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

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16 Abstract

17 Africa's southern Cape is a key region for the evolution of our species, with early symbolic
18 systems, marine faunal exploitation, and episodic production of microlithic stone tools taken
19 as evidence for the appearance of distinctively complex human behavior. However, the
20 temporally discontinuous nature of this evidence precludes ready assumptions of intrinsic
21 adaptive benefit, and has encouraged diverse explanations for the occurrence of these
22 behaviors, in terms of regional demographic, social and ecological conditions. Here, we
23 present a new high-resolution multi-proxy record of environmental change that indicates that
24 faunal exploitation patterns and lithic technologies track climatic variation across the last
25 22,300 years in the southern Cape. Conditions during the Last Glacial Maximum and
26 deglaciation were humid, and zooarchaeological data indicate high foraging returns. By
27 contrast, the Holocene is characterized by much drier conditions and a degraded resource
28 base. Critically, we demonstrate that systems for technological delivery – or provisioning –
29 were responsive to changing humidity and environmental productivity. However, in contrast
30 to prevailing models, bladelet-rich microlithic technologies were deployed under conditions
31 of high foraging returns and abandoned in response to increased aridity and less productive
32 subsistence environments. This suggests that posited links between microlithic technologies
33 and subsistence risk are not universal, and the behavioral sophistication of human populations
34 is reflected in their adaptive flexibility rather than in the use of specific technological
35 systems.

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

38

39 **Introduction**

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

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

66 **Later Stone Age environments and archaeology in the southern Cape**

67 Influenced by both temperate and tropical climate systems (Figure 1), long-term climate
68 change in the southern Cape is characterized by significant and often abrupt fluctuations
69 (Bard and Rickaby, 2009; Chase et al., 2013; Chase and Meadows, 2007; Heaton et al., 1986;

70 Quick et al., 2015; Quick et al., 2016; Talma and Vogel, 1992). Existing evidence indicates
71 that during the Holocene the relative influences of the two dominant synoptic scale moisture-
72 bearing systems – 1) the southern westerly storm track, which expands/shifts northward in the
73 winter, and 2) the tropical easterly flow, which transports moisture from the Indian Ocean
74 during the summer – have varied significantly (Chase et al., 2013; Chase et al., 2015b).
75 However, there is little detailed paleoenvironmental evidence pre-dating the Holocene (Carr
76 et al., 2016b; Chase and Meadows, 2007), and as a result there are contradictory opinions
77 concerning conditions since the LGM (Chase and Meadows, 2007; Deacon and Lancaster,
78 1988; Faith, 2013b; Kohfeld et al., 2013; Partridge et al., 1999; Partridge et al., 2004; Sime et
79 al., 2013; Stone, 2014), to the extent that some studies conclude that the region was
80 exceptionally “harsh” and arid during the LGM (Deacon and Lancaster, 1988; Scholtz, 1986),
81 while others infer greater humidity and highly productive terrestrial environments (e.g. Faith,
82 2013b; Parkington et al., 2000). This uncertainty has fundamentally hindered our
83 understanding of past climate dynamics in the region, and, by extension, the impact of past
84 climate change on hunter-gatherer adaptive and subsistence strategies during both the Later
85 and Middle Stone Age.

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

102 coarse and mask considerable variation, they provide a useful heuristic for discussing broad
103 patterns in technological change across the later LSA.

104 Consistent with the imprecise meaning of the term (Pargeter, 2016), the ELSA,
105 Robberg and Wilton have all been described as ‘microlithic’ (Bousman, 2005; Deacon, 1984;
106 Mitchell, 1988; Wadley, 1993), but based on different characteristics – small flakes in the
107 case of the ELSA, bladelets in the case of the Robberg and backed artefacts in the Wilton
108 (Lombard et al., 2012). The advent of dedicated bladelet production in particular – as
109 characterizes the Robberg – is argued to have presented humans with a significant adaptive
110 advantage during our evolution and dispersal (Ambrose, 2002; Bar-Yosef and Kuhn, 1999;
111 Clarkson et al., 2009; Foley and Lahr, 2003). Some researchers have linked an emphasis on
112 bladelet production with responses to heightened subsistence risk associated with low or
113 declining subsistence resource productivity (Elston and Brantingham, 2002; Petraglia et al.,
114 2009) (for discussion of the risk concept used here see Bamforth and Bleed, 1997). Others
115 have suggested that bladelet production provided benefits under conditions of high residential
116 mobility (Goebel, 2002; Neeley, 2002). Both explanations – increased subsistence risk and
117 increased mobility – have been posited for bladelet-rich systems in southern Africa during
118 globally cooler conditions (Ambrose, 2002; Grosjean et al., 2003; McCall, 2007; McCall and
119 Thomas, 2012; Mellars, 2006; Mitchell, 2000). The Robberg specifically has been associated
120 with increased residential mobility in response to inferred diminishing resource density
121 (Ambrose, 2002; Mitchell, 2000), and has been explained as a risk-dampening response to
122 resource stress (Mackay, 2009). Other researchers, however, have suggested that any tracking
123 between LSA technological systems and paleoenvironmental variation was relatively weak,
124 and occurred only at the broadest scale of environmental change (e.g. Deacon, 1982). The
125 reality of coupling between technology, subsistence conditions and environmental change in
126 this period is thus contested, and with it the viability of high-order explanations for the
127 behavioral significance of artefacts such as bladelets.

128 **Sites and regional setting**

129 To explore the relationship between environmental change and human activities and
130 technology, we focus on sites from the Swartberg mountains of South Africa’s southern
131 Cape, one of the major ranges in the east-west axis of the Cape Fold Mountains (Figure 1).
132 From Seweweekspoort, a deep transversal valley in the central Swartberg mountains, a series
133 of rock hyrax (*Procavia capensis*) middens – stratified accumulations of dried urine and fecal

134 pellets (see Chase et al., 2012) – were identified, and six middens from two sites,
135 Seweweekspoort-1 (SWP-1; 33.3668°S, 21.4144°E) and Seweweekspoort-3 (SWP-3;
136 33.4092°S, 21.4031°), were analysed for this study. SWP-1 is located on a west-facing cliff
137 on the northern slope of the pass (Figure 1). The SWP-1 middens were taken from several
138 locations within the same larger shelter, formed by a ~100 m overhanging cliff. SWP-3 is
139 located on a low eastern cliff in the central section of the valley near the valley bottom, and
140 experiences a more humid microclimate relative to the exposed position of SWP-1.

141

142 <insert Figure 1>

143

144 The SWP-1 site is located in the North Swartberg Sandstone Fynbos, but less than a
145 kilometre to the north is the Matjiesfontein Shale Renosterveld (Mucina and Rutherford,
146 2006). The former, depending on altitude and aspect, is predominantly asteraceous, proteoid
147 and restioid fynbos, while the latter is dominated by asteraceous elements, particularly
148 *Elytropappus rhinocerotis*, *Eriocephalus* sp. and *Euryops* sp., and by an increasing number of
149 succulents, primarily from the Crassulaceae family (Mucina and Rutherford, 2006). At SWP-
150 1, these vegetation types inter-digitate to some extent, with the broad west-facing drainage
151 just north of the site supporting more hydrophilic taxa, such as *Protea*. The north-facing rock
152 shelves directly adjacent to the site maintain only shallow soils and a dominance of
153 succulents. Grasses in the region are a mixture of C₃ (e.g., *Erharta*) and C₄ (e.g., *Aristida*,
154 *Stipagrostis*) varieties (<http://sibis.sanbi.org/faces/DataSources.jsp>; Rutherford et al., 2012;
155 Rutherford et al., 2003; SANBI, 2003). SWP-3 is located in the South Swartberg Sandstone
156 Fynbos, which at the site is primarily proteoid in character. In addition, there are numerous
157 arboreal/Cape thicket elements (e.g., *Podocarpus*, Celastraceae, *Dodonaea*, *Searsia*, *Euclea*,
158 Oleaceae) associated with drainages and the nearby riparian zones of the valley bottom.

159 The Seweweekspoort sites are located 70 km west of the well-stratified late
160 Pleistocene / Holocene archaeological site of Boomplaas Cave. This site is also situated on
161 the flanks of the Swartberg and occupies a very similar climatic regime, making it ideal for
162 exploring linkages between climate, environment, subsistence and technology at high
163 temporal resolution. Located on the southern flanks of the Swartberg range overlooking the
164 Cango Valley, Boomplaas Cave was excavated by Hilary Deacon in the 1970s (Deacon,

165 1979). The excavated sediments were divided into a series of members, some of which were
166 subdivided into units. The site is positioned within a transitional shrubland whose component
167 species vary as a function of temperature and moisture gradients moving upslope from the
168 floor of the valley (Vlok and Schutte-Vlok, 2010). The lowlands to the south are
169 characterized by renosterveld habitats, which give way to fynbos vegetation along the slopes
170 of the Swartberg. Along watercourses and ravines in the Cango Valley are more densely
171 wooded habitats that include sweet thorn trees (*Vachellia (Acacia) karroo*) and ironwood
172 (*Olea* spp.) among others (Moffett and Deacon, 1977). As is also the case at
173 Seweweekspoort, Boomplaas today receives contributions of both winter and summer rainfall
174 (Figure 1). Thus, the limited grasses that do occur in the area today include a mixture of both
175 C₃ and C₄ species.

176 **Materials and methods**

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

190 The fossil pollen content of 82 adjacent, contiguous pollen samples were prepared
191 with standard physical (600 μm sieving and decanting) and chemical (HCl, KOH, HF and
192 acetolysis) methods (Moore et al., 1991). *Lycopodium* tablets were added to the weighed
193 sample to estimate pollen concentrations (Stockmarr, 1971). A minimum pollen sum of 400
194 grains was counted at a magnification of $\times 400$ under a light microscope, and identified with
195 the help of the literature (Scott, 1982; van Zinderen Bakker, 1953, 1956; van Zinderen

196 Bakker and Coetzee, 1959), and photographic and slide reference collections at the
197 Universities of the Free State, Cape Town, and Montpellier.

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

206 Stable isotope results from the different Seweweekspoort rock hyrax middens were
207 combined into a single aggregate record using Local Regression (LOESS) curve fitting of the
208 combined datasets (SOM Figures S2 and S3). As individual middens under the same climate
209 regime may exhibit differences in their isotopic records due to microclimatic influences on
210 individual foraging ranges (i.e., baseline $\delta^{15}\text{N}$ variability), we have adjusted the $\delta^{15}\text{N}$ to
211 account for these differences prior to LOESS curve fitting. Using the SWP-1-1 and SWP-1-
212 4b records as a datum, an estimated offset of 1.5‰ was added to the $\delta^{15}\text{N}$ data from the
213 SWP-3-1 to compensate for the more humid microclimate in which the midden was found,
214 and 0.5‰ and 1‰ were added to SWP-1-5 and SWP-1-2a respectively to account for their
215 more exposed positions.

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

228 Hyraceum $\delta^{15}\text{N}$ is an indicator of changes in ecosystem water-availability (Carr et al.,
229 2016a; Chase et al., 2013; Chase et al., 2015b; Chase et al., 2009; Chase et al., 2011). A
230 positive relationship exists between aridity and $\delta^{15}\text{N}$ in soils, plants and herbivores, with drier
231 conditions correlating with enriched $\delta^{15}\text{N}$ (Carr et al., 2016a), most likely as a result of
232 denitrification processes in arid/semi-arid soils (Handley et al., 1999; Handley et al., 1994;
233 Hartman, 2011; Heaton, 1987; Murphy and Bowman, 2006, 2009; Wang et al., 2010). In the
234 hyraceum samples, the narrowly defined feeding range of the hyraxes (<60 m; Sale, 1965),
235 and the accumulation rates of the middens (~20-60 years/sample) enforce a spatio-temporal
236 averaging that reduces the $\delta^{15}\text{N}$ variability observed in modern ecosystem studies (Carr et al.,
237 2016a), and provides a more reliable index of past water variability (Carr et al., 2016a; Chase
238 et al., 2012).

239 *Boomplaas faunal and archaeological archives*

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

258 Taxonomic abundances (number of identified specimens: NISP) of ungulates from
259 Boomplaas Cave were derived from Faith (2013a), with Klein's (1983) specimen counts used

260 for the uppermost member DGL. Comparable data (minimum number of individuals: MNI)
261 for the Boomplaas microfauna were derived from Avery (1982). To facilitate comparison
262 with the SWP record, we conducted a detrended correspondence analysis (DCA) for both
263 data sets, using the first axis (rescaled from 0 to 100) to broadly summarize faunal
264 composition (Figure 3). The linear trends in both taxonomic groups closely parallel a decline
265 in ungulate grazers (Figure 3), suggesting that the DCA axis 1 scores are related to the
266 replacement of grasslands by more shrubby habitats (see also Faith, 2013a). Broadly parallel
267 changes are also observed in the south coast faunal sequences from Nelson Bay Cave (Klein,
268 1983) and Byneskranskop 1 (Schweitzer and Wilson, 1983) (Figure 1), implying regional
269 shifts in habitat structure.

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

291 are unequivocally a low-ranked prey type, suggests that we can treat tortoises as low-ranked
292 prey in this context.

293

294 <insert Table 1>

295

296 All lithic data are taken from Deacon (1982), standardized to site mean (standardized
297 value = (layer value – site mean) / site standard deviation). We focus on the abundance of
298 bladelets (Figure 3d), and three indicators of technological delivery: ratio of cores to
299 retouched flakes (Figure 3g), total proportions of retouched flakes (Figure 3e), and artefact
300 density measured as total number of artefacts per bucket of excavated sediment following
301 Deacon (1982) (Figure 3h). These last three values function, respectively, as proxies for the
302 transport of retouched flakes vs tool-making potential (mode of technological ‘provisioning’
303 (Kuhn, 1995)), frequency of flake curation, and intensity of site-use (Barton and Riel-
304 Salvatore, 2014; Kuhn and Clark, 2015; Parry and Kelly, 1987; Riel-Salvatore and Barton,
305 2004). Provisioning, which we define as the systems by which stone artefact technologies are
306 delivered in anticipation of future needs, has been argued to mediate the response of mobility
307 to environmental change (Mackay et al., 2014; Wilkins et al., 2017). Under conditions of
308 diminished residential mobility, we expect increases in core transport and artefact density,
309 and lower rates of curation. The inverse is expected when mobility increases and the
310 scheduling of movements becomes harder to predict. If bladelets are a response to
311 diminishing subsistence returns, then their abundance should track humidity and resource
312 productivity inversely. Similarly, if bladelets are positively associated with increasing
313 residential mobility and declining durations of site occupancy then we expect an inverse
314 relationship with artefact density. We also consider the relative abundance of spatially-rare,
315 fine-grained rocks such as silcrete and crypto-crystalline silicates (CCS, subsuming chert and
316 chalcedony) (Figure 3f); it has recently been shown that the abundance of rocks such as
317 silcrete is responsive to increases in overall artefact abundance (Will and Mackay, 2016), and
318 may thus reflect diminished residential mobility and improved scheduling of movements.

319 **Results**

320 *Climate change since the Last Glacial Maximum at Seweweekspoort*

321 The Seweweekspoort record shows substantial changes in both $\delta^{13}\text{C}$ (range 5.1‰) and $\delta^{15}\text{N}$
322 (range 9.5‰) over the last 22,300 years, implying significant changes in vegetation and
323 climate (Figure 2). These changes are coherent with the pollen data from the same material.
324 Across this period, a strong first-order trend is apparent, with cool, humid glacial conditions
325 (indicated by increased cryophilic Fynbos Biome vegetation pollen and lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)
326 transitioning into warmer, but substantially drier conditions during the Holocene (declining
327 fynbos pollen and higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; Figure 2). This aridification coincides with the
328 deglacial decline in Antarctic sea-ice extent (using sea-salt sodium as a proxy) between 19-11
329 ka (Fischer et al., 2007; Levine et al., 2014; Wolff et al., 2010) (Figure 2), which is
330 considered to be a strong determinant on the position of the westerly storm track (Bard and
331 Rickaby, 2009; Stuut et al., 2004). The elevated grass pollen percentages during the last
332 glacial period, coupled with low $\delta^{13}\text{C}$ suggest the increased prevalence of cool growing
333 season C_3 grasses (Vogel, 1978), consistent with the model that much of the precipitation
334 during this period fell during the winter months as a result of increased westerly influence.
335 While recent work has indicated that variability in summer rainfall may have had some
336 significant impact in the winter rainfall zone (Chase et al., 2015a; Chase et al., 2015b), long-
337 term (i.e., glacial-interglacial timescales) precipitation trends in the summer rainfall zone
338 (Chevalier and Chase, 2015) exhibit a clear antiphase relationship with humidity at
339 Seweweekspoort (Figure 2), indicating that tropical systems played a limited role in the
340 region at these timescales.

341

342 <insert Figure 2>

343

344 Within this broad first-order trend of deglacial aridification at Seweweekspoort,
345 significant second-order abrupt episodes of wetter conditions (centred at 14.5, 11 and 4 cal
346 kBP, and the last millennium) indicate major reorganisations of regional climate dynamics. In
347 southern Africa, where rainfall regimes are defined by their strong seasonality, the varying
348 contribution of the non-dominant moisture-bearing system can have a substantial impact on
349 regional environments, shortening or attenuating the impact of often pronounced drought
350 seasons (Chase et al., 2015a). In this context, humid episodes within the last glacial-
351 interglacial transition (LGIT; 18.5-11.7 ka) – previously identified as being a period of
352 exceptionally high effective precipitation in the region (Scholtz, 1986) – can be linked to the

353 warming of both high southern latitudes (Stocker, 1998; Stocker and Johnsen, 2003) and the
354 oceans surrounding southwestern Africa (Barker et al., 2009; Farmer et al., 2005; Kim and
355 Schneider, 2003), including a response to the slow-down of Atlantic Meridional Overturning
356 Circulation (AMOC) during Heinrich stadial 1 (HS1; ~18-14.6 ka) (McManus et al., 2004)
357 (Figure 2).

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

372 *Changing resources and technology*

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

384

385 <insert Figure 3>

386

387 These findings contrast with earlier interpretations from floral (Deacon et al., 1984;
388 Scholtz, 1986) and faunal assemblages (Avery, 1982; Klein, 1972; Klein, 1980, 1983) from
389 southern Cape archaeological sequences, wherein open grassland environments – inferred
390 primarily from a predominance of grazers in large mammal fossil records – were interpreted
391 as signs of increased aridity. Our results support inferences that evidence for grassier
392 vegetation indicates the influence of more/more regular precipitation on the richer soils of the
393 valleys and plains of the southern Cape (Chase, 2010; Faith, 2013b), which currently support
394 relatively xeric karroid vegetation (Cowling, 1983). In contemporary African ecosystems,
395 elevated precipitation is typically associated with increased biomass of large herbivores (Coe
396 et al., 1976; East, 1984), a phenomenon likely to have been enhanced by increased plant
397 nutrient content under reduced atmospheric CO₂ concentrations (Faith, 2011a). The
398 implication for human populations is that cooler, more humid late Pleistocene conditions
399 presented a more productive resource base, including the proliferation of large grazing
400 ungulates.

401 Zooarchaeological evidence from the human-accumulated vertebrate assemblages at
402 Boomplaas Cave (CL4 and above) indicates that aridification through the LGIT is associated
403 with a decline in foraging efficiency. Across the LGIT (CL4 to BRL5), tortoises and leporids
404 increase in abundance relative to ungulates (tortoises: $\chi^2_{\text{trend}} = 90.332$, $p < 0.001$; leporids:
405 $\chi^2_{\text{trend}} = 64.854$, $p < 0.001$). Because ungulates are larger and provide greater energetic returns
406 than tortoises or hares – in which case they should be pursued whenever encountered – these
407 trends imply a decline in their abundances on the landscape. This is also reflected in changes
408 in carcass transport strategies. The average food utility index of large mammal high-survival
409 skeletal elements increases steadily across the LGIT (Spearman's rho = 0.964, $p < 0.001$),
410 indicating a greater emphasis on skeletal parts providing the highest energetic returns. Within
411 an optimal foraging framework, this trend is consistent with an increase in carcass transport
412 distances and/or search times stemming from diminished availability of large game (Cannon,
413 2003; Faith, 2007). These parallel trends imply that the cooler and more humid conditions of
414 the late Pleistocene provided a more productive vertebrate resource base with higher average
415 energetic returns than did the more arid conditions of the early Holocene.

416 The decline in foraging efficiency through the deglaciation reverses through the
417 Holocene. Barring an increase observed in the two upper units (Table 1), leporids decline in
418 abundance relative to ungulates after the peak in BRL5 (~11-12 cal kBP) ($\chi^2_{\text{trend}} = 15.854, p <$
419 0.001). This trend, which is consistent with an increase in ungulate abundances on the
420 landscape, complements a decline in the mean FUI of large mammal skeletal parts
421 (Spearman's $\rho = 0.821, p = 0.034$).

422 From the LGM through the Holocene, there are marked temporal trends in lithic
423 indicators of technological systems at Boomplaas Cave (Figure 3). Though not without some
424 variation, there is a general decline through time in the abundance of bladelets ($\chi^2_{\text{trend}} =$
425 $1323.693, p < 0.001$), cores relative to retouched flakes ($\chi^2_{\text{trend}} = 921.328, p < 0.001$), and
426 fine-grained raw materials ($\chi^2_{\text{trend}} = 775.322, p < 0.001$), coupled with an increase in the
427 frequency of retouched pieces ($\chi^2_{\text{trend}} = 1510.282, p < 0.001$). A relationship between
428 technological systems and the environment is suggested by strong correlations between these
429 indicators and the DCA axis 1 scores derived for both ungulates and microfauna (Figure 3b,
430 c; Table 2). Indeed, all the measures of technological change we employ for the Boomplaas
431 assemblage are significantly correlated with changes in ungulate community composition,
432 and most with the composition of micromammal communities (Table 2). Both sets of axis 1
433 scores track changing frequencies of grassland indicators at the site, as well as the $\delta^{15}\text{N}$ and
434 especially $\delta^{13}\text{C}$ values from Seweweekspoort (Figure 3). It follows that technological change
435 is tracking environmental change, including the patterns of climate-driven environmental
436 change documented in the Seweweekspoort records.

437

438 <insert Table 2>

439

440 During the LGM and early LGIT bladelets are abundant and artefact indicators are
441 consistent with low residential mobility (Figure 3). With the exception of the earliest LGM
442 members (GWA/HCA), for which taphonomic data suggest limited human occupation (Faith,
443 2013a), artefact densities are well above the overall mean at Boomplaas, flake curation is
444 uncommon, and all core to retouched flake values pre-13 ka (CL member units) are higher
445 than all those that follow. Associated high frequencies of rock such as silcrete and CCS
446 before 12 cal kBP (CL + BRL 7) imply regular and predictable access to fine-grained rock

447 through this period (Figure 3). These factors combined imply an emphasis on the transport of
448 tool-making potential to sites.

449 Coincident with the onset of the first-order aridification trend after ~14 ka (BRL
450 member units), artefact densities decrease, as do proportions of fine-grained rock and
451 bladelets. The period is broadly characterised by more common acquisition and reduction of
452 readily available local rocks (quartz and quartzite), with diminishing intensity of site use and
453 little transport of cores or curation of flakes. Investment in technological costs in the later
454 LGIT appears minimal and may reflect greater allocation of energy to search and handling of
455 subsistence packages in response to diminishing ungulate abundance (cf., Hames, 1992;
456 Mackay and Marwick, 2011). From the beginning of the Holocene (BRL3 through to DGL
457 member), and tracking diminishing humidity, artefact densities are low and locally abundant
458 rock continues to dominate, but flake curation becomes markedly more common –
459 technological systems show a much greater emphasis on transportation and maintenance of
460 implements in this period than in the Pleistocene.

461 Conclusions

462 The findings presented here overturn prevailing models of environmental and behavioral
463 change in Africa's southern Cape. A continuous and high-resolution environmental base-line
464 is provided for the first time, indicating a trend from relative humidity during the LGM to
465 increased aridity during the Holocene, with marked shifts in moisture across the LGIT.
466 Rather than being characterised by 'harsh,' conditions (Deacon and Lancaster, 1988; Scholtz,
467 1986), the mesic environments of the late Pleistocene were highly productive, with more
468 extensive grasslands existing in areas now dominated by drought resistant succulent
469 shrublands. Zooarchaeological data indicate proliferation of a diverse ungulate grassland
470 community during this time, suggesting greater resource availability for humans living in the
471 area, and reduced search and handling times for large game. While lithic technologies track
472 these changes, we found no evidence to support an association between the production of
473 bladelets during the LGM/early LGIT (Robberg) and diminished subsistence conditions.
474 Indeed, bladelets seem to have flourished in a period of relative resource abundance. The
475 period of lowest subsistence productivity inferred from the Seweweekspoort data probably
476 occurred during the Holocene, associated with aridification and the concomitant loss of large
477 ungulates and faunal diversity recorded at Boomplaas. This change led to increases in carcass
478 processing at kill sites, as evidenced by more selective transport of high utility body parts,

479 increased reliance on low-ranked prey, and a technological response in which flakes from
480 locally acquired rocks were curated, core transportation was relatively rare, and bladelets
481 were uncommon. In documenting the strong coupling of environmental, subsistence and
482 technological behavior in Later Stone Age foragers, our data reflect the simple observation
483 that all lithic technologies can be adaptive solutions, not only those often assumed to provide
484 particular adaptive benefits. The findings afforded by high resolution analysis of late
485 Pleistocene and Holocene climate imply more generally that the lack of certain kinds of
486 technologies – such as bladelets, backed artefacts and bifacial points - in the earlier stages of
487 human evolution need not carry inherent meaning. The ability of foragers to track rapid
488 climatic and environmental changes with adaptive cultural responses is a better arbiter of
489 cognitive complexity than the deployment of any specific technological system.

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843

844 Table Captions

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

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

851 Figure Captions

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

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

868 **Figure 3:** Comparison of $\delta^{15}\text{N}$ (j) and $\delta^{13}\text{C}$ (i) values from the Seweweekspoort hyrax middens with
869 zooarchaeological records (a-c) of macrofauna (Faith, 2013a; Klein, 1983) and microfauna (Avery,
870 1982), and (d-h) lithic data (Deacon, 1979; Deacon et al., 1984) from Boomplaas Cave. Error bars on
871 the data from Boomplaas reflect potential age ranges (2σ) of each stratigraphic unit.