Carbon Parting' (CP) layers representing geogenic and anthropogenic/biogenic-dominated deposits, respectively. Overall, CP layers dominate the HP deposits with YS layers becoming more common in the post-HP (Fig. 3). The YS layers are generally characterised by fewer artefacts and a relative abundance of micromammal remains (Singer and Wymer, 182). Spiral fracture patterns – which are prevalent in the HP – are also far less common in the YS-dominated post-HP (Table 4). This, and the relative dearth of burnt bone, suggest that these layers were deposited when occupations were less intense or frequent (Reynard, 2022a). Burnt bone is significantly more abundant in the CP (n = 850; 83.6%) compared to the YS layers (n = 216; 16.8%) and dominate the HP (Table 5). Micromorphological samples taken from early HP layers (including layer CPx4) show that the darker deposits here include fragments of shell, burned bone, fat-derived char, wood ash, charcoal, and charred seeds. This section of the sequence was likely a midden that contained dumped materials from hearths and food-related debris (Wurz et al., 2022, p. 13). The CP units are therefore probably associated with increased human activity and input resulting in locally trampled and reworked deposits.

Research suggests that sites in the southern Cape were usually more intensely occupied when the coast was closer (Gravel-Miguel et al., 2022; Reynard, 2022b), which may be what is reflected during the HP at KRM. The fact that deposits indicative of lower occupational intensity are more evident in the post-HP suggests that this period may be associated with more extensive marine regressions. While sea-levels likely sometimes regressed during glacial MIS 4 (the HP), given that MIS 3 was a variable stadial period, it is possible that lower sea-levels also occurred during the post-HP (cf. Cawthra et al., 2018). There is an increase in the relative abundance of *Donax* – a mollusc associated with sandy beaches – in the upper HP layers, suggesting that sandy beaches began dominating the Late HP coast (Thackeray, 1988). Thereafter, shellfish that prefer a sandy/muddy environment are more common in the post-HP than in any other period at KRM (Langejans et al., 2017). Furthermore, Cape dune mole rat is more common in the post-HP than the HP (Van Pletzen-Vos et al., 2019; Reynard and Wurz, 2020) suggesting the presence of dune sand. Coastal and barrier dunes in the southern Cape often form during sea-level highstands, becoming exposed during marine regressions (Bateman et al., 2011; Cawthra et al., 2020). While the precise nature of the KRM landscape during MIS 3 and 4 was likely complex, the depositional history of the Upper Member speaks to a changing coastal environment.

Manganese stained bone is extremely common in the Late HP/post-HP samples (87%), and rare in the Early HP (3.4%) (Table 7). This significant difference suggests that bone in the lower deposits may have undergone different diagenetic process to the later periods. Manganese-stained bone is generally associated with the occurrence of moisture and can be a result of microbial or bacterial activity, water saturation of the sediment or the presence of limestone dissolved by groundwater (McBride, 1994; López-González et al., 2006). The manganese stains on our sample are generally small 'spots', and Thackeray (Thackeray et al., 2005; Thackeray, 2016) suggests that manganese spots on bone may also be a result of lichen growth which proliferates in moist, cool and relatively dark conditions. The lack of severe or extensive manganese-coated bone means that water saturation was probably not significant at that

time. Water-logged bone would likely exhibit more severe manganese staining and other characteristics associated with water immersion (Cukrowska et al., 2005). Bone polish is also common in both the Late and post-HP samples. This could be linked to water abrasion (Bromage, 1984). Currently, water runoff over the cave 1A embankment at KRM after heavy rainfall is relatively common, so it is possible that, in the past, the site may have been affected by fluvial processes. That said, there is little indication of significant water flow through the site at that time, and other taphonomic agents (e.g., sand abrasion linked to increased dune activity) may also result in bone polish.

Evidence of pooling at the site may be linked to prevailing wetter conditions. The fact that manganese is rare in the Early HP suggests that pooling may not have impacted bone specimens during this period and may have only affected samples in the later periods of the Upper Member. Manganese-stained bones also suggest alternating wet and dry periods since both anoxic and oxygenated environments are necessary for the precipitation of manganese oxides (Dal Sasso et al., 2014; Hollund et al., 2018). One possibility is that highly laminated deposits, such as those found in the mid, Late and post-HP, relate to the downward flow of acidic water that preserved microlaminations but dissolved carbonates (Mentzer, 2023). On a broader scale, this could be linked to fluctuating environmental conditions during MIS 3 associated with the post-HP. Whatever the case, the presence of manganese-staining indicates the presence of moisture, which had a significant effect on the deposits during the later HP/post-HP.

6.4.2. Species abundance and the palaeoenvironment

The small sample size of identified taxa makes it challenging to draw palaeoecological inferences with confidence. However, if we compare our taxonomic data with that of the V (Van Pletzen-Vos et al., 2019) and K samples (Klein, 1976), we get a more reliable impression of the prevailing habitat in the Upper Member.

In the HP, larger mammals, such as hartebeest and the giant buffalo, are more common in the taphonomic sample (Table 9). The K and V samples also show an abundance of alcelaphines, eland and buffalo during this period suggesting an open environment dominated by grasses (Table 9; Reynard and Wurz, 2020). This aligns with $\delta^{13}C$ records indicating the occurrence of CAM or C4 photosynthetic modes during MIS 4 in the southern Cape (Braun et al., 2019; Strobel et al., 2022). However, the HP in the south-eastern Cape was probably not a stable environmental period, with evidence of both arid and wetter phases during MIS 4 (Ziegler et al., 2013; Simon et al., 2015; Quick et al., 2016). Unstable environmental conditions are also apparent in speleothem data from Crevice Cave and PP29 near Pinnacle Point, Mossel Bay between c.73 and 64 ka (Bar-Matthews et al., 2010; Braun et al., 2019). Both the K and V samples point to changing environmental conditions in the HP with the presence of browsers such as elephant and kudu and a dominance of eland in the Early HP, and grazers (e.g., hartebeest and wildebeest) in the later period (Klein, 1976; Van Pletzen-Vos et al., 2019).

In the post-HP, larger mammals are rare and small fauna dominate the taphonomic sample (Table 9). The larger ungulates present (buffalo, wildebeest and zebra) are grazers suggesting a grass-dominated landscape. Buffalo, *Hippotragus* and eland are also documented in the K and V samples indicating open environment dominated by grasslands (Klein, 1976; Van Pletzen-Vos et al., 2019). Generally, the Upper Member deposits show similar distributions of ungulates. The key difference in the Upper Member sequence is the smaller sample size in the post-HP compared to the HP. There is some evidence of wetlands in the post-HP with the occurrence of hippo, possible waterbuck and water mongoose in the K and V samples (Klein, 1976; Van Pletzen-Vos et al., 2019). One proposed scenario for the post-HP is a wetland-dominated landscape with barrier dunes – similar to the present-day Wilderness embayment near Knysna on the southern coast – but with a relatively distant coastline (Bateman et al., 2011; Wurz et al., 2018; Reynard and Wurz, 2020). It is tempting to link evidence of wetlands with the prevalence of manganese-stained bone in the post-HP, but this association may be tenuous at best. In any case, given the small sizes of all the KRM samples, it is challenging to infer specific environmental conditions during the post-HP based on the large mammal data. Thus, while there is good data on fluctuating environmental conditions during MIS 3, the KRM large mammal data cannot be used to infer when these changes were evident at the site.

Compared to other MIS 4 and 3 sites in the southern Cape, ungulate richness is relatively high in the Upper Member, and at KRM, it may be associated with expanding grasslands (Reynard and Wurz, 2020). Generally, increasing ungulate richness is tied to increasing precipitation and moisture availability. However, this is only evident when MAP is less than c. 780 mm/yr (Thackeray, 1980; Faith, 2013). At KRM, MAP is about 1000 mm/yr (van Wijk et al., 2017), so it is therefore possible that higher ungulate richness at KRM suggests a dryer environment (see Reynard and Wurz, 2020 for a detailed discussion on this).

6.5. Subsistence behaviour, technology and environmental change

Given the small sample sizes in the post-HP, it is challenging to compare subsistence strategies between the HP and post-HP. There is good evidence that marrow-extraction was an important subsistence strategy in the HP. However, although there is some evidence of both marrow-extraction and meat-drying strategies in the post-HP, the effects of bone density-mediated destruction make these problematic assertions. It is likely that occupational intensity was higher in the HP than in the post-HP (Reynard, 2022a). Broadly similar quantities of lithics occur in the two HP phases with the HP assemblage significantly larger than the post-HP. The phases of the HP are similar in that backed artefacts and a small blade technology occur, but differences in the raw material exploitation and blank production have been noted.

A key question is whether environmental conditions drove changes in subsistence behaviour. To test whether these changes correspond to environmental conditions, we need local, specific environmental data. Micromammal remains are useful proxies for local environments (Avery, 2021). While large mammals reflect broader, regional environments and can be relatively resilient to local-scale environmental change (Reynard, 2021), micromammals are more sensitive to confined, site-specific environmental fluctuations (Avery, 2007). Interestingly, at KRM, micromammal and large mammal data often do not correlate. An increase in browser/mixed-feeder ungulates from MSA I to MSA II suggest a more closed environment, while micromammal analyses show an increase in open grassland over the same period (Nel et al., 2018). Again, this is likely because of scaling, and the resultant variation in territorial ranges between very small and large mammals (Nel et al., 2018, p. 12).

Avery's (1987) micromammal data from KRM corresponds well with other micromammal data for the cave 1 deposits (Nel et al., 2018; Maringa, 2020). It is therefore likely a reliable proxy for local, site-specific environmental conditions during the HP and post-HP. Species that represent open vegetation such as Saunders' vlei rat (*Otomys saundersiae*) and the Hottentot golden mole (*Amblysomus hottentotus*) are common through the KRM sequence but peak in excavation unit BSS5 in the early post-HP. Conversely, species associated with closed environments (e.g., the striped mouse [*Rhabdomys pumilio*] and the laminate vlei rat [*Otomys laminatus*]) are less common then. Fig. 11 shows the Shannon-Weiner index for heterogeneity calculated by Margaret Avery for all the HP and post-HP micromammal samples excavated by Deacon (Avery, 1987). Here, we see a significant drop around samples 15 and 16 (BSS5 and BS units, respectively, in square E50), indicating a major change in environmental conditions at the site then (Fig. 11). Avery (1987) argued that this dip corresponded to MIS 5b, but more recent dates suggest it reflects the shift from MIS 4 to 3 (Table 1).

Interestingly, although our sample does not include units BSS5 and BS, percussion mark frequencies begin to drop significantly in unit CP4 – the layer just above BSS5 and BS (Fig. 11). Fig. 12 shows that percussion mark and trampling mark frequencies peak in the HP, decreasing

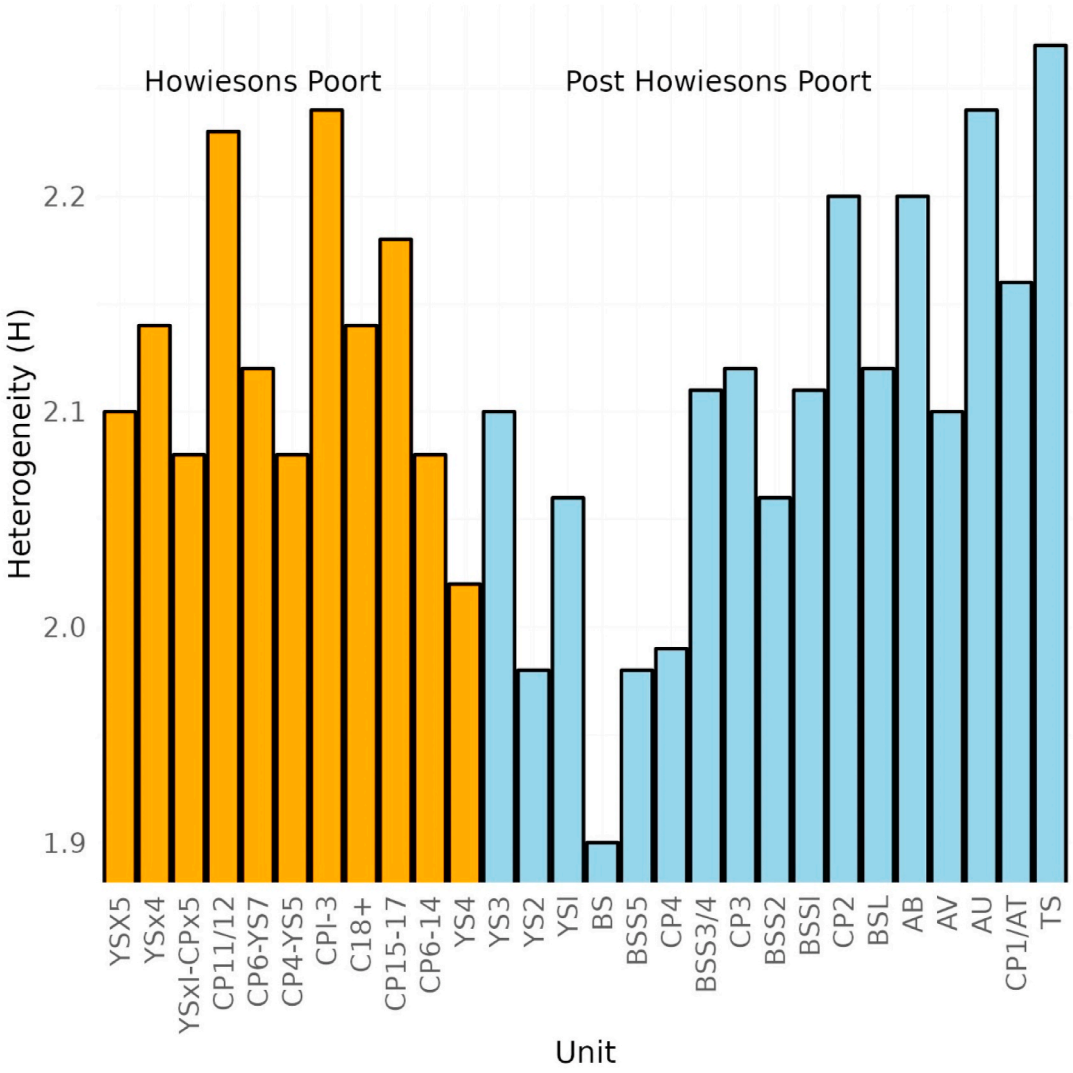


Fig. 11. Shannon-Weiner index for heterogeneity (H) in micromammals for all Howiesons Poort (HP) and post-HP layers at Klasies River (data from Avery, 1987).

significantly in the post-HP. Previous research has shown that trampling marks may be a useful proxy for human occupational intensity (Reynard and Henshilwood, 2018; Reynard, 2022b). Both humans and ungulates can trample bone but in southern African coastal rockshelters trampling marks were likely the result of human activity for two key reasons. Firstly, while ungulates may seek shelter in rock shelters for short stays, most coprolites recovered from Pleistocene caves in the subcontinent belong to carnivores (Zipfel et al., 2023) with many associated with hyena dens (e.g., Brain, 1981; Klein et al., 1991; Rector and Reed, 2010). Carnivores were thus significant occupiers of southern African rockshelters (Brain, 1981), so it is therefore unlikely that ungulates would have also occupied these spaces. At KRM, an almost complete leopard skeleton was recovered during the Wymer excavations (Singer and Wymer, 1982), and it has been argued that leopards often denned at the site (Thackeray, 1990). Secondly, geoarchaeological evidence shows that trampling generally corresponds well with human activities in southern Cape rockshelters (Karkanas and Goldberg, 2010; Haaland et al., 2021). At many sites, a dominance of anthropogenic BSM and anthropogenic artefacts occur in layers with high frequencies of trampled bone (Reynard et al., 2016a; Reynard, 2022b). This is particularly true at KRM where micromorphological analyses indicate that trampled sediment occurs in layers associated with hearths, middening and other evidence of increased human activity (Wurz et al., 2022).

The inverse association between micromammal heterogeneity and percussion mark frequencies in the Upper Member suggests that the onset of MIS 3 may be linked to changes in subsistence behaviour (Fig. 12). At the same time, Wurz (2000) and Villa et al. (2010) note variations in technology through the sequence, and noticeable shifts in raw material procurement (Table 10). From the middle of the HP sequence, flake production increases, and the size of blades becomes larger and less regular in the Late HP. However, the fact that this environmental shift reflected in BSS5 and BS occurs *after* the onset of post-HP type lithics, suggests no correlation between the two. That said, the lower post-HP YS and BS layers are low occupation density accumulations, so larger sample sizes may highlight differences not presently observable.

The taphonomic data suggest an interesting relationship between faunal patterns and the technological shift from the HP to post-HP. Besides KRM, Rose Cottage Cave also shows a gradual shift in technology through the HP and post-HP (Soriano et al., 2007; Villa et al., 2010). Villa et al. (2010) argue that it is unlikely that this trend is a result of demographic factors such as population decline. Instead, they posit that the end of the HP may relate to changes in environmental conditions or subsistence behaviour. Our data show a slight lag between the onset of post-HP technology and changes in the environment at KRM (Fig. 11). This could represent a delay effect between the onset of interstadial climatic changes and its environmental expression. However, as noted earlier, micromammals are relatively sensitive to climatic variation so it

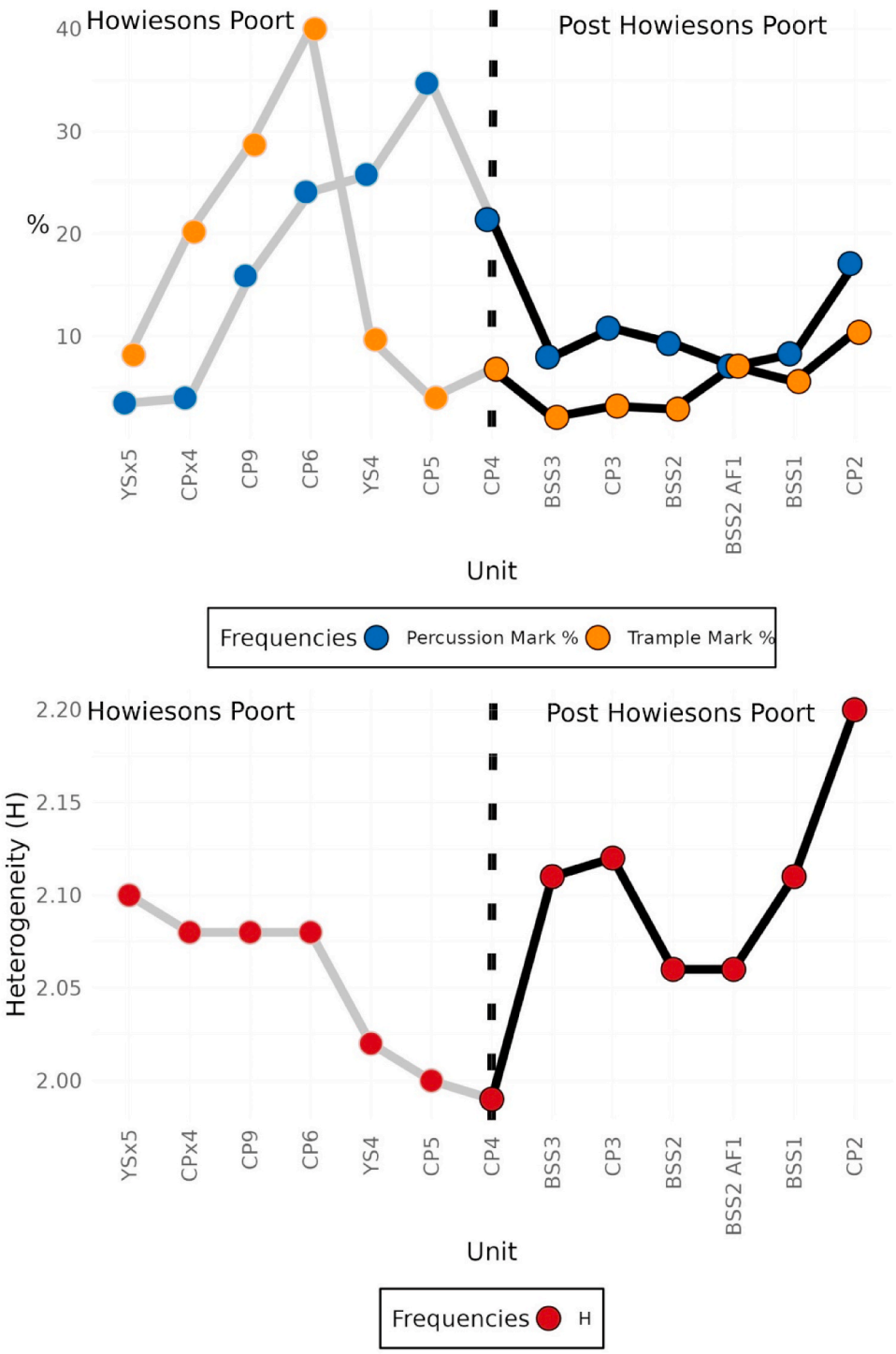


Fig. 12. Percussion mark and trampling mark frequencies (top) compared to micromammal heterogeneity (bottom) in the Howiesons Poort (HP) and post-HP. Black line represents the HP, grey line represents the post-HP. Dotted line represents the HP/post-HP transition. Heterogeneity data from Avery (1987).

seems unlikely that this lag would be extensive. Thus, the corresponding shift in taphonomic patterns and micromammal diversity suggests a connection between changing environmental conditions and subsistence behaviour.

Changes in technology in the Upper Member may be related to shifts in subsistence strategies linked to the (re)introduction and/or development of weaponry. In the Early HP, a bone point with internal fractures related to high-velocity longitudinal impact partially covered with a hard, black residue containing mineral and organic compounds (interpreted as poison residue by Lombard. 2020) was found in the Early HP (Bradfield et al., 2020). Given its close morphological similarity with Historical and traditional San bone arrow heads, the most parsimonious interpretation is that it is an arrowhead. This, and other evidence of arrow tips (e.g. Backwell et al., 2008, 2018; Lombard, 2011), point to the use of bow hunting in the HP at KRM and Sibudu, in addition to other weapon types such as javelins (Bradfield et al., 2019). Based on tip cross-sectional area metrics from a number of sites, Lombard (2020, 2021) argues that HP hunters tended to prefer combining bow and javelin hunting. The larger artefacts from the post-HP suggests a return to the handheld stabbing or thrusting spear as weapon choice (Lombard,

Table 10
Summary of subsistence, technological and environmental trends in the Howiesons Poort (HP) and post-HP at Klasies River.

Period	Subsistence patterns	Technology	Occupational intensity	Environment
Post-HP	Focus on meat-drying & marrow-extraction? Filleting, skinning,	Larger lithics, Blades dominate but different to HP type, Some unifacial points, Quartzite dominated Thrusting spear use?	Lowest occupations: Highest carnivore tooth marks & acid-etched frequencies, Lowest trampled bone frequencies, High carnivore/ungulate ratios	More small fauna, Grazers occur, C3 plant dominance, Warmer with cooler oscillations, Drier
Late HP	Focus on marrow-extraction, Significant increased percussion marks, Disarticulation, Skinning	Small blade and flake technology, Quartzite raw material prominent	High occupations: Carnivore activity rare, Highest frequencies of trampled bone, High frequency of burnt bone	Grazer dominance, Open environment, Humid/drier fluctuations? Cool becoming warmer?
Middle HP	N/A	Small blade technology with the addition of some flake technology, increase of quartz and silcrete raw material, Notches are more prevalent	High occupations? (Low carnivore/ungulate ratios)	Browser/grazer presence, Drier becoming more humid? Cooler/warmer fluctuations
Early HP	Focus on marrow-extraction, Filleting?	Small blade technology, Quartzite dominated, Evidence of bow-and-arrow use	Low to moderate occupations: High carnivore/ungulate ratios, Relatively high frequencies of trampling marks in earliest layer	Presence of browsers (more closed environment), More humid? Cooler temperatures

2021).

6.6. Comparison to other MIS 4/3 sites

Other sites dated to MIS 4/3 also reveal a complex relationship between environmental change and subsistence behaviour. Changes in subsistence behaviour from the early to late HP at Klipdrift Shelter, about 400 km west of KRM in the southern Cape, is evidently related to shifts in occupational intensity driven by environmental conditions (Reynard et al., 2016a). At Klein Kliphuis, in the south-western Cape, there appears to be coherent changes in occupational intensity, technology and woody taxa composition at the MIS 4/3 transition, perhaps related to a reduced availability of humidity in the post-HP (Mackay and Cartwright, 2023). At Diepkloof rockshelter, a near-coastal site in the south-western Cape, the lower Intermediate HP here (unit OB5) is dated to MIS 4, with the late and post-HP deposited during MIS 3 (Tribolo et al., 2013 but see Jacobs et al., 2008, Feathers, 2015; Jacobs and Roberts, 2017 for alternative dates). Skinning marks on carnivore remains in the HP and Still Bay layers at this site suggests that people were exploiting these animals for pelts (Val et al., 2020). Interestingly, while there is little significant change in mammal species through the sequence, there is noticeable increase in shellfish abundance and seal remains during MIS 4 and 3 (Steele and Klein, 2013). This is surprising because, given glacial eustatic sea-level expectations, it is assumed the coastline was significantly further away at this time. If we discount site formation or taphonomic reasons, the presence of shellfish and seal in these deposits suggest that coastal foraging may have been an important aspect of subsistence behaviour during the HP.

Sibudu has a particularly sizeable HP and post-HP assemblage with marked changes in the environment between these periods linked to the MIS 4/3 transition (Clark, 2011). The HP here is dominated by forest-loving species such as blue duiker (*Philantomba monticola*) and vervet monkey (*Cercopithecus pygerythrus*) with post-HP species (e.g., equids and buffalo) reflecting more open, grassier environments (Clark and Plug, 2008; Clark, 2011). Evidence of subsistence intensification in the HP layers, in contrast to the post-HP, suggests that demographic and/or environmental stress may have played a role in differences in subsistence strategies between these periods at Sibudu (Clark, 2011). However, as Clark (2013) notes, layer-specific diachronic analyses of fauna through the HP and post-HP sequences indicate a gradual change in local environment and procurement strategies. The early MIS 3 sites from the summer rainfall zone were under a different climatic control than at KRM though, and in general, there are more sites from the early part of MIS 3 in this region than in the southern Cape (Mitchell, 2008).

7. Conclusion

Sites with substantial deposits such as KRM offer a unique opportunity to explore human-animal interactions in the Late Pleistocene in a more detailed way. At KRM, the MIS 4 and 3 are reflected in the Early HP, Late HP and post-HP technocomplexes, and encompass significant environmental and behavioural changes. In this paper, we report on taphonomic analyses of samples of fauna from the HP and post-HP at KRM, and use it to explore links between subsistence behaviour and environmental change. Our results indicate that humans were the dominant contributor of fauna in both assemblages. The abundance of zoogenic marks on small fauna, and the similarities between our sample and actualistic assemblages, suggests that carnivores were significant bone accumulators in the post-HP. This, and other data, suggest that the post-HP was less intensely occupied than the HP.

Taphonomic data show that subsistence patterns and site formation processes differed between the HP and post-HP. While cut marks are slightly more prevalent in the post-HP, burnt bone, spiral fractures and percussion marks are significantly more common in the HP than the post-HP. Post-depositional taphonomic data suggest different site formation processes between phases in the Upper Member. Significant difference in manganese-stained bone frequencies suggests the Late and post-HP were more impacted by moisture than the Early HP. Although not severe, weathering is prevalent throughout the Upper Member – probably due to the fact that cave 1A is a partially-covered rockshelter where deposits were more exposed than in cave 1.

Larger mammal skeletal-part patterns in both the HP and post-HP are dominated by cranial remains, which may either be a result of taphonomic bias in small samples, or it implies that larger prey were hunted relatively close to the site. Analyses of carcass-part utility suggests that people focused on marrow-extraction in the HP. This is supported by the relatively high percussion mark frequencies in the Late HP sample. In the post-HP, the sample is too small (and bone density-mediated attrition may be too severe) to decipher subsistence patterns with confidence. There is some evidence that both marrow-extraction and meat-drying may have occurred but this must be viewed with caution.

The large mammal fauna data show no significant difference in herbivore abundance between the HP and post-HP. Identified species in our taphonomic samples from the Upper Member, and in the K and V assemblages suggest a dominance of grasslands and open environments in MIS 4 and 3. However, the presence of browsers in the lower layers of the HP in the K sample may point to a slightly more closed environment

in the Early HP. In comparing Avery's (1987) micromammal data with our analyses, we note that major environmental changes occurred at KRM between units BSS5 and BS which are probably linked to the MIS 4/3 transition. Based on the timing of technological developments, this transition appears to have occurred *after* a shift to the post-HP. However, there appears to be a close link between the onset of MIS 3 and changes in anthropogenic patterns at KRM, suggesting that the environment may have played a role in driving shifts in subsistence strategies. The interesting relationships between behaviour and the environment posited by these data warrant further investigation with larger samples of fauna. Currently, our small sample sizes and the lack of middle HP data means our understanding of trends in subsistence strategies in a significant portion of MIS 4, are limited. Future studies would need to explore these patterns in more depth.

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CRediT authorship contribution statement

Jerome P. Reynard: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Formal analysis, Conceptualization. **Alexandra Pearson:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Pamela Akuku:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Sarah Wurz:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

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.

Data availability

Data will be made available on request.

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