Glacial cycles and Palaeolithic adaptive variability on China’s Western Loess Plateau

Christopher Morgan¹, Loukas Barton², Robert Bettinger³, Fahu Chen⁴ & Zhang Dongju⁴

Intensive research on China’s Western Loess Plateau has located 63 Palaeolithic deposits, which together allow the authors to present a general model of hominin occupation from 80,000 to 18,000 years ago. Tools, subsistence and settlement correlate nicely with the climate: the warm wet MIS3 seeing expansion and more organised acquisition of quartz, and the Late Glacial Maximum that followed, a reduction in human presence but possibly an increase in ingenuity.

Keywords: China, climate, MIS3, LGM, lithics

Introduction

Recently, Hill et al. (2009) argued that the last glacial cycle played a major role in the evolution of modern human behaviour, especially in the emergence of non-kin cooperation, the development of larger groups and the evolution of intensive technologies and subsistence strategies (see also Richerson et al. 2009). The advantages associated with these behaviours, they suggested, explain the trend toward increasing human dominance of global ecologies through the Terminal Pleistocene and Holocene. While certainly true in a temporal sense,
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The way cultural adaptations evolved in concert with the environmental changes associated with this cycle is anything but clear. While some posit more-or-less direct relationships between environmental productivity and behavioural changes (e.g. Ambrose 1998), several confounding factors cloud the issue, specifically: the increasingly complex picture of hominid biological evolution in Eurasia (e.g. Krause et al. 2010), catastrophic volcanism (Golovanova et al. 2010) and social factors like the effects of risk sensitivity and group size on innovation, learning and long-term cultural transmission (Henrich 2004; Morgan 2009).

Relative to this context, the goals of the research reported here are twofold. The first is to provide a descriptive summary of work conducted since 2002 by our team of Chinese and American researchers on China’s Western Loess Plateau (WLP), where we have documented a record of human occupation spanning more than 80,000 years and most of the last glacial cycle. The second is to explore the relationship between major climatic shifts and variability in human technological, subsistence and settlement patterns. The idea here is to generate hypotheses that might identify causal connections between climate change, glacial cycling and the evolution of modern human behaviour in East Asia. This is a region that Norton and Jin (2009: 251) identify as critical to understanding the evolution of modern human behaviour, but which is woefully lacking in synthesis. This exploration begins with an overview of the regional palaeoenvironment and archaeology during the last glacial cycle, is followed by a summary of survey, excavation and analysis results and concludes with a consideration of the role of climate change in East Asian Palaeolithic cultural evolution.

Late Quaternary climate, environment and archaeology in north-east Asia

The last glacial cycle spans the MIS5 interglacial through the MIS2 stadial (i.e. the Last Glacial Maximum [LGM]), roughly 130 to 18 kya (Table 1). MIS5 is marked by pronounced climatic variability (Feng & Wang 2006), warm-wet phases and a northward advance of temperate forest/steppe biomes. The shift from warmer-wetter MIS5 interglacial biomes to cold, wet glacial conditions during early MIS4 resulted in the expansion of coniferous forests at the expense of deserts across the WLP (Feng et al. 1998), a trend which reversed after ~60 kya with the transition to MIS3. At this time the forests of the WLP gave way to a forest-steppe patchwork, with broadleaf taxa gradually supplanting coniferous ones (Feng et al. 2007). Across East Asia, technology was remarkably conservative from ~50–13 kya, dominated by an expedient core/flake industry using mostly locally-available and abundant raw materials (Ikawa-Smith 1978). Despite what appears to be technological continuity, however, relatively few archaeological sites or human fossils date between ~100–50 kya (Brown 2001), a phenomenon some attribute to regional abandonments associated with the MIS4 stadial (Ambrose 1998).

By the middle of MIS3 (~45 kya), winters were warmer, the summer phase of the East Asian monsoon was stronger, precipitation penetrated deeper inland (Yu et al. 2007) and wetlands developed across the WLP (Feng et al. 2007) — many containing archaeological sites (Ji et al. 2005). Late MIS3 saw a number of important cultural developments associated with what many consider to be the inception of modern human behaviour. These include the first clear evidence, at upper Zhoukoudian Cave (Norton & Gao 2008) and at Xiaogushan
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Table 1. Generalised WLP palaeoclimatic synthesis.

<table>
<thead>
<tr>
<th>Regime</th>
<th>Dates</th>
<th>Type</th>
<th>Climate</th>
<th>Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>post-LGM</td>
<td>&lt;18 kya</td>
<td>Poststadial</td>
<td>Warm/wet</td>
<td>Steppe-grassland</td>
</tr>
<tr>
<td>LGM (MIS2)</td>
<td>24–18 kya</td>
<td>Stadial</td>
<td>Cold/dry/variable</td>
<td>Artemisia steppe</td>
</tr>
<tr>
<td>MIS3</td>
<td>60–30 kya</td>
<td>Interstadial</td>
<td>Warm/wet (post-45 kya)</td>
<td>Forest-steppe &amp; Wetlands</td>
</tr>
<tr>
<td>MIS4</td>
<td>80–60 kya</td>
<td>Stadial</td>
<td>Cold/wet</td>
<td>Coniferous forest</td>
</tr>
<tr>
<td>MIS5</td>
<td>130–80 kya</td>
<td>Interglacial</td>
<td>Warm/variable</td>
<td>Forest-steppe</td>
</tr>
</tbody>
</table>

in north-eastern China (Chen & Olsen 1990), for symbolic representation and art in the greater region. They also include the proliferation of Upper Palaeolithic stone tool technologies (Brantingham et al. 2001), the expansion of human populations into new environments (Brantingham & Gao 2006) and perhaps the establishment of anatomically modern humans in the region after 45 kya (Su et al. 1999; Goebel 2007) — problematic correlations between behavioural and biological evolution notwithstanding (d’Errico 2003).

Beginning ~24 kya, the LGM (MIS2) was characterised by a weakened summer monsoon, widespread reduction in temperature and humidity (Wünnemann et al. 2007) and pronounced climatic variability (Ditlevsen et al. 1996). Lakes established during MIS3 became saline or disappeared (Yu et al. 2003; Yang et al. 2004). Deserts expanded (Sun et al. 1997; Zhou et al. 2002) and forests gave way to deserts (Herzschuh & Liu 2007). In the WLP, the MIS3 forest-steppe patchwork gave way to a sparsely vegetated Artemisia steppe (Feng et al. 2007). Culturally, the LGM is somewhat enigmatic, the absence of archaeological evidence being viewed by some as a population ‘bottleneck’ that explains the differences between pre- and post-LGM assemblages and site distributions (e.g. Goebel 2002). What little evidence we do have for this timespan suggests that the prepared core technology for producing prismatic microblades for use in composite weapons emerged during the LGM (Elston & Brantingham 2002; Brantingham et al. 2004). Climatic amelioration following MIS2 (after ~18 kya) resulted in the development of modern biomes, mainly a grassland-steppe, with gallery forests and wetlands developing along major water courses periodically through the Holocene (Yu et al. 2000). This period saw the development and spread of intensive human adaptations like microlithic technology, intensive hunting and gathering, and eventually, agriculture (Bettinger et al. 2010a).

The Palaeolithic on the Western Loess Plateau

During six field seasons between 2002 and 2009, surveys, site sampling and excavations were undertaken at multiple Late Pleistocene localities. These focused on the Shui Luo and Qing Shui rivers in the greater Hulu River watershed (Figure 1). Within this region, 63 in situ Palaeolithic deposits ranging from isolated artefacts to substantial deposits of stone tools, faunal remains and features were found in cutbanks or steep exposures on the edge of agricultural terraces. Sites were sampled by collecting artefacts and faunal bone from section walls. Dating samples were taken from cleaned section walls, in most cases by removing charcoal (for AMS) or soil samples in 50mm diameter steel tubes (for OSL) from the palaeosols containing the majority of the cultural deposits, and in a few cases, charcoal directly from cultural features. Ten of the 63 sites have been dated with AMS (Table 2)
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Figure 1. The research area, with sites mentioned in the text.

or OSL (Table 3) to the period in question: 80–13 kya (all dates in calendar years before present). An additional 22 sites have been dated to this same period based on their position in chronologically-sensitive Loess palaeosol sequences (Chen et al. 1997, 1999). Intensive sampling of two of these sites has resulted in collections from pre-LGM (ZJC02) and LGM (ZL05) contexts. Along with the Dadiwan site (Bettinger et al. 2010a & b), which spans this entire period, these sites record nearly 70 000 years of human activity and environmental change. The following briefly describes the most significant finds.

Pre-LGM deposits are found at Zhangjiachuan, Yuweigou and Huagou localities (Figure 2). Site ZJC02, on Zhangjiachuan Ridge, consists of abundant chipped stone and bone in a 3m thick, 7m long section containing at least six strata, from which 205 chipped stone artefacts and 228 pieces of animal bone were recovered, including specimens from large ungulates (e.g. *Bos*). Two OSL dates on loess palaeosols bracket site occupation between 42 and 40 kya; the third dates the basal level of the deposit to 80 kya. The highest density of artefacts at Huagou, a mid-elevation basin, is in and around site HG05, OSL-dated to MIS3 (33 kya). The site contains abundant quartz flakes (several intentionally retouched) and shatter in a wetland palaeosol. At Yuweigou, another mid-elevation basin, are sites YWG01 and YWG02. YWG01 consists of flakes, stone tools and faunal bone in a wetland palaeosol. Faunal remains are few, but include a fossilised *Bos* or *Bison* sp. molar. Two AMS dates on charcoal recovered from wetland palaeosols bracket site occupation between 28.4 and 30.6 kya. Like HG05, YWG01 shows occupation of mid-elevation upland wetland basins ∼30 kya, during the MIS3 interstadial. YWG02 consists of chipped stone artefacts

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Table 2. AMS dates from WLP surveys.

<table>
<thead>
<tr>
<th>Regime</th>
<th>Site</th>
<th>Sample context</th>
<th>$^{14}$C age</th>
<th>Lab</th>
<th>Lab no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>post-LGM</td>
<td>SXK01</td>
<td>Hearth</td>
<td>14 190±80</td>
<td>Beta Analytic</td>
<td>Beta-263913</td>
</tr>
<tr>
<td></td>
<td>SXK01</td>
<td>Hearth</td>
<td>14 410±60</td>
<td>Beta Analytic</td>
<td>Beta-263915</td>
</tr>
<tr>
<td></td>
<td>SXK01</td>
<td>Hearth</td>
<td>14 660±60</td>
<td>Beta Analytic</td>
<td>Beta-263914</td>
</tr>
<tr>
<td>LGM</td>
<td>ZL05$^b$</td>
<td>Feature</td>
<td>16 750±70</td>
<td>Beta Analytic</td>
<td>Beta-197631</td>
</tr>
<tr>
<td></td>
<td>ZL05$^b$</td>
<td>Feature</td>
<td>18 920±520</td>
<td>Lawrence</td>
<td>CAMS 95088</td>
</tr>
<tr>
<td></td>
<td>ZL05$^b$</td>
<td>Feature</td>
<td>20 220±90</td>
<td>Beta Analytic</td>
<td>Beta-197633</td>
</tr>
<tr>
<td></td>
<td>ZL05$^b$</td>
<td>Feature</td>
<td>21 180±100</td>
<td>Beta Analytic</td>
<td>Beta-197632</td>
</tr>
<tr>
<td>MIS3</td>
<td>HLG01</td>
<td>Palaeosol</td>
<td>22 590±70</td>
<td>Lawrence Livermore</td>
<td>CAMS135381</td>
</tr>
<tr>
<td></td>
<td>HLG01</td>
<td>Palaeosol</td>
<td>22 730±230</td>
<td>Lawrence Livermore</td>
<td>CAMS134380</td>
</tr>
<tr>
<td></td>
<td>YWG01</td>
<td>Palaeosol</td>
<td>23 700±110</td>
<td>Lawrence Livermore</td>
<td>CAMS135380</td>
</tr>
<tr>
<td></td>
<td>YWG01</td>
<td>Palaeosol</td>
<td>26 020±720</td>
<td>Lawrence Livermore</td>
<td>CAMS134377</td>
</tr>
<tr>
<td></td>
<td>ZS08$^b$</td>
<td>Palaeosol</td>
<td>27 730±150</td>
<td>Beta Analytic</td>
<td>Beta-210740</td>
</tr>
<tr>
<td></td>
<td>YWG02</td>
<td>Palaeosol</td>
<td>&gt;45 700</td>
<td>Lawrence Livermore</td>
<td>CAMS134378</td>
</tr>
<tr>
<td></td>
<td>HLG01$^c$</td>
<td>Palaeosol</td>
<td>46 240±1090</td>
<td>Lawrence Livermore</td>
<td>CAMS135382</td>
</tr>
<tr>
<td></td>
<td>YWG02</td>
<td>Palaeosol</td>
<td>&gt;53 000</td>
<td>Lawrence Livermore</td>
<td>CAMS135379</td>
</tr>
</tbody>
</table>

$^a$ All AMS dates on charcoal. Except where noted, dates calibrated to a 2σ confidence interval with OxCal4.1 (Bronk Ramsey 2001, 2009) using the IntCal09 calibration curve (Reimer et al. 2009). See Barton et al. 2008 for sample locations.

$^b$ Previously reported in Barton et al. 2007.

$^c$ Upper range of calibration is outside the range of IntCal09; mid-point for calibrated age derived from the 2σ upper range provided by CalPal using the Hulu 2007 comparison curve (Weninger et al. 2007) and a lower 2σ range generated by OxCal4.1 and the IntCal09 calibration curve.

as well as abundant bone and charcoal. AMS and OSL dates bracket artefact-bearing strata between 24 and 80 kya, indicating occupation mainly during MIS3.

LGM and post-LGM deposits are found mainly along the Shui Luo and Qing Shui rivers. The Shui Luo contains site ZL05, which consists of two discrete chipped stone concentrations, a quartz bipolar anvil, and possibly the remains from small seed processing (Chenopodiaceae) (Barton et al. 2007). AMS dates indicate occupation during the LGM ($\sim$25.3–19.9 kya). The Qing Shui contains site SXK01 (Figure 2). It consists of abundant quartz artefacts, faunal bone and two hearths in a well-developed palaeosol. It also contains a crude CCS pebble core similar in morphology to those used in microblade production. The hearths have been AMS-dated to between 17.9 and 17.2 kya.

Controlled excavation data come from the Dadiwan site, also on the Qing Shui, excavated in 2004, 2006 and 2009 (Bettinger et al. 2010a & b; Zhang et al. 2010). In total, we have excavated 31.8m³ of deposit, reaching the base of the cultural sequence at 9.9m. Artefact distributions, 88 radiocarbon and five OSL dates justify dividing the deposit into six
Table 3. OSL dates from WLP surveys.*

<table>
<thead>
<tr>
<th>Regime</th>
<th>LGM</th>
<th>MIS 3</th>
<th>MIS 4/5</th>
</tr>
</thead>
<tbody>
<tr>
<td>site</td>
<td>YWG02</td>
<td>DJG01</td>
<td>HG05</td>
</tr>
<tr>
<td></td>
<td>ZJC02</td>
<td>CWG01</td>
<td>ZJC02</td>
</tr>
<tr>
<td>U,ppm:</td>
<td>3.14±0.10</td>
<td>2.65±0.11</td>
<td>2.90±0.10</td>
</tr>
<tr>
<td>Th,ppm:</td>
<td>14.9±0.18</td>
<td>11.5±0.15</td>
<td>11.9±0.15</td>
</tr>
<tr>
<td>K,%:</td>
<td>2.58±0.10</td>
<td>1.74±0.08</td>
<td>2.07±0.09</td>
</tr>
<tr>
<td>Ed(Gy):</td>
<td>99.82±2.72</td>
<td>91.45±5.11</td>
<td>114.10±5.80</td>
</tr>
<tr>
<td>Aliquot:</td>
<td>11/15</td>
<td>11/12</td>
<td>15/15</td>
</tr>
<tr>
<td>Depth (m):</td>
<td>10</td>
<td>3.3</td>
<td>6.5</td>
</tr>
<tr>
<td>Cosmic ray rate (Gy/Ka):</td>
<td>0.09</td>
<td>0.19</td>
<td>0.12</td>
</tr>
<tr>
<td>Dose rate (Gy/Ka):</td>
<td>4.16±0.32</td>
<td>3.08±0.23</td>
<td>3.44±0.27</td>
</tr>
<tr>
<td>Age (Ka):</td>
<td>23.99±1.95</td>
<td>29.72±2.80</td>
<td>32.92±3.02</td>
</tr>
</tbody>
</table>

components (Figure 3). Of note in the Palaeolithic portion of this sequence (Components 1–4) is a long period (Component 1) of apparently sporadic, low-intensity occupation during MIS4/5 and early MIS3 (from before 80 to 42 kya), a more substantial occupation (Component 2) during late MIS3 (42–33 kya), near abandonment of the site (Component 3) during the LGM (33–20 kya), and substantial increases in artefact density and diversity in the terminal Pleistocene (20–13 kya) (Component 4) — most notably the introduction of a cryptocrystalline silicate (CCS: e.g. chert) microlithic technology.

**Analytical results**

The following presents a heuristic analysis of Palaeolithic technology, subsistence, and settlement using data generated between 2002 and 2009. It is geared towards identifying correlations between behavioural patterns and major climatic shifts by dividing the entire collection into subpopulations based on temporal assignation: MIS4/5; MIS3; LGM (MIS2) and post-LGM.

**Technology**

Technological change is indicated by 1143 stone artefacts predominantly made of quartz, much less commonly of quartzite, trace amounts of other low quality materials (termed ‘other’), and CCS. Artefacts are mainly waste flakes and shatter, but also cores, unmodified
Figure 3. Dadiwan lithic densities per 100mm level (oldest on the right).

pebbles and cobbles (termed ‘other’), and tools exhibiting either use-wear or retouch (Figure 4). Size and artefact type vary substantially over time. Mean artefact length diminishes significantly ($F = 62.59; p < 0.0001$): MIS4/5 ($\bar{X} = 23.2$ mm); MIS3 ($\bar{X} = 17.1$ mm); LGM ($\bar{X} = 5.9$ mm) and post-LGM ($\bar{X} = 6.4$ mm). Raw material is dominated in all periods by quartz, but proportions drop from a peak of 91% of the assemblage during MIS3 to 62% post-LGM. CCS materials (representing microlithic technology) show the reverse trend, first appearing during the LGM but comprising nearly 40% of the post-LGM assemblage (Figure 5). These differences in material type are significant ($\chi^2 = 270.68; p < 0.001$). Artefact types also vary significantly ($\chi^2 = 165.58; p < 0.001$), with shatter dominating MIS4/5 assemblages; a diverse range of artefact types, including cores and tools (any artefact showing evidence of use-wear or retouch), associated mainly with MIS3 and flakes (including CCS microlithic blades struck from prepared microcores) characterising LGM and post-LGM assemblages (Figure 5). These results indicate that a crude quartz technology, mostly large shatter probably resulting from bipolar reduction, dominates the MIS4/5 assemblage. MIS3 saw a more organised focus on core acquisition, core reduction and more intensive use of waste materials as expedient and retouched tools. LGM and post-LGM assemblages show a marked increase in the frequency of flakes relative to shatter and the introduction of a CCS-based microlithic technology.

Subsistence

Direct subsistence proxies are 1028 faunal specimens ranging from ostrich shell to animal bone to antler. Due to generally poor preservation, taxon identification is rare, but these are mainly from large prey genera — *Cervus, Equus, Bison* and *Bos*. Temporal distribution is somewhat skewed by the larger samples recovered from ZJC02, mainly an MIS3 occupation (comprising 23% of the total faunal assemblage), and Dadiwan, which tracks faunal exploitation through the Late Pleistocene (comprising 75% of the assemblage). Not surprisingly, most faunal remains (72.7%) are from post-LGM contexts, to some degree probably a function of preservation bias in younger deposits. But there are also almost no specimens ($n = 12$) from LGM contexts and fairly abundant remains from MIS3 and even
MIS4/5 contexts (26.1%). This probably indicates a pre-LGM hunting focus, a hypothesis summarily supported by the fact that three other pre-LGM sites contain identifiable large mammalian faunal remains (YWG02, HLG04 and CWG01). The data from the LGM are inconclusive, but following the LGM there appears to have been a reorganisation of subsistence behaviours linked to intensive hunting (Barton et al. 2009).
Settlement

Settlement intensity and pattern show substantial variation. Settlement intensity, reflected in the number of AMS and OSL-dated sites per period, indicates few MIS4/5 sites, abundant MIS3 sites, very few LGM sites and a rebound in site frequency following the LGM (Figure 6). These frequencies corroborate the trend seen in the Dadiwan cultural chronology (Figure 3), with initial, MIS4/5 low-intensity occupation, intensive use of the region during MIS3, less intensive use during the LGM, and a post-LGM rebound in occupational intensity.

Settlement pattern is also intriguing (Table 4). MIS4/5 sites are found exclusively in ridgetop settings. MIS3 sites are found in multiple settings, but mainly in upper-elevation basins that probably featured wetlands or lakes during the MIS3 interstadte, as shown by the
wetland palaeosols associated with many of these sites. LGM sites, though few, are found only adjacent to major rivers, as are post-LGM sites. Equally intriguing is the distribution of hearths, such as those at post-LGM site SXK01. These resemble a similar feature at site PY02, which sits atop LGM Malan Loess, and TX04, AMS dated to 19.6 kya (Bettinger et al. 2005). While the sample is admittedly small (three sites), that hearths are associated only with terminal LGM/post-LGM occupations may indicate that these occupations were more extended, more intensive, or perhaps focused more on food preparation and processing.

**Synthesis and discussion**

The preceding describes a pattern of cultural development that generally corresponds to broader East Asian sequences during the last glacial cycle. In the earliest part of the sequence, initial human/hominid occupation of the WLP is rare but appears to date to before 80 kya — late MIS5 or perhaps early MIS4 — and therefore may be associated with environmental amelioration associated with the MIS5 interglacial. Importantly, deposits dating to this period (~80 kya) help fill the early part of a ~100–50 kya gap in East Asian archaeological sequences. Like most of the rest of East Asia, technological behaviours during MIS4/5 and into MIS3 are remarkably consistent, focused on an expedient, mostly quartz-based core/lake technology that persisted for 40 000 years or more. Temporal resolution
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on the WLP is, however, presently too coarse to ascertain the degree to which the area was abandoned during the MIS4 glacial, though currently no WLP components, except perhaps those at Dadiwan, date between 80 and 60 kya.

Consistent with worldwide estimates for the spread of modern human behaviour, there is abundant evidence for late MIS3 (after ∼50 kya) occupation and behavioural change both at Dadiwan and other WLP sites. MIS3 technology and settlement patterning may indicate the spread or development of new, Upper Palaeolithic stone tool technologies and human expansion into new, previously-unexploited environments. In contrast, LGM occupations are few, characterised by a narrow environmental focus and the possible inception of microblade production using prepared-core techniques seen elsewhere in East Asia during and immediately after this time. The dearth of LGM sites may also correspond to an East Asian population ‘bottleneck’ related to pre-to-post LGM cultural discontinuities. The abundance and diversity of post-LGM assemblages, components and sites is consistent with Terminal Pleistocene/Early Holocene population rebound and economic intensification seen throughout East Asia (Barton et al. 2007).

If the preceding synopsis of cultural development in the WLP is accurate, then it is clear that significant behavioural changes are temporally correlated with major climatic shifts affiliated with glacial cycling: initial occupations are during the MIS5 interglacial; there is little or no evidence of glacial MIS4 occupation; fundamental behavioural changes are associated with large and/or intensive MIS3 interstadial occupations; there is little evidence of occupation during the LGM stadial and post-LGM behavioural changes are profound. Pre-MIS3 data are admittedly somewhat inconclusive, but later data are consistent with a four-part hypothesis that: (1) a wet-warm MIS3 interstadial provided abundant and predictable resources which supported relatively large WLP hunter-gatherer populations; (2) LGM environmental decline and resource depression severely reduced population density; (3) novel behavioural adaptations were adopted or developed during the LGM; and (4) the intensive behaviours that developed during the LGM became entrenched in larger post-LGM populations. In particular, MIS3 and the LGM had pronounced effects on the evolution of modern behaviour in the region.

Though a coarse history of hominid biogeography on the WLP correlates well with general trends in climate change, we hypothesise that the details of human cultural evolution in the region are more probably the results of complex interactions between resource abundance, population density, social organisation and change in the capacity of humans to transmit and retain information. Increases in the frequency of dated components and the diversity of behaviours during MIS3 might well reflect the combined effects of increased biotic productivity and an influx (or at least saltation) of Eurasian Upper Palaeolithic people and/or behaviours after 50 kya (Brantingham et al. 2001). Declines in the frequency of dated components during the LGM might be explained by lower human population density, itself a function of biotic productivity. However, fundamental changes in technology and settlement/subsistence patterns during this time suggest more complex interactions were at play. It is conceivable that modern humans may not have penetrated the region until well into the LGM, introducing novel blade technologies and perhaps other behaviours as they did so. Alternatively, we speculate that population size and different modes of culture transmission worked in concert with reduced biotic productivity and pronounced climatic variability to
generate behavioural innovation. Theoretically, natural selection should favour individual (trial-and-error) learning over social (specifically, frequency-dependent) learning when environments change rapidly (Aoki et al. 2005). Novel, albeit often unsuccessful, behaviours would thus probably have emerged regularly in smaller LGM groups. However, since small groups may also limit the maintenance of complex cultural behaviours (Henrich 2004), and because social learning is not favoured under volatile change, innovations were short-lived and unlikely to spread. If social learning characterised by a combination of success-based and frequency-dependent behavioural selection indeed dominates in less volatile environments (e.g. McElreath et al. 2008), perhaps post-glacial stabilisation facilitated the rapid spread of the few novel LGM adaptations that survived this period in larger, post-glacial populations. In any event, it is clear that fundamental behavioural changes are temporally correlated with glacial cycling on the WLP and that critical developments during and after MIS3 demand further consideration of the effects of environmentally-mediated population size on social learning, cultural transmission and the spread of modern human behavioural innovations.

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