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Climatic controls on Later Stone Age human adaptation in Africa's southern Cape

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Abstract

Africa’s southern Cape is a key region for the evolution of our species, with early symbolic systems, marine faunal exploitation, and episodic production of microlithic stone tools taken as evidence for the appearance of distinctively complex human behavior. However, the temporally discontinuous nature of this evidence precludes ready assumptions of intrinsic adaptive benefit, and has encouraged diverse explanations for the occurrence of these behaviors, in terms of regional demographic, social and ecological conditions. Here, we present a new high-resolution multi-proxy record of environmental change that indicates that faunal exploitation patterns and lithic technologies track climatic variation across the last 22,300 years in the southern Cape. Conditions during the Last Glacial Maximum and deglaciation were humid, and zooarchaeological data indicate high foraging returns. By contrast, the Holocene is characterized by much drier conditions and a degraded resource base. Critically, we demonstrate that systems for technological delivery – or provisioning – were responsive to changing humidity and environmental productivity. However, in contrast to prevailing models, bladelet-rich microlithic technologies were deployed under conditions of high foraging returns and abandoned in response to increased aridity and less productive subsistence environments. This suggests that posited links between microlithic technologies and subsistence risk are not universal, and the behavioral sophistication of human populations is reflected in their adaptive flexibility rather than in the use of specific technological systems.

Keywords: paleoclimate; paleoecology; rock hyrax middens; microlithic; macrofauna; Boomplaas Cave

Introduction

South Africa's southern coastal margin is a key region for the evolution and development of our species (Ambrose, 2002; Ambrose and Lorenz, 1990; Brown et al., 2012; Henshilwood et al., 2004a; Henshilwood et al., 2002; Marean, 2010; Powell et al., 2009). The southern Cape archaeological record has reframed the debate about the evolution of human behavior, providing early examples of engravings, ornaments, heat treatment of tool-stone and the focussed consumption of marine resources (Delagnes et al., 2016; Henshilwood et al., 2004b; Henshilwood et al., 2002; Henshilwood et al., 2014; Marean, 2014). The region also exhibits regular technological turnover through the last 100,000 years, with the intermittent production of bladelets, bifacial points and backed artefacts and the use of fine-grained rock, interspersed with periods lacking regular retouched flake forms and dominated by locally available rocks such as quartzite and quartz (Deacon, 1984; Wilkins et al., 2017). The links between these variable technological and subsistence records and their environmental context – necessary to arguments about the evolution of human adaptation – remain surprisingly unclear (Deacon, 1982; Roberts et al., 2016). This reflects the region's particular climatic dynamism (Chase and Meadows, 2007) coupled with disagreement concerning the interpretation of its paleoenvironmental archives (e.g. Chase and Meadows, 2007; Deacon and Lancaster, 1988; Faith, 2013b; Marean et al., 2014).

In this paper, we focus on the Later Stone Age record in the southern Cape, for which - in contrast with the Middle Stone Age - high resolution environmental and archaeological data are now available. We explore the strength of coupling between environments, subsistence behavior and lithic technology over the last 22,300 years to understand whether, and how closely, human behavior tracked environmental change. Spanning the transition from the Last Glacial Maximum (LGM; 26.5-19 ka; Clark et al., 2009) to the Holocene (11.7 ka to present Lowe et al., 2008), and episodes of the use of bladelet-rich technological systems, our data also have a bearing on broader debates about the role of what are often termed 'microlithic' technologies in issues of human adaptation and expansion.

Later Stone Age environments and archaeology in the southern Cape

Influenced by both temperate and tropical climate systems (Figure 1), long-term climate change in the southern Cape is characterized by significant and often abrupt fluctuations (Bard and Rickaby, 2009; Chase et al., 2013; Chase and Meadows, 2007; Heaton et al., 1986; Quick et al., 2015; Quick et al., 2016; Talma and Vogel, 1992). Existing evidence indicates that during the Holocene the relative influences of the two dominant synoptic scale moisture-bearing systems – 1) the southern westerly storm track, which expands/shifts northward in the winter, and 2) the tropical easterly flow, which transports moisture from the Indian Ocean during the summer – have varied significantly (Chase et al., 2013; Chase et al., 2015b). However, there is little detailed paleoenvironmental evidence pre-dating the Holocene (Carr et al., 2016b; Chase and Meadows, 2007), and as a result there are contradictory opinions concerning conditions since the LGM (Chase and Meadows, 2007; Deacon and Lancaster, 1988; Faith, 2013b; Kohfeld et al., 2013; Partridge et al., 1999; Partridge et al., 2004; Sime et al., 2013; Stone, 2014), to the extent that some studies conclude that the region was exceptionally "harsh" and arid during the LGM (Deacon and Lancaster, 1988; Scholtz, 1986), while others infer greater humidity and highly productive terrestrial environments (e.g. Faith, 2013b; Parkington et al., 2000). This uncertainty has fundamentally hindered our understanding of past climate dynamics in the region, and, by extension, the impact of past climate change on hunter-gatherer adaptive and subsistence strategies during both the Later and Middle Stone Age.

In the southern Cape, the Later Stone Age archaeological sequence is typically divided into several industries or technocomplexes: early Later Stone Age (ELSA ~<40-24 cal kBP), Robberg (~24-12 cal kBP), Oakhurst (~12-8 cal kBP) and Wilton (~8-2 cal kBP), followed by the arrival of Khoikhoi herders in the last 2000 years (Deacon et al., 1984; Deacon, 1978; Lombard et al., 2012; Mitchell, 1988). The ELSA is associated with the production of small flakes, often through bipolar reduction of cores, though it otherwise lacks unifying characteristics and has been described as a period of technological heterogeneity (Mitchell, 1988; Wadley, 1993). The Robberg presents more coherent characteristics, including the production of large numbers of bladelets (small, elongate flakes usually less than 24 mm long) produced both from dedicated bladelet cores and from those worked by bipolar reduction (Mitchell, 1988). The Robberg also sees more concentrated, if episodic, use of fine-grained rocks such as a silcrete and chert than the preceding or subsequent phases (Deacon, 1978; Deacon, 1982). The Oakhurst (or Albany) is typified by fewer bladelets, larger flakes, a range of scraper forms and declining use of fine-grained rock, while the Wilton features both scrapers and backed artefacts and highly variable patterns of raw material use (Deacon, 1972; Deacon, 1978; Lombard et al., 2012). While these units are coarse and mask considerable variation, they provide a useful heuristic for discussing broad patterns in technological change across the later LSA.

Consistent with the imprecise meaning of the term (Pargeter, 2016), the ELSA, Robberg and Wilton have all been described as ‘microlithic’ (Bousman, 2005; Deacon, 1984; Mitchell, 1988; Wadley, 1993), but based on different characteristics – small flakes in the case of the ELSA, bladelets in the case of the Robberg and backed artefacts in the Wilton (Lombard et al., 2012). The advent of dedicated bladelet production in particular – as characterizes the Robberg – is argued to have presented humans with a significant adaptive advantage during our evolution and dispersal (Ambrose, 2002; Bar-Yosef and Kuhn, 1999; Clarkson et al., 2009; Foley and Lahr, 2003). Some researchers have linked an emphasis on bladelet production with responses to heightened subsistence risk associated with low or declining subsistence resource productivity (Elston and Brantingham, 2002; Petraglia et al., 2009) (for discussion of the risk concept used here see Bamforth and Bleed, 1997). Others have suggested that bladelet production provided benefits under conditions of high residential mobility (Goebel, 2002; Neeley, 2002). Both explanations – increased subsistence risk and increased mobility – have been posited for bladelet-rich systems in southern Africa during globally cooler conditions (Ambrose, 2002; Grosjean et al., 2003; McCall, 2007; McCall and Thomas, 2012; Mellars, 2006; Mitchell, 2000). The Robberg specifically has been associated with increased residential mobility in response to inferred diminishing resource density (Ambrose, 2002; Mitchell, 2000), and has been explained as a risk-dampening response to resource stress (Mackay, 2009). Other researchers, however, have suggested that any tracking between LSA technological systems and paleoenvironmental variation was relatively weak, and occurred only at the broadest scale of environmental change (e.g. Deacon, 1982). The reality of coupling between technology, subsistence conditions and environmental change in this period is thus contested, and with it the viability of high-order explanations for the behavioral significance of artefacts such as bladelets.

Sites and regional setting

To explore the relationship between environmental change and human activities and technology, we focus on sites from the Swartberg mountains of South Africa’s southern Cape, one of the major ranges in the east-west axis of the Cape Fold Mountains (Figure 1). From Seweweekspoort, a deep transversal valley in the central Swartberg mountains, a series of rock hyrax (*Procavia capensis*) middens – stratified accumulations of dried urine and fecal pellets (see Chase et al., 2012) – were identified, and six middens from two sites, Seweweekspoort-1 (SWP-1; 33.3668°S, 21.4144°E) and Seweweekspoort-3 (SWP-3; 33.4092°S, 21.4031°), were analysed for this study. SWP-1 is located on a west-facing cliff on the northern slope of the pass (Figure 1). The SWP-1 middens were taken from several locations within the same larger shelter, formed by a ~100 m overhanging cliff. SWP-3 is located on a low eastern cliff in the central section of the valley near the valley bottom, and experiences a more humid microclimate relative to the exposed position of SWP-1.

<insert Figure 1>

The SWP-1 site is located in the North Swartberg Sandstone Fynbos, but less than a kilometre to the north is the Matjiesfontein Shale Renosterveld (Mucina and Rutherford, 2006). The former, depending on altitude and aspect, is predominantly asteraceous, proteoid and restioid fynbos, while the latter is dominated by asteraceous elements, particularly *Elytropappus rhinocerotis*, *Eriocephalus* sp. and *Euryops* sp., and by an increasing number of succulents, primarily from the Crassulaceae family (Mucina and Rutherford, 2006). At SWP-1, these vegetation types inter-digitate to some extent, with the broad west-facing drainage just north of the site supporting more hydrophilic taxa, such as *Protea*. The north-facing rock shelves directly adjacent to the site maintain only shallow soils and a dominance of succulents. Grasses in the region are a mixture of C_3 (e.g., *Erharta*) and C_4 (e.g., *Aristida*, *Stipagrostis*) varieties (http://sibis.sanbi.org/faces/DataSources.jsp; Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003). SWP-3 is located in the South Swartberg Sandstone Fynbos, which at the site is primarily proteoid in character. In addition, there are numerous arboreal/Cape thicket elements (e.g., *Podocarpus*, Celastraceae, *Dodonaea*, *Searsia*, *Euclea*, Oleaceae) associated with drainages and the nearby riparian zones of the valley bottom.

The Seweweekspoort sites are located 70 km west of the well-stratified late Pleistocene / Holocene archaeological site of Boomplaas Cave. This site is also situated on the flanks of the Swartberg and occupies a very similar climatic regime, making it ideal for exploring linkages between climate, environment, subsistence and technology at high temporal resolution. Located on the southern flanks of the Swartberg range overlooking the Cango Valley, Boomplaas Cave was excavated by Hilary Deacon in the 1970s (Deacon, 1979). The excavated sediments were divided into a series of members, some of which were subdivided into units. The site is positioned within a transitional shrubland whose component species vary as a function of temperature and moisture gradients moving upslope from the floor of the valley (Vlok and Schutte-Vlok, 2010). The lowlands to the south are characterized by renosterveld habitats, which give way to fynbos vegetation along the slopes of the Swartberg. Along watercourses and ravines in the Cango Valley are more densely wooded habitats that include sweet thorn trees (*Vachellia* (*Acacia) karroo*) and ironwood (*Olea* spp.) among others (Moffett and Deacon, 1977). As is also the case at Seweweekspoort, Boomplaas today receives contributions of both winter and summer rainfall (Figure 1). Thus, the limited grasses that do occur in the area today include a mixture of both C_3 and C_4 species.

Materials and methods

Rock hyrax middens accumulate over thousands of years and preserve continuous records of past climate change (Chase et al., 2012). The six middens from Seweweekspoort sites SWP-1 and SWP-3 were selected for analysis because they are composed almost entirely of hyraceum (no visible fecal pellets). Our experience suggests that such middens have superior stratigraphic integrity compared to more pellet-rich middens. Representative portions of the middens were processed as described in Chase et al. (2013; 2012). Radiocarbon age determinations (*n*=36) were processed at the ^{14}CHRONO Centre, Queen's University Belfast using accelerator mass spectrometry (AMS) (Supplementary Online Material [SOM] Figure S1; Table S1). The radiocarbon ages were corrected for isotope fractionation using the AMS measured δ^{13}C and calibrated using the SHCal13 calibration data (Hogg et al., 2013). The Bacon 3.0.3 software package (Blaauw and Christen, 2011) was used to generate all age-depth models (SOM Figure S1). Results indicate that these sequences continuously span the last 22,300 years.

The fossil pollen content of 82 adjacent, contiguous pollen samples were prepared with standard physical (600 µm sieving and decanting) and chemical (HCl, KOH, HF and acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed sample to estimate pollen concentrations (Stockmarr, 1971). A minimum pollen sum of 400 grains was counted at a magnification of ×400 under a light microscope, and identified with the help of the literature (Scott, 1982; van Zinderen Bakker, 1953, 1956; van Zinderen Bakker and Coetzee, 1959), and photographic and slide reference collections at the Universities of the Free State, Cape Town, and Montpellier.

The bulk stable nitrogen (^{15}N) and carbon (^{13}C) isotope contents of 767 overlapping hyraceum samples were measured at the Department of Archaeology, University of Cape Town following Chase et al. (2010; 2009; 2011; 2012), with contiguous/overlapping samples obtained from two series of offset 1 mm holes. For the stable isotope analyses, the standard deviation derived from replicate analyses of homogeneous material was better than 0.2‰ for both nitrogen and carbon. Nitrogen isotope results are expressed relative to atmospheric nitrogen (SOM Figure S2). Carbon isotope results are expressed relative to Vienna PDB (SOM Figure S3).

Stable isotope results from the different Seweweekspoort rock hyrax middens were combined into a single aggregate record using Local Regression (LOESS) curve fitting of the combined datasets (SOM Figures S2 and S3). As individual middens under the same climate regime may exhibit differences in their isotopic records due to microclimatic influences on individual foraging ranges (i.e., baseline $\delta^{15}N$ variability), we have adjusted the $\delta^{15}N$ to account for these differences prior to LOESS curve fitting. Using the SWP-1-1 and SWP-1-4b records as a datum, an estimated offset of 1.5‰ was added to the $\delta^{15}N$ data from the SWP-3-1 to compensate for the more humid microclimate in which the midden was found, and 0.5‰ and 1‰ were added to SWP-1-5 and SWP-1-2a respectively to account for their more exposed positions.

The carbon isotopic composition of the hyraceum is representative of vegetation around a midden site (Carr et al., 2016a) and provides information on 1) the relative contribution of C_3, C_4 and CAM plants (Smith, 1972) to the animals' diet, and 2) variations in plant water-use efficiency (WUE) as a function of climate (Ehleringer and Cooper, 1988; Farquhar et al., 1989; Farquhar and Richards, 1984; Pate, 2001). Throughout the broader region, the distribution of C_3 and C_4 grasses tracks the proportion of winter versus summer rainfall (Vogel, 1978). As mentioned, at Seweweekspoort today, grasses are a mosaic of C_3 and C_4 varieties (Rutherford et al., 2012; Rutherford et al., 2003; SANBI, 2003), and where aspect and soil depth limit soil water content, CAM plants become increasingly abundant. As C_3 plants are depleted in ^{13}C compared with most CAM and all C_4 plants, higher $\delta^{13}C$ values indicate more abundant warm season (C_4) grasses and/or succulent plants (CAM), and generally warmer/more arid conditions.

Hyraceum $\delta^{15}N$ is an indicator of changes in ecosystem water-availability (Carr et al., 2016a; Chase et al., 2013; Chase et al., 2015b; Chase et al., 2009; Chase et al., 2011). A positive relationship exists between aridity and $\delta^{15}N$ in soils, plants and herbivores, with drier conditions correlating with enriched $\delta^{15}N$ (Carr et al., 2016a), most likely as a result of denitrification processes in arid/semi-arid soils (Handley et al., 1999; Handley et al., 1994; Hartman, 2011; Heaton, 1987; Murphy and Bowman, 2006, 2009; Wang et al., 2010). In the hyraceum samples, the narrowly defined feeding range of the hyraxes (<60 m; Sale, 1965), and the accumulation rates of the middens (~20-60 years/sample) enforce a spatio-temporal averaging that reduces the $\delta^{15}N$ variability observed in modern ecosystem studies (Carr et al., 2016a), and provides a more reliable index of past water variability (Carr et al., 2016a; Chase et al., 2012).

Boomplaas faunal and archaeological archives

The Boomplaas sequence spans much of the last >65,000 years (Deacon, 1982), though we focus here on the fauna and flaked stone artifacts from the upper stratigraphic units corresponding in age with the Seweweekspoort record (SOM Table S2). We use these data to explore the relationship between the paleoenvironmental changes documented at Seweweekspoort and mammal community composition, foraging efficiency, and technological organization. Ages for Boomplaas follow Deacon (1982), calibrated using SHCal13 (Hogg et al., 2013). These published data do present limitations, as they do not adequately bracket each stratigraphic unit. In an effort to maximize their utility, and estimate likely intervals of time that each unit may represent, we derived depths from the published stratigraphic diagrams and calculated a general age-depth model for the sequence. While apparently quasi-continuous, with a relatively constant depositional rate, the nature of the sequence, in terms of lithology, suggests more sporadic deposition. In plotting each unit, we have included both minimum and maximum weighted mean ages as well as potential minimum and maximum ages of the units considering potential sources of error related to radiocarbon calibration and assumptions of accumulation rates (SOM Figure S4). This highlights the clear need to initiate a systematic revision of the chronologies of many archaeological sites in the region (e.g. Loftus et al., 2016; Sealy et al., 2016) to enable more robust inter-site and inter-regional comparisons.

Taxonomic abundances (number of identified specimens: NISP) of ungulates from Boomplaas Cave were derived from Faith (2013a), with Klein's (1983) specimen counts used for the uppermost member DGL. Comparable data (minimum number of individuals: MNI) for the Boomplaas microfauna were derived from Avery (1982). To facilitate comparison with the SWP record, we conducted a detrended correspondence analysis (DCA) for both data sets, using the first axis (rescaled from 0 to 100) to broadly summarize faunal composition (Figure 3). The linear trends in both taxonomic groups closely parallel a decline in ungulate grazers (Figure 3), suggesting that the DCA axis 1 scores are related to the replacement of grasslands by more shrubby habitats (see also Faith, 2013a). Broadly parallel changes are also observed in the south coast faunal sequences from Nelson Bay Cave (Klein, 1983) and Byneskranskop 1 (Schweitzer and Wilson, 1983) (Figure 1), implying regional shifts in habitat structure.

Humans are the primary accumulator of the Boomplaas Cave macrofauna from stratum CL4 and above (Faith, 2013a; see also Faith, 2011). This allows us to explore how the environmental changes documented at SWP translate to changes in foraging efficiency. Based on models grounded in optimal foraging theory, we examine two zooarchaeological indicators of foraging efficiency. These include the relative abundance of small-bodied and presumably low-ranked prey (leporids and tortoises) and the average food utility index (FUI; Metcalfe and Jones, 1988) – a proxy for energetic returns (e.g., meat, fat, marrow) of various ungulate body parts – of large mammal (size classes 3 and 4: 84 to 900 kg) skeletal elements (data from Faith, 2011b). Given the evidence for attrition at Boomplaas Cave (Faith and Thompson, in press), we follow Cleghorn and Marean's (2004) taphonomic model of bone survivorship and restrict analysis to the long-bones (femur, tibia, humerus, radius, and metapodials) and skull elements (crania and mandibles). Building on previous studies conducted elsewhere (e.g., Grayson, 1991, 2005; Broughton, 1994, 1999; Cannon, 2003; Faith, 2007; Munro 2004;), we predict that declining foraging efficiency will be characterized by (1) increasing frequencies of low-ranked prey, reflecting declining availability of high-ranked prey (e.g., large game) on the landscape, and (2) increasing mean FUI values, reflecting intensified field processing due to an increase in carcass transport distances and/or search times. We recognize that because tortoises are slow-moving and easily captured, they might be considered a high-ranked prey type that should be collected whenever encountered (e.g. Stiner et al., 2000). However, the significant positive correlation between their abundances and those of leporids (Spearman's ρ: $r_s = 0.814$, $p \leq 0.001$), which are unequivocally a low-ranked prey type, suggests that we can treat tortoises as low-ranked prey in this context.

<insert Table 1>

All lithic data are taken from Deacon (1982), standardized to site mean (standardized value = (layer value – site mean) / site standard deviation). We focus on the abundance of bladelets (Figure 3d), and three indicators of technological delivery: ratio of cores to retouched flakes (Figure 3g), total proportions of retouched flakes (Figure 3e), and artefact density measured as total number of artefacts per bucket of excavated sediment following Deacon (1982) (Figure 3h). These last three values function, respectively, as proxies for the transport of retouched flakes vs tool-making potential (mode of technological 'provisioning' (Kuhn, 1995)), frequency of flake curation, and intensity of site-use (Barton and Riel-Salvatore, 2014; Kuhn and Clark, 2015; Parry and Kelly, 1987; Riel-Salvatore and Barton, 2004). Provisioning, which we define as the systems by which stone artefact technologies are delivered in anticipation of future needs, has been argued to mediate the response of mobility to environmental change (Mackay et al., 2014; Wilkins et al., 2017). Under conditions of diminished residential mobility, we expect increases in core transport and artefact density, and lower rates of curation. The inverse is expected when mobility increases and the scheduling of movements becomes harder to predict. If bladelets are a response to diminishing subsistence returns, then their abundance should track humidity and resource productivity inversely. Similarly, if bladelets are positively associated with increasing residential mobility and declining durations of site occupancy then we expect an inverse relationship with artefact density. We also consider the relative abundance of spatially-rare, fine-grained rocks such as silcrete and crypto-crystalline silicates (CCS, subsuming chert and chalcedony) (Figure 3f); it has recently been shown that the abundance of rocks such as silcrete is responsive to increases in overall artefact abundance (Will and Mackay, 2016), and may thus reflect diminished residential mobility and improved scheduling of movements.

Results

Climate change since the Last Glacial Maximum at Seweweekspoort

The Seweweekspoort record shows substantial changes in both $\delta^{13}C$ (range 5.1‰) and $\delta^{15}N$ (range 9.5‰) over the last 22,300 years, implying significant changes in vegetation and climate (Figure 2). These changes are coherent with the pollen data from the same material. Across this period, a strong first-order trend is apparent, with cool, humid glacial conditions (indicated by increased cryophilic Fynbos Biome vegetation pollen and lower $\delta^{13}C$ and $\delta^{15}N$) transitioning into warmer, but substantially drier conditions during the Holocene (declining fynbos pollen and higher $\delta^{13}C$ and $\delta^{15}N$; Figure 2). This aridification coincides with the deglacial decline in

Antarctic sea-ice extent (using sea-salt sodium as a proxy) between 19-11 ka (Fischer et al., 2007; Levine et al., 2014; Wolff et al., 2010) (Figure 2), which is considered to be a strong determinant on the position of the westerly storm track (Bard and Rickaby, 2009; Stuut et al., 2004). The elevated grass pollen percentages during the last glacial period, coupled with low $\delta^{13}C$ suggest the increased prevalence of cool growing season C_3 grasses (Vogel, 1978), consistent with the model that much of the precipitation during this period fell during the winter months as a result of increased westerly influence. While recent work has indicated that variability in summer rainfall may have had some significant impact in the winter rainfall zone (Chase et al., 2015a; Chase et al., 2015b), long-term (i.e., glacial-interglacial timescales) precipitation trends in the summer rainfall zone (Chevalier and Chase, 2015) exhibit a clear antiphase relationship with humidity at Seweweekspoort (Figure 2), indicating that tropical systems played a limited role in the region at these timescales.

<insert Figure 2>

Within this broad first-order trend of deglacial aridification at Seweweekspoort, significant second-order abrupt episodes of wetter conditions (centred at 14.5, 11 and 4 cal kBP, and the last millennium) indicate major reorganisations of regional climate dynamics. In southern Africa, where rainfall regimes are defined by their strong seasonality, the varying contribution of the non-dominant moisture-bearing system can have a substantial impact on regional environments, shortening or attenuating the impact of often pronounced drought seasons (Chase et al., 2015a). In this context, humid episodes within the last glacial-interglacial transition (LGIT; 18.5-11.7 ka) – previously identified as being a period of exceptionally high effective precipitation in the region (Scholtz, 1986) – can be linked to the warming of both high southern latitudes (Stocker, 1998; Stocker and Johnsen, 2003) and the oceans surrounding southwestern Africa (Barker et al., 2009; Farmer et al., 2005; Kim and Schneider, 2003), including a response to the slow-down of Atlantic Meridional Overturning Circulation (AMOC) during Heinrich stadial 1 (HS1; ~18-14.6 ka) (McManus et al., 2004) (Figure 2).

While the influence of the westerly storm track may have diminished as the Subtropical Front shifted poleward (Barker et al., 2009), increased evaporation from warmer oceans and the invigoration of the southern African monsoon system would have augmented the summer rain component in what was then primarily a winter rainfall regime, reducing rainfall seasonality and drought stress. At Seweweekspoort, peaks in humidity at 14.5 and 11 cal kBP typify this, with reductions in fynbos vegetation under slightly warmer conditions, and with increased grass cover as a function of more regular rains promoting shallow rooting vegetation. With the onset of the Holocene, as warming continued, the combination of tropical and temperate systems that resulted in these phases of LGIT humidity broke down. Changes in global boundary conditions resulted in 1) a more permanent southerly position of the westerly storm track, and less winter rain, and 2) strong regional warming that intensified potential evapotranspiration, enhancing drought stress (Chevalier and Chase, 2016). Combined, these factors are interpreted to have driven the marked aridification exhibited in the Seweweekspoort records (Figure 2).

Changing resources and technology

The climatic changes robustly identified at Seweweekspoort are strongly reflected in our newly synthesised faunal and archaeological records (Figure 3). Large mammals and microfauna from Boomplaas Cave indicate open and grassy environments during the LGM, giving way to shrublands across the Pleistocene-Holocene transition; a phase marked by large mammal extinctions and shifts in faunal community composition throughout the region (Faith and Behrensmeyer, 2013). These changes are evident in the DCA axis 1 scores (Figure 3). The abundance of ungulate grazers and axis 1 scores at the site closely tracks $\delta^{13}C$, $\delta^{15}N$ (Figure 3), and changes observed in the pollen record at Seweweekspoort (Figure 2). Likewise, the carbon isotope composition of tooth enamel from Boomplaas grazers parallels the $\delta^{13}C$ shifts at Seweweekspoort, with predominantly C_3 grasses consumed during the LGM giving way to increased C_4 grasses during the LGIT (Sealy et al., 2016).

<insert Figure 3>

These findings contrast with earlier interpretations from floral (Deacon et al., 1984; Scholtz, 1986) and faunal assemblages (Avery, 1982; Klein, 1972; Klein, 1980, 1983) from southern Cape archaeological sequences, wherein open grassland environments – inferred primarily from a predominance of grazers in large mammal fossil records – were interpreted as signs of increased aridity. Our results support inferences that evidence for grassier vegetation indicates the influence of more/more regular precipitation on the richer soils of the valleys and plains of the southern Cape (Chase, 2010; Faith, 2013b), which currently support relatively xeric karroid vegetation (Cowling, 1983). In contemporary African ecosystems, elevated precipitation is typically associated with increased biomass of large herbivores (Coe et al., 1976; East, 1984), a phenomenon likely to have been enhanced by increased plant nutrient content under reduced atmospheric CO_2 concentrations (Faith, 2011a). The implication for human populations is that cooler, more humid late Pleistocene conditions presented a more productive resource base, including the proliferation of large grazing ungulates.

Zooarchaeological evidence from the human-accumulated vertebrate assemblages at Boomplaas Cave (CL4 and above) indicates that aridification through the LGIT is associated with a decline in foraging efficiency. Across the LGIT (CL4 to BRL5), tortoises and leporids increase in abundance relative to ungulates (tortoises: $\chi^2_{\text{trend}} = 90.332$, $p < 0.001$; leporids: $\chi^2_{\text{trend}} = 64.854$, $p < 0.001$). Because ungulates are larger and provide greater energetic returns than tortoises or hares – in which case they should be pursued whenever encountered – these trends imply a decline in their abundances on the landscape. This is also reflected in changes in carcass transport strategies. The average food utility index of large mammal high-survival skeletal elements increases steadily across the LGIT (Spearman's rho = 0.964, $p < 0.001$), indicating a greater emphasis on skeletal parts providing the highest energetic returns. Within an optimal foraging framework, this trend is consistent with an increase in carcass transport distances and/or search times stemming from diminished availability of large game (Cannon, 2003; Faith, 2007). These parallel trends imply that the cooler and more humid conditions of the late Pleistocene provided a more productive vertebrate resource base with higher average energetic returns than did the more arid conditions of the early Holocene.

The decline in foraging efficiency through the deglaciation reverses through the Holocene. Barring an increase observed in the two upper units (Table 1), leporids decline in abundance relative to ungulates after the peak in BRL5 (~11-12 cal kBP) ($\chi^2_{\text{trend}} = 15.854$, $p < 0.001$). This trend, which is consistent with an increase in ungulate abundances on the landscape, complements a decline in the mean FUI of large mammal skeletal parts (Spearman's rho = 0.821, $p = 0.034$).

From the LGM through the Holocene, there are marked temporal trends in lithic indicators of technological systems at Boomplaas Cave (Figure 3). Though not without some variation, there is a general decline through time in the abundance of bladelets ($\chi^2_{\text{trend}} =$

1323.693, $p < 0.001$), cores relative to retouched flakes ($\chi^2_{\mathrm{trend}} = 921.328$, $p < 0.001$), and fine-grained raw materials ($\chi^2_{\mathrm{trend}} = 775.322$, $p < 0.001$), coupled with an increase in the frequency of retouched pieces ($\chi^2_{\mathrm{trend}} = 1510.282$, $p < 0.001$). A relationship between technological systems and the environment is suggested by strong correlations between these indicators and the DCA axis 1 scores derived for both ungulates and microfauna (Figure 3b, c; Table 2). Indeed, all the measures of technological change we employ for the Boomplaas assemblage are significantly correlated with changes in ungulate community composition, and most with the composition of micromammal communities (Table 2). Both sets of axis 1 scores track changing frequencies of grassland indicators at the site, as well as the δ^{15}N and especially δ^{13}C values from Seweweekspoort (Figure 3). It follows that technological change is tracking environmental change, including the patterns of climate-driven environmental change documented in the Seweweekspoort records.

<insert Table 2>

During the LGM and early LGIT bladelets are abundant and artefact indicators are consistent with low residential mobility (Figure 3). With the exception of the earliest LGM members (GWA/HCA), for which taphonomic data suggest limited human occupation (Faith, 2013a), artefact densities are well above the overall mean at Boomplaas, flake curation is uncommon, and all core to retouched flake values pre-13 ka (CL member units) are higher than all those that follow. Associated high frequencies of rock such as silcrete and CCS before 12 cal kBP (CL + BRL 7) imply regular and predictable access to fine-grained rock through this period (Figure 3). These factors combined imply an emphasis on the transport of tool-making potential to sites.

Coincident with the onset of the first-order aridification trend after ~14 ka (BRL member units), artefact densities decrease, as do proportions of fine-grained rock and bladelets. The period is broadly characterised by more common acquisition and reduction of readily available local rocks (quartz and quartzite), with diminishing intensity of site use and little transport of cores or curation of flakes. Investment in technological costs in the later LGIT appears minimal and may reflect greater allocation of energy to search and handling of subsistence packages in response to diminishing ungulate abundance (cf., Hames, 1992;

Mackay and Marwick, 2011). From the beginning of the Holocene (BRL3 through to DGL member), and tracking diminishing humidity, artefact densities are low and locally abundant rock continues to dominate, but flake curation becomes markedly more common – technological systems show a much greater emphasis on transportation and maintenance of implements in this period than in the Pleistocene.

Conclusions

The findings presented here overturn prevailing models of environmental and behavioral change in Africa's southern Cape. A continuous and high-resolution environmental base-line is provided for the first time, indicating a trend from relative humidity during the LGM to increased aridity during the Holocene, with marked shifts in moisture across the LGIT. Rather than being characterised by 'harsh,' conditions (Deacon and Lancaster, 1988; Scholtz, 1986), the mesic environments of the late Pleistocene were highly productive, with more extensive grasslands existing in areas now dominated by drought resistant succulent shrublands. Zooarchaeological data indicate proliferation of a diverse ungulate grassland community during this time, suggesting greater resource availability for humans living in the area, and reduced search and handling times for large game. While lithic technologies track these changes, we found no evidence to support an association between the production of bladelets during the LGM/early LGIT (Robberg) and diminished subsistence conditions. Indeed, bladelets seem to have flourished in a period of relative resource abundance. The period of lowest subsistence productivity inferred from the Seweweekspoort data probably occurred during the Holocene, associated with aridification and the concomitant loss of large ungulates and faunal diversity recorded at Boomplaas. This change led to increases in carcass processing at kill sites, as evidenced by more selective transport of high utility body parts, increased reliance on low-ranked prey, and a technological response in which flakes from locally acquired rocks were curated, core transportation was relatively rare, and bladelets were uncommon. In documenting the strong coupling of environmental, subsistence and technological behavior in Later Stone Age foragers, our data reflect the simple observation that all lithic technologies can be adaptive solutions, not only those often assumed to provide particular adaptive benefits. The findings afforded by high resolution analysis of late Pleistocene and Holocene climate imply more generally that the lack of certain kinds of technologies – such as bladelets, backed artefacts and bifacial points - in the earlier stages of human evolution need not carry inherent meaning. The ability of foragers to track rapid climatic and environmental changes with adaptive cultural responses is a better arbiter of cognitive complexity than the deployment of any specific technological system.

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Table Captions

Table 1: Zooarchaeological indicators of foraging efficiency at Boomplaas Cave. These include the relative abundance of tortoises (%), leporids (%), and mean food utility index (FUI) of high-survival body parts belonging to size 3-4 mammals.

Table 2: The correlation (Spearman’s ρ) between lithic technological indicators and faunal community composition (DCA Axis 1 scores) for ungulates and microfauna at Boomplaas Cave. Significant values in bold.

Figure Captions

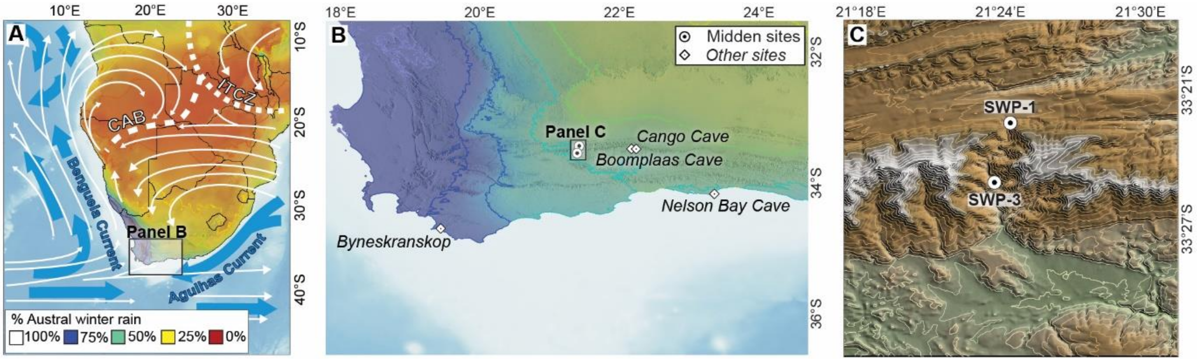

Figure 1: (A) Map of southern Africa showing seasonality of rainfall and climatic gradients dictated by the zones of summer/tropical (orange) and winter/temperate (blue) rainfall dominance. Winter rainfall is primarily a result of frontal systems embedded in the westerly storm track. Major atmospheric (white arrows) and oceanic (blue arrows) circulation systems and the austral summer positions of the Inter-Tropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB) are indicated. The location of the study site in the transitional southern Cape region is shown. (B) Map of southwest African coastal region with the Seweweekspoort sites and other key palaeoenvironmental and archaeological sites indicated (shading as for panel 'A'). (C) Topographical map of Seweweekspoort, with the SWP-1 and SWP-3 sites indicated.

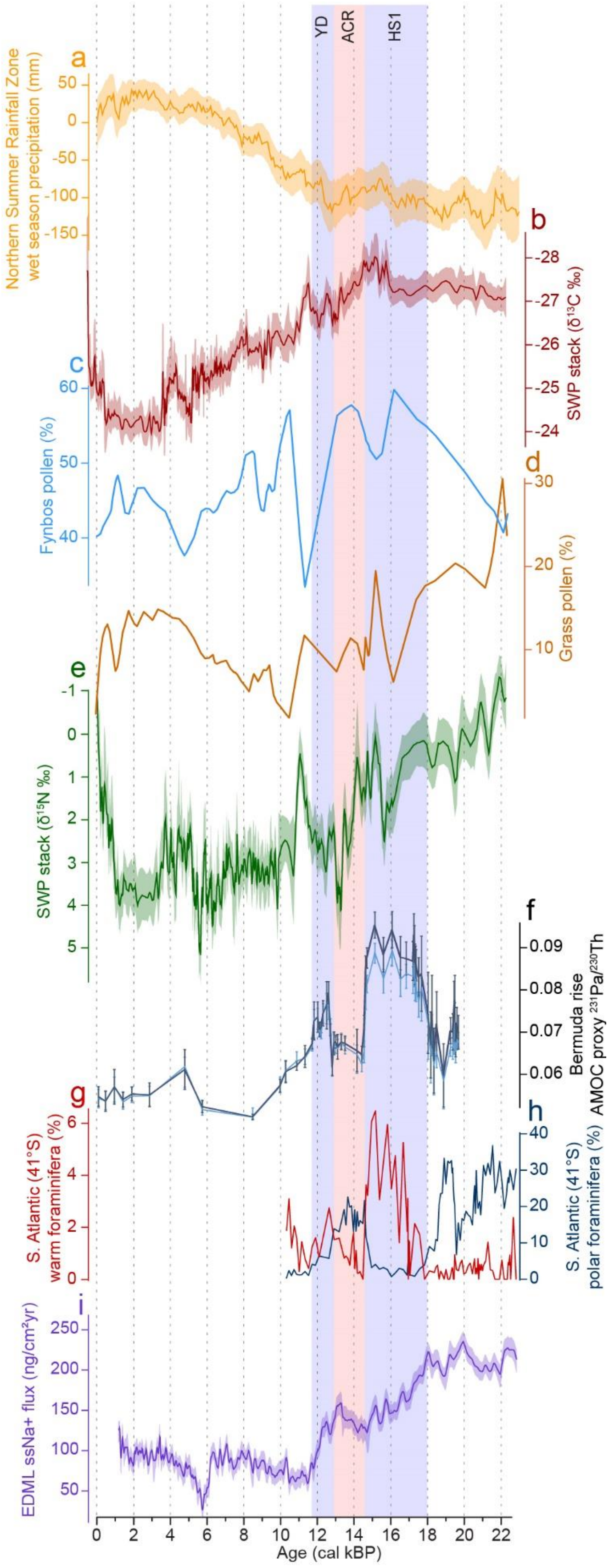

Figure 2: Comparison of δ^{15}N (e),δ^{13}C values (b), fynbos (c) and grass (d) pollen percentages from the Seweweekspoort hyrax middens with relevant palaeoenvironmental records including the northern summer rainfall zone wet season precipitation reconstruction (a; Chevalier and Chase, 2015), the Bermuda Rise record of Atlantic Meridional Overturning Circulation (AMOC) strength and the northward oceanic transport of heat (f; McManus et al., 2004), foraminifera records indicating conditions in the ocean to the south of the Africa (g, h; Barker et al., 2009) and sea salt sodium concentrations from the EPICA DML ice core in Antarctica (i; Fischer et al., 2007).

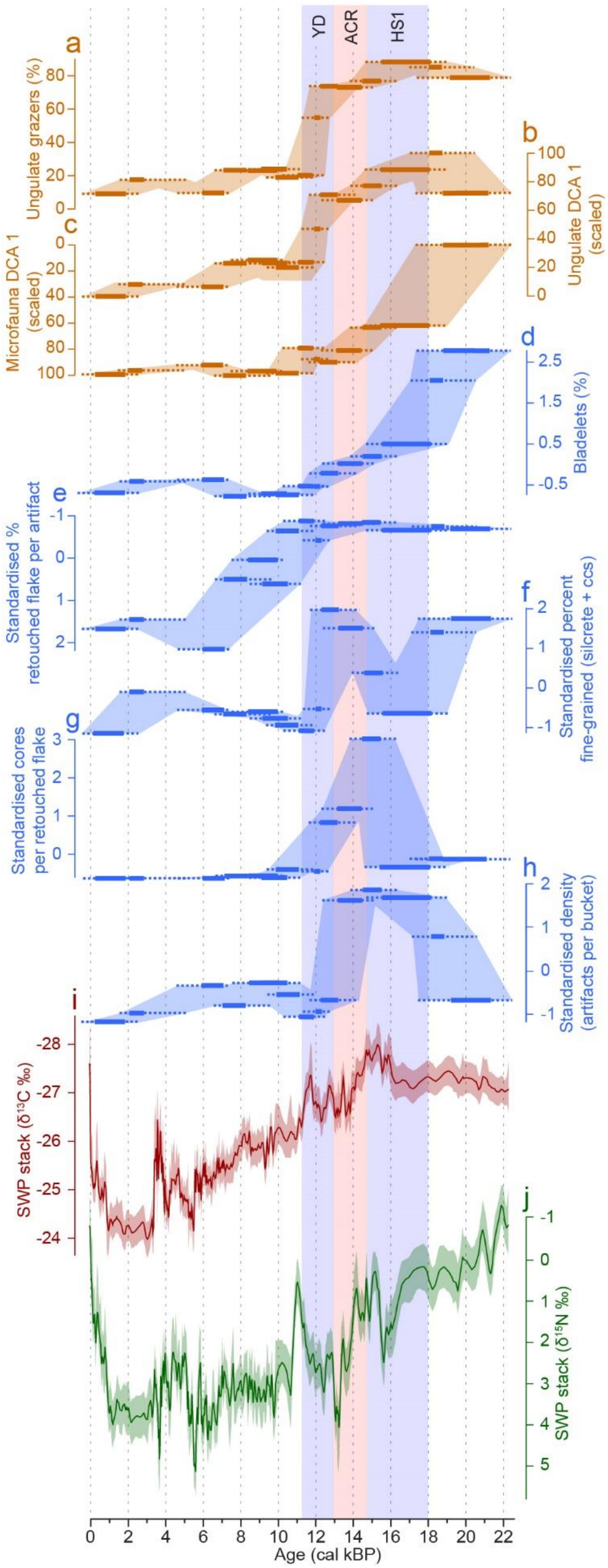

Figure 3: Comparison of δ^{15}N (j) and δ^{13}C (i) values from the Seweweekspoort hyrax middens with zooarchaeological records (a-c) of macrofauna (Faith, 2013a; Klein, 1983) and microfauna (Avery, 1982), and (d-h) lithic data (Deacon, 1979; Deacon et al., 1984) from Boomplaas Cave. Error bars on the data from Boomplaas reflect potential age ranges (2σ) of each stratigraphic unit.

Supplementary Information

Material and methods

The Seweweekspoort middens were selected for analysis because they are composed almost entirely of hyraceum (no visible pellets). Our experience suggests that such middens have superior stratigraphic integrity compared to more pellet-rich middens. Representative portions of the middens were processed according to the methods described by Chase et al. (Chase et al., 2013; Chase et al., 2012). Radiocarbon age determinations were processed at the ^{14}CHRONO Centre, Queen's University Belfast using accelerator mass spectrometry (AMS) (Figure S1; Table S1). The radiocarbon ages were corrected for isotope fractionation using the AMS measured $\delta^{13}C$ and calibrated using the SHCal13 calibration data (Hogg et al., 2013). The Bacon 3.0.3 software package (Blaauw and Christen, 2011) was used to generate all age-depth models (Figure S1). Stable isotope analysis of bulk midden samples were performed at the Department of Archaeology, University of Cape Town according to the methods described in Chase et al. (2010; 2009; 2011; 2012), with a contiguous/overlapping samples obtained from two series of offset 1 mm holes. For the stable isotope analyses, the standard deviation derived from replicate analyses of homogeneous material was better than 0.2 ‰ for both carbon and nitrogen. Carbon isotope results are expressed relative to Vienna PDB. Nitrogen isotope results are expressed relative to atmospheric nitrogen.

Table S1: Radiocarbon ages were calibrated using the SHCal13 calibration data (Hogg et al., 2013), except for the surface sample from SWP-1-4b, which was not calibrated, and UBA-19558, which was calibrated with CALIBomb using SHCal13 and the SHZ1_2 dataset of Hua et al. (Hua et al., 2013).

Sample	**^{14}C age BP**	**F^{14}C**	**1 sigma error**	**95.4 % (2σ) cal age ranges**		**relative area under distribution**	**median probability (cal BP)**
				lower cal range BP	**upper cal range BP**		
SWP-1-1							
UBA-16698	3067		32	3078	3094	0.02947	3222
				3108	3129	0.031819	
				3138	3349	0.938712	
UBA-18638	4509		40	4892	4900	0.006407	5131
				4915	4927	0.009555	
				4959	5299	0.984038	
UBA-18639	5322		35	5940	5977	0.111729	6068
				5981	6183	0.888271	
UBA-18640	6226		33	6954	7178	0.982768	7082
				7219	7236	0.017232	
UBA-18641	8535		39	9447	9540	1	9502
SWP-1-2a							
UBA-22927	10243		39	11721	11733	0.009155	11886
				11748	12040	0.990845	
UBA-18645	13621		60	16145	16620	1	16359
UBA-18646	17143		83	20377	20894	1	20627
UBA-18647	18746		95	22372	22837	1	22564
SWP-1-4b top							
surface	modern		1				
UBA-19558		1.0181	0.0043	-7	-6	1	
UBA-19559	975		27	775	782	0.020244	853
				787	919	0.979756	
UBA-22921	1543		25	1314	1426	1	1378
UBA-22922	2238		25	2117	2123	0.008228	2231
				2148	2319	0.991772	
SWP-1-4b bottom							
UBA-19560	11138		47	12811	13076	1	12961
UBA-22924	12190		41	13836	14166	1	14030
UBA-19561	12626		55	14547	15185	1	14923

UBA-22925	12618	46	14586	15164	1	14917
UBA-19562	13425	67	15855	16313	1	16102

SWP-1-5

UBA-19565	410	21	328	378	0.344762	456
			391	401	0.018871	
			439	497	0.636367	
UBA-22742	1657	35	1415	1582	1	1504
UBA-22743	3428	28	3512	3528	0.013505	3629
			3558	3719	0.986495	
UBA-22744	4973	29	5596	5728	1	5651
UBA-22745	6216	29	6959	7168	1	7077
UBA-22746	7559	32	8206	8263	0.154807	8348
			8290	8403	0.845193	
UBA-22747	8292	35	9035	9047	0.011584	9224
			9088	9329	0.882282	
			9342	9403	0.106134	
UBA-22748	8609	35	9480	9564	0.955713	9535
			9567	9597	0.044287	
UBA-19566	9341	42	10296	10360	0.074017	10496
			10366	10597	0.897515	
			10624	10650	0.028468	

SWP-3-1

UBA-19320	3405	32	3482	3535	0.122002	3604
			3547	3694	0.877998	
UBA-19321	3509	40	3612	3848	1	3741
UBA-19322	4661	65	5051	5191	0.201609	5354
			5213	5481	0.745676	
			5532	5578	0.052715	
UBA-19323	5454	46	6014	6081	0.097688	6221
			6104	6158	0.115457	
			6171	6301	0.786855	
UBA-21381	6212	30	6956	7167	1	7074
UBA-21382	7840	32	8455	8502	0.081029	8574
			8506	8642	0.918971	
UBA-19324	9354	52	10296	10359	0.069114	10512
			10367	10668	0.930886	
UBA-19325	10717	52	12553	12718	1	12651
UBA-19326	12874	84	15060	15648	1	15310

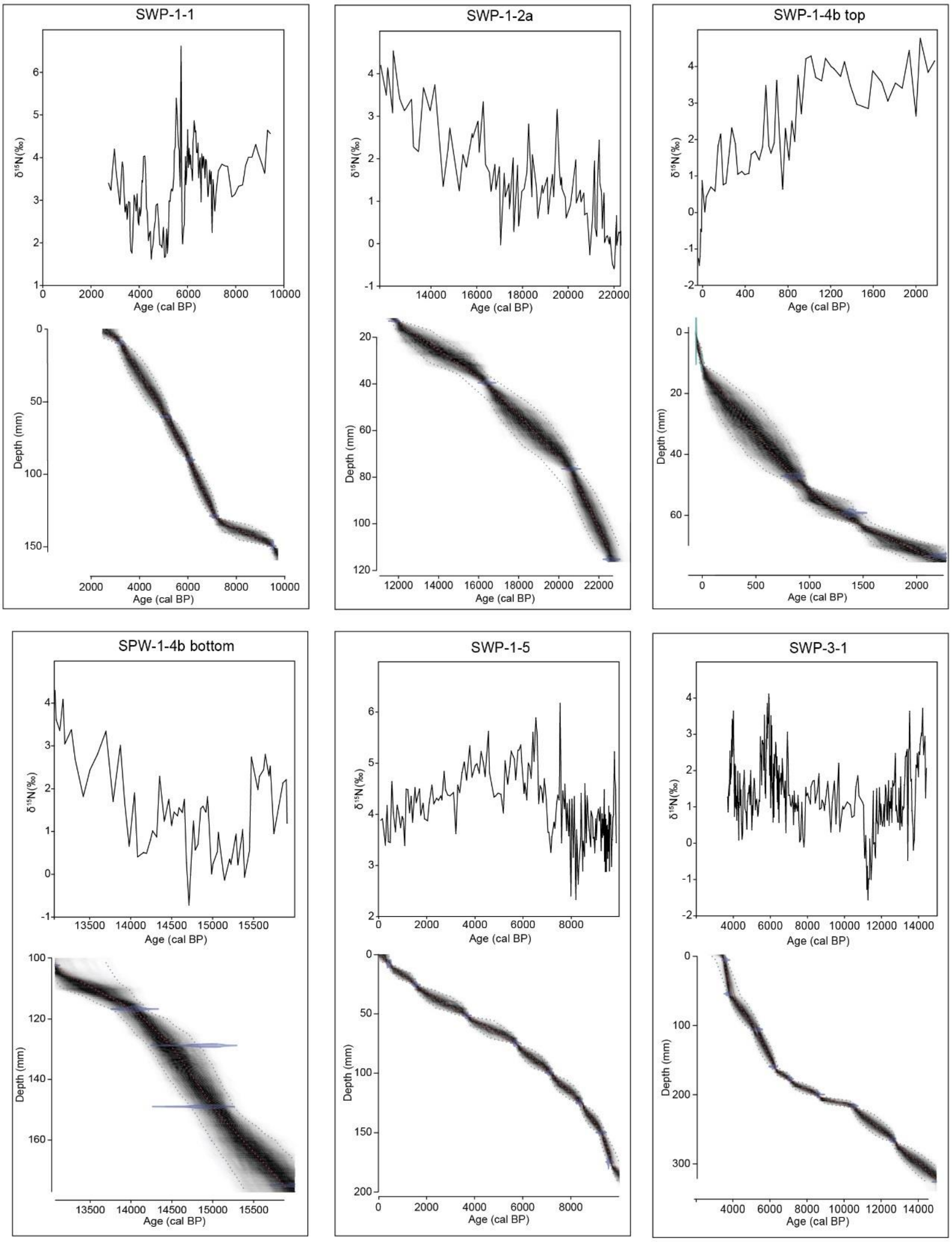

Figure S1: Stable nitrogen isotope results from the Seweweekspoort rock hyrax midden considered in this study with associated age models. Age-depth models were generated using the Bacon 3.0.3 software package (Blaauw and Christen, 2011).

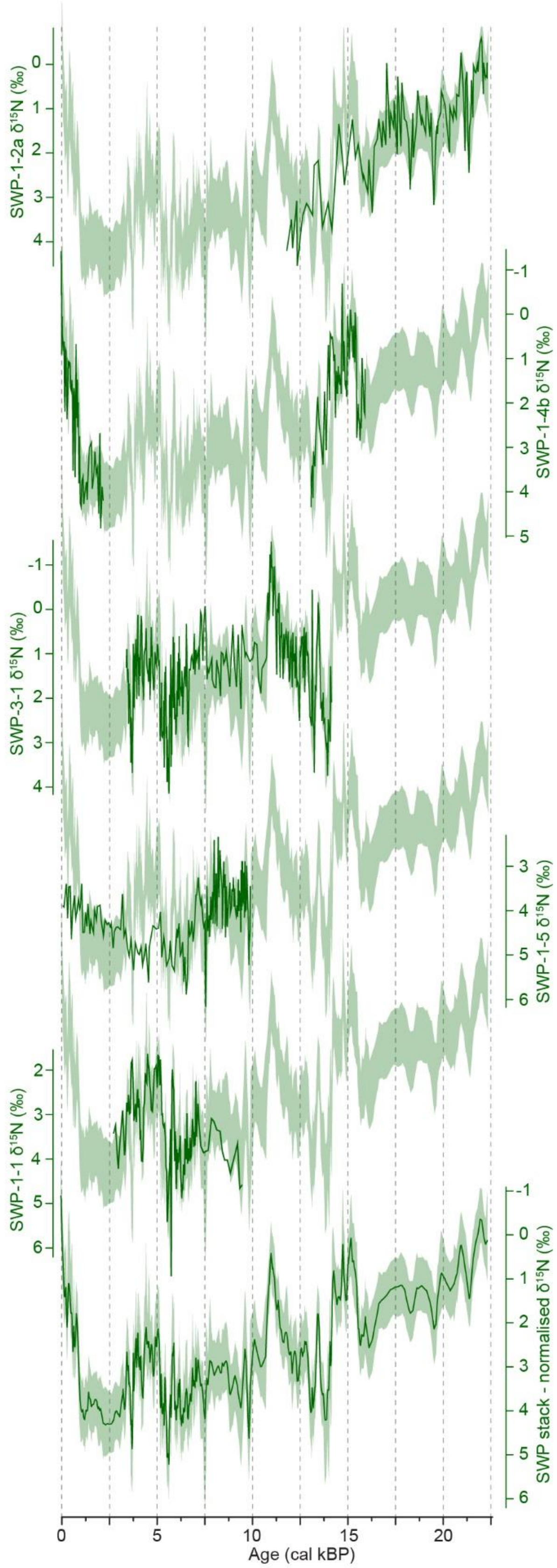

Figure S2: Stable nitrogen isotope results from the Seweweekspoort rock hyrax midden shown individually in relation to the aggregate record obtained using Local Regression (LOESS) curve fitting of the combined datasets. For comparability, 1.5‰ was added to the δ^{15}N data from the SWP-3-1 to compensate for the more humid microclimate, relative to the SWP-1 site, in which the midden was found.

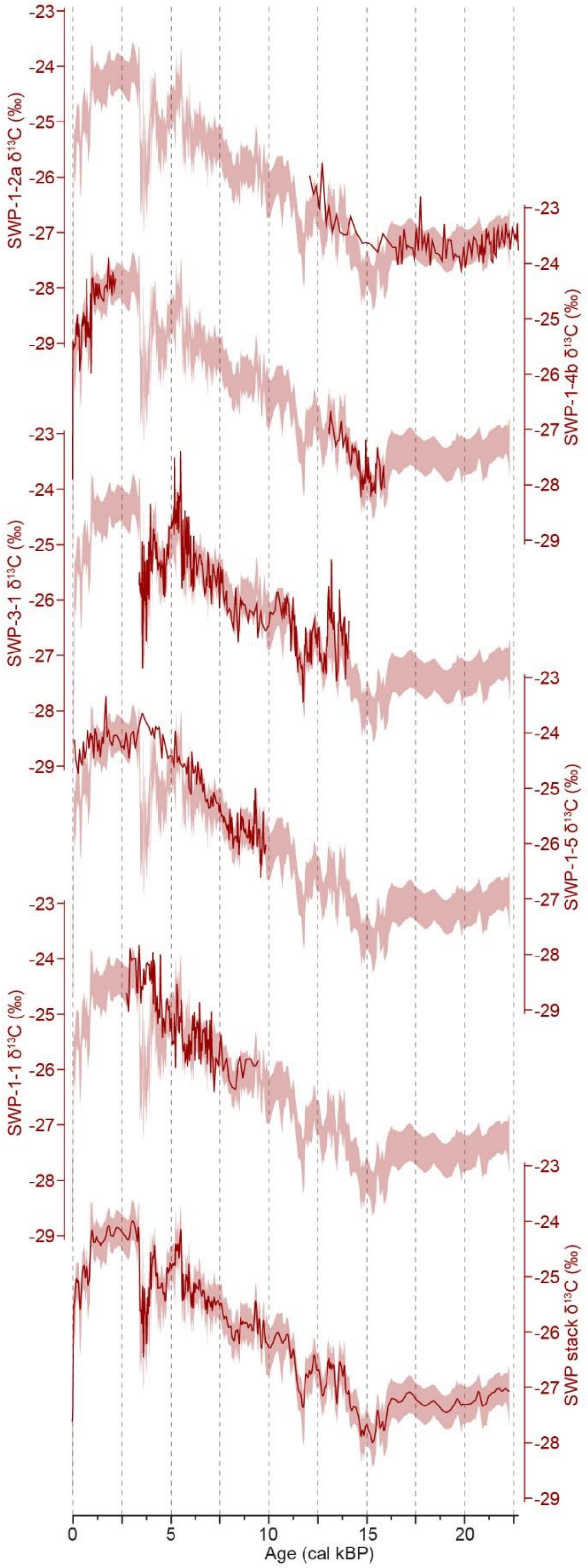

Figure S3: Stable carbon isotope results from the Seweweekspoort rock hyrax midden shown individually in relation to the aggregate record obtained using Local Regression (LOESS) curve fitting of the combined datasets.

Faunal and archaeological archives

Taxonomic abundances of ungulates from Boomplaas Cave were derived from Faith (Faith, 2013), with Klein's (Klein, 1983) data used for the uppermost member DGL. Comparable data for the Boomplaas microfauna were derived from Avery (Avery, 1982). We conducted a detrended correspondence analysis (DCA) for both data sets, using the first axis (rescaled from 0 to 100) to broadly summarize faunal composition (Figure 3). The linear trends in both taxonomic groups closely parallel a decline in ungulate grazers (Figure 3), suggesting that the DCA Axis 1 scores are related to the replacement of grasslands by more shrubby habitats (see also Faith, 2013). Parallel changes are also observed at Nelson Bay Cave (Klein, 1983) and Byneskranskop 1 (Schweitzer and Wilson, 1983), implying regional shifts in habitat structure.

Zooarchaeological indicators of foraging efficiency at Boomplaas Cave (Table S2), including the relative abundance of small-bodied prey (leporids and tortoises) and the average utility of high-survival body parts (following the taphonomic model of bone survivorship outlined in Cleghorn and Marean (Cleghorn and Marean, 2004)), were derived from Faith (Faith, 2011). Despite small body size, because tortoises are slow-moving and easy to capture, they might be considered a high-ranked prey type that should be collected whenever encountered (e.g. Stiner et al., 2000). While this makes tortoises a somewhat ambiguous indicator, the parallel increase in leporids – unequivocally a low-ranked prey type – across the LGIT more definitively suggests a decline in foraging efficiency that parallels changing body part representation for large-bodied prey.

Table S2:. Zooarchaeological indicators of foraging efficiency at Boomplaas Cave. These include the relative abundance of tortoises (%), leporids (%), and mean food utility index of high-survival body parts belonging to size 3-4 mammals (FUI).

Stratum	% Tortoises	% Leporids	FUI
BLD3	74.6	30.9	1405
FBL/BLA	79.1	28.7	1737
BRL/BRL1	61.8	10.4	1465
BRL2	71.7	13.5	1910
BRL3	78.1	24.2	1610
BRL4	74.1	24.2	2245
BRL5	80.3	36.2	2432
BRL6	68.2	15.2	2246
BRL7	70.9	22.3	2188
CL1	68.9	8.5	2028
CL2	71.9	3.6	2037

CL3	47.1	4.4	1840
CL4	54.5	0.0	1458

Ages for Boomplaas follow Deacon (1982), calibrated using SHCal13 (Hogg et al., 2013). All lithic data are taken from Deacon (1982), standardised to site mean (standardised value = (layer value – site mean) / site standard deviation). We use core to tool ratios to track changes in the way in which technology was delivered; alternative measures such as core to flake ratios may increase or decrease with changing intensity of core reduction independent of delivery systems. All the measures of technological change we employ for the Boomplaas assemblage are significantly correlated with changes in ungulate community composition, and most with the composition of micromammal communities (Table S3).

As with the faunal data, the technological trends noted for Boomplaas are replicated at Byneskranskop (Schweitzer and Wilson, 1983) (Table S4) and Nelson Bay Cave (Deacon, 1982) (Table S5) (methods as per Boomplaas), with the exception of changes in artefact density. Given the coastal location of these two sites, changes in artefact density – effectively number of artefacts per unit sediment – are likely to have been influenced by changes in sedimentation associated with sea level fluctuations (Chase and Thomas, 2007). Microlithic technologies in the forms of bladelets do reappear at Byneskranskop and Nelson Bay Cave during the more arid conditions of the mid-Holocene, along with backed artefacts, reinforcing arguments for the diversity of contexts in microlithic systems were deployed (Hiscock et al., 2011).

Table S3: The correlation between lithic technological indicators and faunal community composition (DCA Axis 1 scores) for ungulates and microfauna at Boomplaas Cave. Significant values in bold.

	Ungulates		Microfauna	
	r_s	p	r_s	p
%Bladelets	**-0.696**	**0.004**	**0.878**	**<0.001**
Core/tool	**-0.842**	**<0.001**	**0.680**	**0.015**
Tool/aft	**0.732**	**0.002**	**-0.674**	**0.012**
CCS+Silcrete	**-0.604**	**0.017**	0.484	0.094
Density	**-0.618**	**0.014**	0.355	0.234

Table S4: Technological measures of the assemblage from Byneskranskop. Ages following (Loftus et al., 2016).

Layer	Age (cal yr BP)	Core/tool	Tool/aft	CCS+Silcrete	Density	Bladelets
1	1715-1870	-0.568	-0.232	-0.954	-0.834	-1.084
2	3450-3818	-0.616	1.608	-0.142	-1.253	-0.868
3		-0.589	1.579	0.325	-0.581	0.740
4	3720-3970	-0.605	1.380	0.387	-0.682	-0.696
5	6015-6290	-0.665	1.591	1.947	0.031	0.845
6	6315-6495	-0.617	1.223	1.542	0.090	1.119
7	5905-6180	-0.564	0.650	0.828	0.218	1.665
8	6285-6410	-0.578	0.314	1.339	1.017	0.540
9	6740-6945	-0.593	0.162	0.845	0.634	0.752
10		-0.511	-0.350	0.537	0.194	-0.475
11	6505-6740	-0.522	-0.708	-0.010	2.304	1.288
12	8342-8725	-0.457	-0.509	0.413	1.936	-0.548
13		-0.196	-0.711	-0.557	-0.448	-0.514
14	10796-11245	0.053	-0.988	-1.174	-0.939	-1.372
15	11245-11695	1.926	-1.004	-1.439	-1.315	-1.359
16		0.963	-1.002	-1.359	-1.013	-1.046
17	13855-14320	0.168	-0.992	-0.689	-0.728	0.290
18		0.886	-0.986	-1.254	0.534	-0.827
19	16060-16535 16550-17105	3.086	-1.025	-0.583	0.835	1.549

Table S5: Technological measures of the assemblage from Nelson Bay Cave. Ages following (Loftus et al., 2016).

Layer	Age (cal yr BP)	Core/tool	Tool/aft	CCS+Silcrete	Density	Bladelets
Ivan	5330-5655 5590-5730	-1.037	3.073	1.597	1.370	-0.369
BSC		-0.891	0.163	-0.034	1.920	-0.499
Rice A	9030-9400	-0.849	0.006	-1.443	-0.611	-0.650
Rice B	9305-9520 9460-9545	-0.610	-0.039	-1.404	-0.707	-0.636
Jake	10275-10590	0.082	-0.301	-1.536	-0.541	-0.650
BSBJ	11405-11975	0.260	-0.476	-1.572	-0.576	-0.634
CS	11825-12400	2.730	-0.590	-1.295	-0.742	-0.612
BSL	12020-12515 13775-14135	-0.501	-0.334	1.464	-0.532	0.000
GSL		0.133	-0.525	1.266	-0.794	0.440
YSL	17645-18050	0.412	-0.499	3.105	1.213	2.775
YGL	21960-22485 22615-23355	0.271	-0.477	-0.150	1.370	0.834

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