

# *Beyond arrows on a map: the dynamics of Homo sapiens dispersal and occupation of Arabia during Marine Isotope Stage 5*

Article

Accepted Version

Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0

Nicholson, S. L., Hosfield, R. ORCID: <https://orcid.org/0000-0001-6357-2805>, Groucutt, H. S., Pike, A. W. G. and Fleitmann, D. (2021) Beyond arrows on a map: the dynamics of Homo sapiens dispersal and occupation of Arabia during Marine Isotope Stage 5. *Journal of Anthropological Archaeology*, 62. 101269. ISSN 0278-4165 doi: 10.1016/j.jaa.2021.101269 Available at <https://centaur.reading.ac.uk/96426/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.jaa.2021.101269>

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

[www.reading.ac.uk/centaur](http://www.reading.ac.uk/centaur)

## **CentAUR**

Central Archive at the University of Reading

Reading's research outputs online

**Author's Original Manuscript – Postprint**

This is an Author's Accepted Manuscript (text and tables only) of an article published as: Nicholson, S.L., Hosfield, R., Groucutt, H.S., Pike, A.W.G. & Fleitmann, D. 2021. Beyond arrows on a map: the dynamics of Homo sapiens dispersal and occupation of Arabia during Marine Isotope Stage 5.

*Journal of Anthropological Archaeology* 62: 101269

7 Samuel Luke Nicholson<sup>1</sup>, Rob Hosfield<sup>1</sup>, Huw S. Groucutt<sup>2,3</sup>, Alistair W.G. Pike<sup>4</sup>,  
8 Dominik Fleitmann<sup>5</sup>

9 <sup>1</sup>. Department of Archaeology, University of Reading, United Kingdom.

10 <sup>2</sup>. Extreme Events Research Group, Max Planck Institutes for Chemical Ecology, the  
11 Science of Human History, and Biogeochemistry, Jena, Germany.

12 <sup>3</sup>. Department of Archaeology, Max Planck Institute for the Science of Human History,  
13 Jena, Germany.

14 <sup>4</sup>. Department of Archaeology, University of Southampton, United Kingdom.

15 <sup>5</sup>. Quaternary Environmental Geology, Department of Environmental Sciences,  
16 University of Basel, Switzerland.

17

18 Corresponding authors:

19 Sam Nicholson

20 [sam.nicholson@reading.ac.uk](mailto:sam.nicholson@reading.ac.uk)

21 Rob Hosfield

22 [r.hosfield@reading.ac.uk](mailto:r.hosfield@reading.ac.uk)

23

# Beyond arrows on a map: the dynamics of *Homo sapiens* dispersal and occupation of Arabia during Marine Isotope Stage 5

## Abstract

Arabia occupies a crucial central position between Africa and Eurasia. The northward expansion of the monsoonal rain-belt and the formation of grasslands during Marine Isotope Stage (MIS) 5 provided favourable conditions for *H. sapiens* to occupy and traverse now arid areas of Arabia. While “Green Arabia” may have been a crucial stepping-stone on the way to *H. sapiens* global settlement, the occupation of Arabia is an important area of study in itself and could offer vital perspectives into human-environment interactions. In particular, Green Arabia can offer a unique insight into processes of human dispersal, occupation and extirpation in an environmentally fluctuating landscape. Here we synthesise archaeological, palaeoclimate and ethnographic data to develop a holistic model for the occupation of Green Arabia and offer targets for future research. We suggest that, on broad timescales, the resource availability and carrying capacity of Green Arabia facilitated rapid population expansion and occupation across Arabia. On human time-scales, dispersal was probably a slow process due to the requirements of metapopulation structures, likely consisting of many “micro-dispersals” spanning numerous generations. Transitions to more arid conditions were probably echoed by local hominin extirpations, dispersals into surrounding regions and retraction to resource-retaining core areas.

## 1. Introduction

*Homo sapiens* occupation of Arabia during MIS 5 is becoming an important topic in the debate of human dispersals from Africa. Until recently, it was considered that MIS 5 *H. sapiens* dispersals were restricted to the East Mediterranean Levant; with

“successful” expansions into broader Eurasia only occurring ~65-50 ka (Mellars, 2006; Shea, 2008; Klein, 2009; Mellars et al., 2013). However, mounting evidence shows that dispersals during MIS 5 may have had a longer-term impact on human distribution than previously considered (Petruglia et al., 2007; Liu et al., 2015; Rabett, 2018). These dispersals were probably facilitated by substantial increases of rainfall, abundant freshwater resources and grassland environments in Saharo-Arabia during MIS 5 warm substages (MIS 5e: 128-121 ka, 5c: 104-97 ka and 5a: ~82-77 ka) (Burns et al., 1998, 2001; Fleitmann et al., 2011; Rosenberg et al., 2011, 2012, 2013; Matter et al., 2015; Groucutt et al., 2018; Nicholson et al., 2020).

The role of Arabian environments is crucial for exploring dispersal models, given their position between sub-Saharan Africa and Eurasia (Fig. 1). Yet, owing to the early stages of research in the area, there has been a tendency to view Arabia as part of a network of prehistoric highways to the rest of Eurasia (Armitage et al., 2011; Rosenberg et al., 2011; Bae et al., 2017; Tierney et al., 2017). While useful when discussing broad changes in human distribution, this ‘arrows on maps’ approach obscures nuanced discussions of how *H. sapiens* dispersed (into Arabia and also back into Africa), traversed and occupied landscapes on “human” timescales. Such approaches can also obscure the specific local ecological and environmental characteristics that are critical in understanding introduction, occupation and extirpation.

To stimulate new discussions, we combine palaeoenvironmental, archaeological and ethnographic data to provide new insights into human-environment interactions within Green Arabia. The aim of this paper is to review the current state of knowledge and also, and more importantly, develop a more nuanced perspective and a new model for *H. sapiens* dispersal and occupation of Arabia. While the examples given are focussed

towards Arabia, such discussions may be useful for understanding dispersal at broader geographical scales and in other landscape settings. In a similar fashion to White (2006) and Hosfield (2016), this paper is speculative and aims to stimulate new questions and targets for future research.

## **2. Arabian Climate and Palaeoclimate**

### **2.1. Current climates and environments of Arabia**

The current climate of Arabia is governed by two major weather systems: the Mediterranean frontal system in winter (December, January and February) and the African/Indian Summer Monsoon in summer (June, July and August). Precipitation over much of the peninsula averages  $<200 \text{ mm yr}^{-1}$ , largely delivered in winter by the Winter Mediterranean Cyclonic system (WMCs). The African and Indian Summer Monsoons currently only penetrate the southernmost tips of Yemen and Oman, following the annual migration of the Inter-Tropical Convergence Zone (ITCZ) (Glennie and Singhvi, 2002; Weyhenmeyer et al., 2002). Annual precipitation is greatest in the highlands of Yemen, where rainfall may reach over  $500 \text{ mm yr}^{-1}$ . Temperatures across the Peninsula may reach well in excess of  $40^{\circ}\text{C}$  during summer and can fall below freezing in winter. Evaporation over much of the peninsula is close to or greater than annual precipitation. The resultant low effective moisture (precipitation – evaporation) means that vegetation across most of the peninsula is sparsely distributed, which is also exaggerated by recent overgrazing. The densest and most diverse vegetation occurs within the highlands of Yemen, Hajar, Dhofar and Jebel Akhdar, focussed around streams, valleys and the south facing slopes prone to occasional mists (Miller and Cope, 1996). However, localised rains that penetrate deep into the soils are echoed by opportunistic vegetation blooms, even in the sandy deserts. Standing

waterbodies and perennial rivers are not common and usually small in size. Localised rains and low carrying capacity of sands often allow the formation of interdunal ephemeral closed lakes and streams within the endoreic basins of Arabia. This means that, while indeed there are often water sources available, they are frequently scattered and spatiotemporally variable (e.g., Petraglia et al., 2020).

## 2.1 Palaeoclimate and environment of Arabia during MIS 5 wet periods

Substantial increases of precipitation across the Saharo-Arabian deserts occurred during MIS 5e (~128 to 121 ka BP), 5c (~104 to 97 ka BP) and 5a (~82 to 77 ka BP). Analysis of speleothem fluid inclusion  $\delta^{18}\text{O}$  and  $\delta D$  from Yemen and Oman indicate that enhanced precipitation was delivered by the ASM and ISM (Fleitmann et al., 2003b; Nicholson et al., 2020). Substantial enhancements in the intensity and spatial extent of the monsoonal rain-belt were a result of increased summer insolation and reduced glacial-boundary conditions (Fleitmann et al., 2011; Rosenberg et al., 2013; Nicholson et al., 2020). Speleothem growth at Mukalla and Hoti Cave is coherent with the formation of Mediterranean sapropels S5 (128.3 – 121.5 ka BP), S4 (107.8 – 101.8 ka BP) and S3 (85.8 – 80.8 ka BP) and negative shifts in Soreq Cave  $\delta^{18}\text{O}_{\text{ca}}$  (Bar-Matthews et al., 2003; Grant et al., 2012, 2016, 2017). These respond to increased precipitation in the Ethiopian Highlands and the “source effect”, caused by discharge of low- $\delta^{18}\text{O}$  monsoon-driven freshwater runoff from the Nile, respectively (Bar-Matthews et al., 2003; Grant et al., 2017). Further correspondence is observed with marine sediment cores from the Gulf of Aden (RC09-166: Tierney et al., 2017 and KL-15: Fleitmann, 1997), the Red Sea (KL-11: Fleitmann, 1997; Siddall et al., 2003) and the Mediterranean (ODP 967: Larrasoana et al., 2003; Williams et al., 2015; Grant et al., 2017); all records show substantial changes of Saharo-Arabian continental wetness (Fig. 2), recoding precipitation amount, surface runoff and soil humidity. While



some palaeolake deposits and alluvial records do have ages that overlap with colder substages (e.g., Rosenberg et al., 2011, 2013; Parton et al., 2015a, 2018; Groucutt et al., 2018), the intervening periods of MIS 5d and 5b are generally characterised by a return to more arid conditions (Fleitmann et al., 2011; Grant et al., 2017; Nicholson et al., 2020).

The ASM and ISM increased annual precipitation to 600-300 mm yr<sup>-1</sup> over much of Arabia (Otto-Bliesner, 2006; Fleitmann et al., 2011; Jennings et al., 2015; Fig. 2A). The ASM monsoon rain-belt reached as far north as the Nafud Desert, as determined by palaeolake activation and climatic modelling (Waldmann et al., 2010; Rosenberg et al., 2013; Jennings et al., 2015), and perhaps contributed to the catchment of palaeolake Mudawwara at 29°N during MIS 5e (Petit-Maire et al., 2010). Precipitation was lowest in the northern areas of Arabia, receiving annual rainfall of 300-200 mm yr<sup>-1</sup> and in some places even less (Jennings et al., 2015). This resulted in meridional (more in the south) and zonal (more in the west) precipitation gradients across Arabia. The zonal precipitation gradient, for instance, was caused by the incursion of the ASM into western Arabia (Herold and Lohmann, 2009; Rosenberg et al., 2013; Gierz et al., 2017; Nicholson et al., 2020). In combination with speleothem fluid inclusion  $\delta^{18}\text{O}$  and  $\delta D$  values, seasonal stalagmite  $\delta^{18}\text{O}_{\text{Ca}}$  and  $\delta^{13}\text{C}_{\text{Ca}}$  cycles (stalagmite H13 from Hoti Cave) indicate a shift to a summer-dominated precipitation regime. However, winter rains continued to deliver additional precipitation over Arabia (Gierz et al., 2017) and were enhanced in the Levant (Vaks et al., 2010; Orland et al., 2019). The dominance of summer rainfall across Arabia led to a distinct “wetter” summer and “drier” winter seasonality (Gierz et al., 2017; Nicholson et al., 2020). As well as increased summer precipitation, increased cloud cover of the monsoon system resulted in reduced evaporation (Herold and Lohmann, 2009) and led to increased effective moisture

during the summer. The Dhofar region of Oman – which is prone to increased cloud cover, misting and vegetation blooms in the summer, despite rainfall remaining low – is frequently used as an analogue for periods of enhanced precipitation (e.g., Rose et al., 2019).

It is important to note that there were variations in the duration and intensity of different wet periods. Speleothem  $\delta^{18}\text{O}_{\text{Ca}}$  (Mukalla and Hoti caves: Fleitmann et al., 2011; Nicholson et al., 2020), marine sediment core  $\delta D_{\text{leaf-wax}}$  (RC09-166: Tierney et al., 2017) and grainsize data (KL-11 and KL-15: Fleitmann, 1997) indicate that MIS 5e experienced the longest and most intense increase in monsoonal precipitation. The ASM was intensified for ~6.8 kyrs as indicated by the deposition of sapropel S5 (Grant et al., 2017) and Nile outflow was ~8.8 times higher than today (Amies et al., 2019). While MIS 5c and 5a lasted for similar periods of ~6 and 5 kyrs respectively, they were characterized by more positive  $\delta^{18}\text{O}_{\text{Ca}}$  (Fleitmann et al., 2011; Nicholson et al., 2020) and  $\delta D_{\text{leaf-wax}}$  (Tierney et al., 2017) compared to MIS 5e, indicating that rainfall was less intense than MIS 5e. To place these MIS 5 sub-stages in context, speleothem  $\delta^{18}\text{O}_{\text{Ca}}$  from all Late Pleistocene wet periods were more negative (increased rainfall) than the Holocene Humid Period (HHP), in which increased rainfall supported human occupation in the now arid interiors of the Sahara and Arabia (Kuper and Kropelin, 2015; Groucutt et al., 2020; Petraglia et al., 2020).

Extensive surveys and GIS analyses of the Arabian Peninsula have shown that increased precipitation activated widespread palaeolake and river systems (Breeze et al., 2015, 2016). In southern Arabia, this is exemplified by palaeolakes Mundafan, Khujaymah and Saiwan (Rosenberg et al., 2011, 2012; Groucutt et al., 2015c; Tab. 1), further lakes and sabkhas in the central Rub' al Khali (Matter et al., 2015) and alluvial/fluvial deposits in the UAE (Parton et al., 2015a). Southern Arabian

172 palaeolakes typically contain the ostracod *Darwinula stevensoni* and the mollusc *Unio*  
173 sp., both require fresh and open running water conditions and diverse lacustrine flora  
174 and fauna communities (Rosenberg et al., 2011, 2012; Matter et al., 2015). In addition,  
175 the presence of *D. stevensoni* shows these lakes were perennial, retaining freshwater  
176 during dry seasons (Rosenberg et al., 2011, 2012). Phytolith data from Mundafan  
177 shows that grasslands, with some woody cover, were present in the nearby vicinity  
178 (Groucutt et al., 2015d).

179 In northern Arabia, extensive studies of the Jubbah basin have been crucial to  
180 characterising local environmental shifts in response to climate changes. Lake  
181 formation in the Jubbah basin occurred during MIS 5 (Parton et al., 2018; Tab. 2) with  
182 smaller interdunal lakes close by (Rosenberg et al., 2013). Despite a seasonal  
183 precipitation regime (Nicholson et al., 2020), rainfall was sufficient to sustain perennial  
184 freshwater lakes and riverine systems with diverse flora and fauna communities  
185 (Rosenberg et al., 2011, 2012; Breeze et al., 2015; Matter et al., 2015; Parton et al.,  
186 2018). Colder temperatures in winter months would have been echoed by reduced  
187 evaporation, perhaps aiding the perennial character of these waterbodies. Minor  
188 winter rainfall also likely contributed to maintaining year-round standing waterbodies,  
189 but most recharge would have occurred in the summer months by the ASM  
190 (Rosenberg et al., 2013). Additional deep lakes in northern Arabia include Al Wusta,  
191 B'r Hayzan and Khall Amayshan; their diatom and palaeontological records indicate  
192 environments and climates typically reflecting those of Jubbah (Rosenberg et al.,  
193 2013; M. Stewart et al., 2020b). GIS mapping has identified further large lake basins  
194 within 100 km of Jubbah (Breeze et al., 2015, 2017) and that wetlands and lakes were  
195 probably more numerous in the western Nafud than elsewhere in northern Arabia

(Breeze et al., 2017), and supported multiple phases of hominin occupation (Scerri et al., 2015).

While palaeolakes have been (and will continue to be) vital to characterising the environments of Green Arabia, improved dating must be a target for future research. OSL dating of palaeolake sediments is difficult, due to factors such as the challenge of estimating environmental dose rates in such dynamic environments (Clark-Balzan et al., 2017). Underlying sands are often dated as they consist of aeolian material theoretically good for OSL dating, and it can be argued that they would have become stabilised by the increased rainfall that led to lake formation shortly afterwards. While in some cases this is true (Groucutt et al., 2018), it is possible for lake deposition to occur on top of much older sands (M. Stewart et al., 2020a). Furthermore, compared to other records (such as speleothems), dating of palaeolakes suffers from considerable age uncertainties (often in excess of 10% of the absolute age) and are often “wobble-matched” to speleothem ages (e.g., Rosenberg et al., 2013). Thus, unlike speleothem records (e.g., Nicholson et al., 2020), it is very difficult to construct precise palaeoclimate records from lake sequences. The challenges include identifying major hiatuses and seasonal differences in precipitation, assessing whether lakes were diachronic, or assigning lakes to specific MISs and their substages. While Bayesian approaches can be used to mitigate uncertainties (e.g., Groucutt et al., 2018), their applicability can be limited by small sample sizes with sometimes significant age reversals, which could provide artificial and misleading ages.

Nevertheless, the presence of perennial waterbodies supported large faunal communities across Arabia. Excavations at Al Wusta (late MIS 5) have yielded remains of *Hippopotamus*, *Kobus*, *Pelorovis* and *H. sapiens*, as well as ostrich

eggshells (Groucutt et al., 2018). Large tooth marks on the fossils also indicate a diverse carnivore guild was present (Groucutt et al., 2018). Similar taxa have been identified at the nearby site of Khall Amayshan ( $117 \pm 8$  ka BP: Rosenberg et al., 2013) including, Elephantidae, Hippopotamidae, ostrich eggshell, Equidae, Bovidae and Hippotraginae (M. Stewart et al., 2020b). Three important points to take from the presence of *Hippopotamus* are 1) freshwater bodies were at least 2 m deep and likely perennial; 2) sufficient foraging and vegetation would have been present within 1-3 km of these lakes; and 3) the lakes would have included gently sloping banks and beaches (Jablonski, 2004), which would have made them easily accessible to other animals (including humans). Additionally, a mixture of juvenile and adult (interpreted to represent a herd) elephant prints (as well as fossils eroding from the sediments) were identified at the Alathar palaeolake ( $112 \pm 10$  to  $121 \pm 11$  ka BP), suggesting that substantial biomass was located in the nearby vicinity (M. Stewart et al., 2020a).

The palaeontological records of southern Arabia seemingly match the pattern of northern Arabia: Alcelaphinae, Bovinae, *Arabitragus jayakari*, Cervidae and Equidae have been uncovered from Late Pleistocene deposits in the Rub' Al Khali (McClure, 1984; Stewart et al., 2019). While many of these deposits were originally dated to MIS 3, they have since been re-dated to MIS 5 via the OSL and TT-OSL methods (Rosenberg et al., 2011, 2012). These taxa demonstrate that temperate to semi-arid grasslands were located near to perennial waterbodies, with sufficient vegetation resources to support communities of large herbivores.

Increased effective moisture and soil humidity suggest that vegetation density was enhanced across the Saharo-Arabian deserts during MIS 5 warm substages. In Arabia, grasslands were present both in close proximity to lakes (Rosenberg et al., 2013; Groucutt et al., 2015c, 2018) and elsewhere (Bretzke et al., 2013; Nicholson et

al., 2020). Phytolith analysis of sediments recovered from MIS 5e archaeological contexts (assemblage C) of Jebel Faya, UAE, included Pooids, Panicoids, Chloridoids and long grasses. Cyperaceae, Asteraceae, Palmae and other grasses were also present in small quantities – evincing mixed C<sub>3</sub>/C<sub>4</sub> grassland (Bretzke et al., 2013). Speleothem growth at both Mukalla and Hoti Cave indicate that effective moisture and soil humidity were much greater in MIS 5e, and soils had formed in the now desert areas of Yemen. Calcite carbon isotope ratios ( $\delta^{13}\text{C}_{\text{ca}}$ ) at Mukalla Cave (-8 to -2‰) fall within C<sub>3</sub>/C<sub>4</sub> grassland signatures (Nicholson et al., 2020). However, there remain three key uncertainties:

1) Speleothem  $\delta^{13}\text{C}_{\text{ca}}$  and phytolith analyses cannot identify species-level floral compositions. Without species level assignments, it is not possible to establish plant based Mutual Climate Range estimates, or provide a detailed insight into the floral resources available to humans.

2) Environmental records are sparsely distributed; meaning the majority of the “green” transformation of the Arabian landmass is based on interpolation or analogues with the Sahara (e.g., Larrasoana et al., 2013). This interpretation is complicated by two factors; a recent Red Sea dust source record which demonstrates the Arabia-Nubian shield became the dominant dust source during MIS 5 warm substates, indicating some areas remained relatively dry (Hartman et al., 2020). Additionally, the archaeological and palaeontological records of northern Africa (where predicted precipitation matched northern Arabia) suggest a model of semi-isolated populations and show that some areas remained arid or semi-arid (Scerri et al., 2014b). It is therefore not self-evident that Arabia was completely “green”.

And, 3) there is little knowledge of spatio-temporal environmental variability and seasonal differences in vegetation, which may have influenced seasonal survival strategies. Annual  $\delta^{13}\text{C}_{\text{ca}}$  cycles of stalagmite H13 (Hoti Cave) indicate seasonal differences in drip-rate as a result of a drying of the aquifer and reduced soil moisture, which was likely echoed by a vegetation response. But there are no direct examples of seasonal vegetation variability. Understanding environmental responses to seasonal precipitation, both across space and time, must be a target for future research.

Another issue to consider is that our discussions of Arabian environments and their suitability for dispersal have typically been limited to climate and vegetation feedback (Erlandson and Braje, 2015; Nicholson et al., 2020). Groucutt (2020a) has recently stressed the importance of other factors – with an emphasis on volcanism – on shaping both the environment and topography of Arabia. For example, while eruptions can often have negative short-term effects (contamination of water, deterioration of patch quality), there are also long-term positives, such as creating particularly fertile areas. Eruptions were fairly common throughout MIS 5, with notably high frequencies during early (~130 ka BP) and late MIS 5 (~90-80 ka BP) (Groucutt, 2020a). While the impact of these on humans in Arabia is not understood, it certainly raises questions concerning the variable nature of environments, their impact on human populations within “green” phases, as well as human adaptation, resilience and/or localised extirpations.

In summary, pronounced shifts of Arabian environments during MIS 5 were primarily influenced by expansions and contractions of the monsoon domain on orbital timescales. These resulted in the expansion of grassland environments and allowed *H. sapiens* to expand into the now arid interiors. However, there remain many

uncertainties and key questions for the future. For example, were lakes diachronic, or, similar to today, was there high variability in their availability? In the Arabian interior, what were environments like beyond riparian zones? How heterogenous was the landscape – both spatially and throughout the duration of these green periods – and what sort of microenvironments were present? What other topographic features played a role in shaping the environments available to humans? All-encompassing studies of environmental and topographic heterogeneity will be of key importance for moving beyond simplistic narratives of *H. sapiens* dispersals and occupations of Arabia.

## 2.2 Archaeology

Due to the scarcity of recovered hominin fossils, archaeological finds provide the main record of human activity in Arabia. Middle Palaeolithic (MP) assemblages characterise the early Late Pleistocene archaeological record of Arabia, found mostly in the now-arid interior (Fig. 3). While a large portion of these are surface finds, of those that have been excavated, most have been derived from palaeolake sediments, or deposits on the margins of palaeolakes (Petraglia et al., 2012; Groucutt et al., 2015b, 2015d, 2016), and close to fluvial channels (Breeze et al., 2015).

### 2.2.1 Northern Arabia

In northern Arabia, several Middle Palaeolithic assemblages have been described from the Jubbah Basin. The upper assemblage at the site of Jebel Qattar-1 (JQ-1) dates to ca. 75 ka BP, and features a focus on centripetal Levallois reduction, with both preferential and recurrent methods used (Petraglia et al., 2011; 2012). Other core reduction methods are present in small frequencies, such as discoidal. Retouched forms include side retouched flakes and a small retouched point. These characteristics



are reminiscent of the African MSA and the Levantine MIS 5 Middle Palaeolithic (Groucutt et al., 2015b). Another site, Jebel Umm Sanman (JSM-1), consists of a surface scatter and small published excavations. Available OSL dates loosely constrain the assemblage to late MIS 5 or shortly after (Petraglia et al., 2012). The assemblage again features a focus on centripetal Levallois technology. A larger excavation was conducted at the site of JKF-1, but OSL dating the deposit again proved challenging, and resulted in an age range of 50-90 ka BP (Petraglia et al., 2012). While the core technology is rather amorphous, reflecting the frequent use of small quartz pebbles, the main reduction process involved the primarily unidirectional reduction of quartzite blocks to produce convergent Levallois flakes (Groucutt et al., 2015c). JKF-1 therefore demonstrates a rather different set of characteristics to JQ-1 and JSM-1, and reflects more similarities with MIS 3 sites from the region (e.g., Jennings et al., 2016). In addition to these sites, a variety of surface Middle Palaeolithic sites have been recovered, such as JKF-12 (e.g., Groucutt et al., 2017).

While research on the Middle Palaeolithic assemblages of Jubbah is ongoing, what can we say about the character and meaning of technological variability observed? Some aspects of this probably have a pragmatic basis. For instance, as mentioned the frequent use of small quartz pebbles at JKF-1 seems to have influenced reduction. Perhaps a wider impact, however, concerns differential reduction intensity. Groucutt et al. (2017) explored how reduction intensity (measured as the scar density index) varied with distance from raw material sources, and found a positive relationship. This explains why the JQ-1 assemblage is so small and reduced. Such factors, however, occur within an umbrella of centripetal Levallois technology.

Quantitative comparison of Jubbah lithic assemblages (JKF-1, JKF-12 and JSM-1) with assemblages from NE Africa highlighted that, while there were some similarities

343 in core preparation techniques, high levels of technological variability mitigates against  
344 a simple interpretation (e.g. a single dispersal out of Africa echoed by a single techno-  
345 cultural complex). Instead, the variability was taken to reflect occupation by multiple  
346 populations at different times (Scerri et al., 2014a). However, given the nature of the  
347 burial contexts, current dating inaccuracies between these assemblages, as well as  
348 their temporal distribution, discussions of cultural hetero/homogeneity are not without  
349 uncertainty. Overall, while an MIS 5 occupation of the Jubbah area by hominin groups  
350 using centripetal Levallois technology is clear, further assessments are required to  
351 distinguish whether groups were present at other points, and indeed whether there  
352 were multiple occupations within MIS 5.

353 Similarities to Jubbah are apparent across northern Arabia. The Al Wusta  
354 archaeological assemblage (dated to late MIS 5 and the only assemblage discussed  
355 here with direct association to a *H. sapiens* fossil) again emphasises a focus on  
356 centripetal Levallois reduction, similar to those of east and NE Africa and the Levant  
357 (Groucutt et al., 2018). Interestingly, the assemblage was mostly comprised of chert  
358 artefacts (65%), showing that morphological similarities with the Jubbah assemblages  
359 transcend raw material choices. Elsewhere in northern Arabia, Middle Palaeolithic  
360 assemblages of the Najd appear more homogenous than in southern Arabia, although  
361 there are still differences between assemblages. For example, whereas cores from  
362 sites ABY-1 and SHW-11 were characterised by preferential centripetal Levallois  
363 reduction, AZA-2 was characterised by recurrent centripetal reduction. Additionally,  
364 QAN-1 possessed the only example of a Saudi Arabian assemblage dominated by  
365 discoidal reduction. The new sites presented by Groucutt et al. (2016) lack  
366 chronometric dating which, given that humans repeatedly occupied Arabia throughout  
367 the Pleistocene (Bailey et al., 2015; Scerri et al., 2018a), means addressing spatio-

temporal variability from these assemblages is not straightforward. However, the variability does suggest that expectations of a single defining stone tool culture moving into Arabia are overly simplistic. Instead, it is apparent that different reduction strategies were employed within northern and central Arabia, likely reflecting differences in cultural traditions, mobility strategies or durations of individual occupations. Nevertheless, these findings present a clear indication that the Middle Palaeolithic record of northern Arabia is dominated by a focus on centripetal Levallois technology, as found with *Homo sapiens* in the Levant and northeast Africa (Groucutt et al., 2015b). This is likely influenced by dispersals from these regions into Arabia, as well as back into Africa and/or the Levant following returns to desert conditions.

An additional line of evidence for human activity comes from the identification of seven hominin footprints from a remnant of the Alathar palaeolake, dated between  $112 \pm 10$  and  $121 \pm 11$  ka BP (likely MIS 5e). M. Stewart et al. (2020a) suggest that these can be assigned to *H. sapiens* on the basis of the size of the prints, plus the spread of *H. sapiens* into Arabia and adjacent regions and absence of Neanderthals in the Levant during MIS 5. The recovery context, spatial distribution and orientation of the prints provide a snapshot of very high-resolution behavioural patterns from a rapidly forming site. The various orientation and scatter of the prints around the lake were interpreted to reflect non-directional activities, though these were mostly oriented in a southward direction. Combined with the absence of butchery practices on animal fossils and absence of stone tools, it was suggested that Alathar was, at this time, only briefly visited by humans. The absence of stone tools (while potentially related to poor surface preservation) contrasts other lake sites, which document more intensive usage of lake margin habitats, suggesting that the Alathar prints provides a unique record of human activity in Arabia.

### 2.2.2 Southern Arabia

The archaeology of southern Arabia is somewhat more variable than northern Arabia. Artefacts uncovered at the Mundafan palaeolake (~100-80 ka) included Levallois cores characterised by recurrent centripetal (30%) and preferential with centripetal preparation (22%) strategies (Groucutt et al., 2015d). Flakes were described as standardised and typically ovoid or rectangular in shape. Additionally, a high retouched component was present, which is typically uncommon in the Arabian Middle Palaeolithic. Further undated Middle Palaeolithic sites at Mundafan share a similar technology (Crassard et al., 2013), and lack other forms of technology such as the Nubian Levallois method.

In Dhofar, in the southwest of Oman, a rather different kind of Middle Palaeolithic technology dominates. Here numerous assemblages, particularly in western Dhofar near the spring at Mudayy, demonstrate a focus on the Nubian Levallois reduction method (Rose et al., 2011; Usik et al., 2013). The findings are virtually all surface scatters, except at the site of Aybut al Auwal where a single Nubian Levallois core and a few other lithics were found redeposited in a fluvial channel (Rose et al., 2011). To the discoverers these sites, as well as occasional hints of Nubian Levallois technology in Saudi Arabia (e.g., Crassard and Hilbert, 2013), provide evidence for long distance movement between the Nile Valley and southern Arabia. Groucutt (2020b) has suggested an alternative explanation, that the Dhofar Middle Palaeolithic possibly represents convergent evolution of Nubian Levallois technology, which is found from South Africa to India and over a ca. 200,000 year period. Given the minimum age of ca. 107 ka from Aybut al Auwal, it may be that MIS 5e or earlier dispersals retracted to reliable water sources in southern Arabia and developed distinctive local cultural trajectories. While currently poorly chronologically constrained, the varied Palaeolithic

418 assemblages from southern Arabia certainly indicate a complex demographic history  
419 (e.g., Jagher, 2009; Delagnes et al., 2012; Bailey et al., 2015).

420 Further regional artefact variability is confirmed at Jebal Faya, UAE. This site is a  
421 notable exception to the general Arabian record, with artefacts recovered from rock  
422 shelter sediments and an occupation history spanning from MIS 5e to MIS 3 (Armitage  
423 et al., 2011; Bretzke et al., 2014). Assemblage C, dated to  $127 \pm 16$  and  $123 \pm 10$  ka  
424 (MIS 5e), contained artefacts with a variety of reduction strategies including the  
425 production of volumetric blades and Levallois debitage, bifaces, and retouched forms.  
426 Qualitative characteristics of this assemblage were considered similar to artefacts  
427 recovered from sites such as Muguruk, Kenya (Armitage et al., 2011). Indeed, while  
428 apparently diverse in its characteristics, the dominant characteristic of Assemblage C  
429 seems to be the focus on bifacial reduction, which is unusual for the Arabian Middle  
430 Palaeolithic. Assemblage B, however, contained little evidence of bifacial and  
431 Levallois reduction, with the exception of a few convergent flakes which are similar to  
432 Levallois points (Armitage et al., 2011). Further variability was observed in  
433 assemblage A dated to  $40.2 \pm 3.0$  and  $38.6 \pm 3.1$  ka (MIS 3); assemblage A contained  
434 a diverse range of reduction strategies and retouched morphologies including the  
435 production of denticulates, side scrapers, end scrapers, and burins. Flakes were  
436 produced from platform cores, which contrasts the apparent absence of prepared  
437 platforms from Assemblage C (Armitage et al., 2011). The difference between artefact  
438 types, as well as densities, have been interpreted to relate to differences in techno-  
439 cultures (Armitage et al., 2011) and “distinct traditions in spatial behaviour” (Bretzke  
440 and Conard, 2017) between occupation phases. In summary, the assemblages of  
441 Jebel Faya are not only different from each other, but also seemingly differ from other  
442 Arabian assemblages.

### 2.2.3 Summary

Overall, there is a high degree of spatial variability in stone tool assemblages across Arabia (e.g., Fig. 4). Ongoing analysis of the archaeological record of Arabia suggests that sites in northern Arabia are repeatedly similar to those from NE Africa and the Levant (Petruglia et al., 2012; Scerri et al., 2014b; Groucutt et al., 2019), whereas those in the south repeatedly feature localised characteristics (Armitage et al., 2011; Delagnes et al., 2012). We posit three, not necessarily mutually exclusive, potential explanations for this:

1) multiple populations, with entirely different techno-cultures, entered Arabia during various MIS 5 substages, perhaps from different routes (via the Sinai Peninsula or the Bab al Mandab strait).

2) *H. sapiens* populations entered southern Arabia by crossing the Bab al Mandeb strait on to an exposed continental shelf during periods of low sea-levels (Parker and Rose, 2008; Bailey et al., 2015). Low sea-levels, however, are typically related to drier periods (Rosenberg et al., 2011) and thus initial dispersals would take place prior to the onset of MIS 5e, 5c and 5a (e.g., Rohling et al., 2013). In this instance, widespread population expansions into the Arabian interiors would occur with the onset of wetter conditions (Armitage et al., 2011).

3) Arabian assemblages, particularly those in the south, represent a high degree of localisation following an initial dispersal into northern Arabia.

In terms of entry points into Arabia, it is important to consider that Arabian wet phases in the warm substages of MIS 5 (Fleitmann et al., 2011; Nicholson et al., 2020) occurred when sea-levels were higher than the intervening periods (Rosenberg et al.,

2012; Grant et al., 2014). During the intervening stadials, an expansion of the desert likely inhibited widespread dispersals into Arabia. There is also currently no evidence from Arabia or NE Africa for relevant sea-faring technologies. We take this pattern to suggest a northern dispersal route into Arabia, followed by southward movements into Arabia following green palaeohydrological corridors (e.g., Breeze et al., 2016). We interpret the archaeological signature of the north to represent initial dispersed populations, which quickly diversified and adapted to local environments. As populations expanded southwards into Arabia, local techno-cultural characteristics developed in response to increasing distance from initial populations and local environmental and cultural factors. This pattern was likely repeated during each MIS 5 wet period, as each substage was likely represented by a new wave of settlement. However, only a handful of dated sites are currently available for analysis and few are temporally aligned. It is therefore vital to increase the spatio-temporal resolution and variability of the Arabian archaeological record to test this. The current available methods and the nature of preservation in these environments means that producing such a database will be challenging. Furthermore, many reports from Arabian archaeological sites classify assemblages based on qualitative morphological features; there is currently only one example of inter-site quantitative morphological comparison (e.g., Scerri et al., 2014b). Further analysis comparing many assemblages are needed to generate key information on inter-assemblage morphological variability across Arabia.

Analysis and interpretation of the Arabian and Levantine records is also complicated by survey biases and taphonomic issues. One is geography – the Levant is less than one-tenth the size of Arabia. Another consideration is that the history and intensity of extensive Palaeolithic archaeological survey in Arabia is much younger than that of

491 the Levant. Simply put, we may have much fewer pieces of the puzzle in Arabia.  
492 Assemblages that actually or potentially display similarities to other regions (i.e., the  
493 Levant and NE Africa [Groucutt et al., 2019], or East Africa [Armitage et al., 2011])  
494 may be the only pieces yet identified in a much more complicated puzzle. What of  
495 population links between Mesopotamia and NE Arabia? Did these exist and did the  
496 Euphrates and Tigris rivers act as population corridors between these regions (e.g.,  
497 Breeze et al., 2016; Bretzke and Conard, 2017)? If so, to what extent did these  
498 demographic links shape stone tool assemblages and morphologies? Another  
499 pertinent consideration is the recovery context and the impact on geomorphic,  
500 hydrological and physiographic factors. Most of the dated and stratified archaeological  
501 assemblages from Arabia were found in alluvial, fluvial and lacustrine sediments (apart  
502 from Jebel Faya). However, surface sites have been located across Arabia (Rose et  
503 al., 2011; Groucutt et al., 2016). These, and areas comprised of drift sands, would  
504 have experienced greater reworking than stratified alluvial, fluvial and lacustrine  
505 sediments. The resulting variations in assemblage formation and composition are  
506 partially shaping our understanding of the prehistoric settlement of Arabia.

507 It is important to note that many objects (e.g. bone tools, wood tools, eggshells) do not  
508 readily preserve but could have been crucial to surviving Green Arabia. For example,  
509 Ostrich eggs could have been used as water containers, and facilitated temporary  
510 movement away from waterbodies. While ostrich eggshell fragments were uncovered  
511 at Mundafan (Groucutt et al., 2015d), it cannot be discerned whether these were used  
512 by humans. Also, animal skins and bladders could have been used to carry water and  
513 are commonly used today. Again, these do not readily preserve in the archaeological  
514 record. Additionally, the archaeological record of Arabia does not provide evidence of  
515 symbolic practices, which are commonly associated with rock shelters and caves in



regions with dense *H. sapiens* occupation histories. Across Africa, it is clear that the MSA included specialised hunting tools, use of aquatic resources, bone tools, microlithic technologies, long distance trade, art and decoration, use of pigment, specialised hunting, structure building, social organisation and systematic processing (Mcbrearty and Brooks, 2000; Blegen, 2017; Scerri, 2017; Brooks et al., 2018). While evidence of all of these are not available from Arabia, hints of long-distance sourcing/transfer comes from occasional examples of putatively exotic raw materials in available assemblages (Petruglia et al., 2012). However, further research needs to be done on characterising raw material source, and distinguishing primary and secondary (e.g. fluvial) raw material sources. Given that *H. sapiens* dispersed from NE Africa, it is likely that many behaviours present in Middle to Late Pleistocene Africa were key components of their behavioural repertoire. Conversely, our interpretation that *H. sapiens* were highly mobile (see below) could suggest that costly symbolising practices were not effective in these settings. Nevertheless, finding specific examples from Arabia is necessary for understanding the range of *H. sapiens* behavioural variability. This must be a target of future research.

### **3. *H. sapiens* in Green Arabia**

In order to understand how humans became established, survived and retracted in Arabia, it is necessary to synthesise the environmental and archaeological records with reference to ecological, anthropological and biological datasets. Here, we address the processes of dispersal into Arabia, the dynamics of long-term survival, and population decline in the face of fluctuating climates.

#### **Dispersal**

Dispersal differs from migration, being defined as “a strategy to increase fitness in a heterogeneous landscape by changing the environment in which an organism lives” (Bowler and Benton, 2005: 218). One of the most crucial factors when discussing the distribution of organisms and their introduction into new areas is the resources available to enhance their reproductive fitness. Both periods of increased rainfall (Shultz and Maslin, 2013; Maslin et al., 2014) and aridity (deMenocal, 1995) have been considered to influence hominin adaptation and dispersal on long time-scales through their impacts on changing resources and population dynamics. Whereas transitions to aridity promote dispersal or extirpation due to reduced resources – namely, water, flora and fauna (deMenocal, 1995) – periods of increased rainfall (and vegetation) promote population expansions within the hominin food chain, resulting in hominin population increases and, ultimately, dispersal/adaptation/extinction due to competition pressure (Shultz and Maslin, 2013; Maslin et al., 2014). The palaeoenvironmental record of Arabia clearly highlights that increased resources (water, vegetation and other animals) meant carrying capacity was greatly enhanced and offered new habitats for dispersal during wet periods. On the other hand, returns to aridity may have had a push and/or extirpating effect on resident populations. Another consideration is that shorter events within both ‘wetter’ and ‘drier’ phases, and how these might have stimulated potentially short-lived and rapid dispersals and declines.

This is consistent with recent considerations of *source* and *sink* population dynamics (Dennell et al., 2011; Dennell, 2017). A population sink is described as a region in which reproduction is too low to replace individuals. These are typically located in areas in which resource availability is either scarce or highly variable. On the other hand, source areas are regions in which reproduction outweighs the replacement of

individuals, due to resource abundance or stability. Dennell (2017: 5390) explains that “Demographic expansion thus depends greatly upon (i) extinction rates in sink populations at the edge of the inhabited range and (ii) the ability of the main source populations to support sink populations, especially those at the edge of the range. This becomes difficult when population densities are low and intergroup distances are high”. With regards to Arabia, we may infer that rates of extinction were severely lowered at the edge of original habitats (such as sub-Saharan Africa and NE Africa) in green phases such as early MIS 5e, due to increased resources promoted by monsoonal rainfall. This facilitated former sink populations to become new source populations and allowed expansion into newly habitable areas.

It must also be considered that human populations typically form metapopulations, which can be defined as “a group of spatially separated populations occupying a nexus of favourable patches” (Smith, 2013: 75). Humans can be characterised by “tight” metapopulations, which maintain cohesion through kinship, ideology, culture and additional forms of identity over large distances (Dennell, 2017; Scerri et al., 2018b, 2019). The examples given above of long-distance cultural exchange throughout the MSA suggest that human metapopulations were maintained over >100s of kms (Blegen, 2017; B. A. Stewart et al., 2020). Dennell (2017) highlights two main benefits of species that settle areas as part of a broader metapopulation. Firstly, resilience to stochastic events and environmental/resource variability at the metapopulation level. Whereby groups comprising a metapopulation are more widely distributed in a landscape, mitigating against a metapopulation extinction. Secondly, a trial-and-error basis of settling new habitats in which a “failing” group can be replaced or repopulated by groups from the broader metapopulation. Smith (2013) and Dennell (2017) highlight that this trial-and-error basis allows multiple groups to settle new habitats in a short

period of time, where sufficient inter-group connectivity mitigates against local extinctions. If this model was relevant to Green Arabia dispersals then we should expect to see evidence that Arabian populations with cultural similarities likely maintained some contact over considerable distances. There is currently a suggestion for imported material into the Jubbah basin; however, further examples of long-distance exchange are required to understand the specific inter-connectivity of Arabian populations.

In summary, it is likely that dispersal and settlement of Arabia was a response to feedback effects between resource availability, patch carrying capacity and population pressure. Increasing rainfall across the southern limits of Saharo-Arabia, in which *H. sapiens* were likely already present, meant populations gradually expanded, resulting in increased pressure for dispersal into the new surrounding areas. We may describe this almost as a continuous dispersal, whereby populations expanded gradually into new areas with higher carrying capacities, which facilitated local population growth. Over time, local competition pressure forced expansion into additional new habitats. As rains were predominantly derived from the ASM and ISM monsoons, one likely aspect is that, as populations likely entered northern Arabia, the easiest expansion route was southwards towards greater water availability and food resources. Although the specifics of mobility were likely structured by lakes, rivers and other waterbodies (such as the Wadi Al-Batin) could have provided corridors towards the eastern coast of Arabia (Breeze et al., 2016; Petraglia et al., 2020). As populations moved southwards, increasing differentiation due to separation from a metapopulation and autochthonous development may explain the localisation of stone tool assemblages in these regions. Additionally, northward dispersals into the Levant were likely aided by increased winter (Vaks et al., 2010) and (particularly during MIS 5e) summer (Petit-

614 Maire et al., 2010; Torfstein et al., 2015; Orland et al., 2019) precipitation across the  
615 southern Levant. This dual source of rainfall could mean that human mobility patterns  
616 differed, though, more information on the specific duration and impact of summer  
617 rainfall is required from the Levant.

618 Another important factor concerns whether Arabia was already occupied when  
619 humans dispersed into the area in MIS 5. Whether other human populations (or  
620 species) were already present could have had a dramatic impact on how *H. sapiens*  
621 settled Arabia (e.g., Dennell 2017). Evidence of Oldowan and Acheulean artefacts  
622 across Arabia likely suggest that pre-MIS 5 occupations had occurred (Groucutt and  
623 Petraglia, 2012). Recent dating of the Saffaqah archaeological deposits conform to  
624 this, placing an Acheulean occupation during late MIS 7 and possibly extending into  
625 MIS 6 (Scerri et al., 2018a). Identification of *H. sapiens* at Apidima (Greece: Harvati et  
626 al., 2019) and Misliya (Israel: Hershkovitz et al., 2018, but see Sharp and Paces, 2018)  
627 caves, argued to date to MIS 7 and MIS 6 respectively, suggest that *H. sapiens* had  
628 dispersed from Africa prior to MIS 5, and Arabia would have been along this dispersal  
629 pathway. If these fossils and dates are accepted then, it is possible that *H. sapiens*  
630 occupied Arabia during MIS 7 or 6.

631 Yet, debates on whether there were long-term refugia in Arabia have not produced  
632 clear results (e.g., Rose, 2010; Bretzke and Conard, 2017). It must be considered that  
633 the majority of dated sites from Arabia have been excavated from palaeolake  
634 sediments, which are strongly aligned to interglacial periods. In other words, a failure  
635 to identify archaeological material from glacial periods is to be expected if lakes were  
636 less frequent. While indeed alluvial aggradation in Oman suggests MIS 6 was  
637 characterised by perhaps long-term, albeit less intense precipitation ~160-150 ka BP  
638 (Parton et al., 2015a), absence of stalagmite growth in both the Negev (with exemption

of one sample dated to  $157.2 \pm 3.8$  ka BP; Vaks et al., 2010) and southern Arabia (Nicholson et al., 2020) highlight that precipitation was generally lower between during MIS 6. In this case, Arabia may have been particularly challenging for hominin occupation prior to 130 ka BP, or perhaps characterised by a low intensity occupation in isolated areas such as the Yemeni highlands. For now, our working model is that Arabia was frequently occupied during Arabian green phases throughout the Middle Pleistocene (Scerri et al., 2018a; Nicholson et al., 2020); whereas returns to aridity saw depopulations (see below). Therefore, it is very likely that Arabia was devoid of other humans when *H. sapiens* first entered during MIS 5e. In this case, if settlement and occupation across Green Arabia was uncontested, it was perhaps more rapid than it might have otherwise been.

#### Occupation

But what can we say about the more intricate processes of occupying Green Arabia? We have discussed the broad environmental outlines of Arabia, yet many fundamental aspects are currently not known. For example, while some areas would have become grassland environments with water sources, the attractiveness and stability of these landscapes is currently poorly constrained. Many Arabian Palaeolithic archaeological sites are located close to palaeolakes (Petraglia et al., 2012; Groucutt et al., 2015c, 2018; Scerri et al., 2015); although Jebel Faya is a notable exception, wadis and lakes have been identified within 5 km of the site (Armitage et al., 2011; Bretzke et al., 2013). The perennial nature of the palaeolakes made these attractive habitats, which included the provision of freshwater during the drier winter months. These could have also provided rich opportunities for hunters (human and non-human) to ambush prey that are drawn to the water (Hitchcock et al., 2019). Yet, the discovery of hippo fossils – arguably one of the most dangerous land mammals, killing ca. 500 people a year –

and evidence of a diverse carnivore guild during late MIS 5 and other Pleistocene sites (Groucutt et al., 2018; Stewart et al., 2019) indicate that small lakes in Arabia also came with challenges.

A further complicating factor is that we currently have little information on the character of edible plant resources for *H. sapiens* in Arabia. For example, bushed or wooded lake shores and river margins of East Africa tend to host mesophilic plants and other plants producing berries, nuts and seeds (Lind and Morrison, 1974; Sept, 1994; Marean, 1997). Drier soils, escarpments and inselbergs contain a plethora of carbohydrate rich plants with underground storage organs (USOs – including rhizomes, tubers, corns and bulbs; Vincent 1985); these are generally nutritious, palatable and visible year-round, requiring little to no processing (Gott and Murray, 1982; Vincent, 1985). As such, these are staple constituents of the year-round diet of traditional societies across Africa (Vincent, 1985; Marean, 1997). Their wide usage by traditional societies and identification of charred rhizomes (*Hypoxis*) at Border Cave (Wadley et al., 2020) may suggest these were a crucial source of year-round nutrition in the past. These could have been extremely useful resources during the drier seasons of Green Arabia, when other vegetation resources declined. However, the specific characteristics of the flora of Green Arabia must be a target for future research.

In any case, given the predominantly grassland character of Green Arabia during pluvial periods and the palaeontological record (e.g., Groucutt et al., 2018; Stewart et al., 2019), it is likely that meat was also a significant component of the hominin diet. As well as the spread of animals from places such as Africa using the same semi-arid landscapes followed by humans, i.e. the ‘fellow travellers’, there could also have been rich animal resources already present within Arabia. As Foley (1987) noted, in

689 important ways plants vary more than animals, and so rapid spread without significant  
690 adaptation could have occurred. Foley (1987: 263) commented that a “deer is very  
691 much like an antelope”, and so for human groups moving into Arabia they would have  
692 encountered grasslands rich in bovids at least broadly similar to those with which they  
693 were familiar. As described above, it is quite possible that humans arriving during MIS  
694 5 entered a region in which other human were absent for tens of thousands of years  
695 due to the prevailing harsh environmental conditions of MIS 6. In such a situation,  
696 humans may have faced a ‘naïve fauna’ (e.g., Dennell, 2018), and as a result been  
697 able to expand rapidly before animals changed their behaviour.

698 Data compiled by Binford (2001) and Kelly (2013) illustrates clear relationships  
699 between productivity and aspects of human demography and behaviour. Ethnographic  
700 studies indicate that arid and semi-arid environments are associated with highly  
701 mobile populations living in large ranges, with low population densities. Most hunter  
702 gatherer groups – i.e. excluding rare examples such as the sedentary groups of the  
703 north American coast – live at densities of 0.1 to 1 person per km<sup>2</sup> (Kelly, 2013), and  
704 sometimes at less than a tenth of this. Likewise, societies with a high reliance on meat  
705 tend to be highly mobile and live at low population densities (Grove, 2009). There are  
706 however caveats to the kinds of datasets presented in sources such as Binford (2001)  
707 and Kelly (2013). For example, most studied societies are from the Americas, with  
708 very few samples from Asia, and none from northern Africa and the Middle East. But  
709 even accounting for regional specifics, the broad pattern of how demographic and  
710 behavioural dynamics relate to the environments offers us an approximation of past  
711 patterns. It is clear from the data presented by Kelly (2013: 80-84) that low primary  
712 biomass is associated with large total areas for hunter gatherer groups and large total  
713 distances covered annually. In the more marginal areas of northern Arabia – which



were at the limits of the monsoonal rains during periods such as MIS 5 – we can expect pioneering human groups to have been highly mobile and with large ranges.

Another consideration is that, while virtually all studied human groups have been expanding in population size at a relatively rapid rate (i.e. often more than 1% a year; Gurven and Davison, 2019), it is clear that hunter-gatherer populations remained relatively small in the long run. There must, therefore, have been periodic phases of catastrophic mortality (Gurven and Davison, 2019). Arabia probably exemplifies such processes, as the opening of a window of opportunity in northern Arabia could have led to rapid population expansion south- and eastwards (as above), but also environmental fluctuations (e.g., brief arid periods) were likely reflected by sudden population declines. For example, climate records from the Holocene Humid Period demonstrate that Green Arabia was prone to sudden and brief periods of aridity (such as the 8.2 kyr event; Fleitmann et al., 2003a), which were likely echoed by population declines (Petraglia et al., 2020). While current palaeoclimate records from MIS 5e, 5c and 5a are not of sufficient resolution to detect brief periods of aridity, it is probable that variable climatic factors continued to exert control on population.

The specific geological and environmental aspects of Arabia are also significant for human occupations. The deserts of Arabia are typically characterised by either rocky surfaces or deep sand (Miller and Cope, 1996). This contrasts with somewhere like Australia, where a thin sand cover means small water holes are abundant, allowing widespread occupation as long as populations are at low density and are highly mobile (e.g., Smith, 2013). Current evidence suggests that in some areas of Arabia there was little occupation for broad periods of the past, due to a lack of water. Examples of this include areas in northern Arabia which were not proximal to palaeolakes and feature a very sparse archaeological record (Breeze et al., 2017), and a paucity of evidence

for post-Acheulean occupation in the Dawadmi area of central Arabia (Jennings et al., 2015; Groucutt et al., 2016; Shipton et al., 2018). It is our impression that populations in Pleistocene Arabia were relatively tethered to water sources, such as lakes and rivers. These would have occurred at varying scales. It is the deep basins that contained palaeolakes, such as Jubbah in the Nafud Desert, which have produced archaeological findings covering every major period of human prehistory from the Acheulean onwards (Scerri et al., 2015, 2018a). Middle Palaeolithic sites, which mostly date to MIS 5, are significantly closer to palaeorivers than would be expected by a random distribution (Breeze et al., 2015). The connection between human demography/behaviour and the palaeohydrological structure of Arabia is therefore clear at a broad scale. The fact that Arabia is a tilted plateau – rising steeply along the entire western margin, dropping away gradually to the east – means that during Pleistocene humid periods an extensive network of rivers formed across the peninsula (Breeze et al., 2015, 2016). What is unclear is the finer scale mechanics of this process, such as the mobility patterns which allowed survival in highly seasonal environments. This must on some level have meant retraction to perennial water sources, yet as discussed above there would have been competition for these and so the specific mobility and social strategies employed are currently unclear.

## Decline

An important aspect for understanding *H. sapiens* occupation in Arabia is what happened following climatic optima. As climates deteriorated during MISs 5e-5d and 5c-5b and 5a-4, reduced resources and lowered habitat carrying capacity would have increased competition pressure, resulting in population declines via dispersals, retractions and local extirpations (Bretzke and Conard, 2017). This may have included “back to Africa” dispersals, for which analogues may be drawn from MIS 4-3 genetic

764 data (Soares et al., 2012; Hervella et al., 2016). Additionally, absence of clean genetic  
765 splits throughout the Pleistocene suggest ongoing gene flow for tens of thousands of  
766 years (Groucutt et al., 2015a; Bergström et al., 2020). For the most part, however, we  
767 expect that depopulations were complex processes with varying human responses.

768 Depopulations during drier periods are supported by a lack of continuity in the  
769 archaeological record at sites in the north (Groucutt et al., 2015b) and also large  
770 occupation gaps at Jebel Faya (Armitage et al., 2011; Bretzke and Conard, 2017).  
771 While lack of continuity in northern Arabia lake sites may partly be a result of  
772 taphonomic processes and the favourable preservation biases of wet periods,  
773 punctuated archaeological phases at Jebel Faya provides additional evidence for a  
774 reduced human presence on the Arabian Peninsula during drier periods. However,  
775 evidence of occupation during MIS 3 complicates the rather simplistic picture that  
776 humans could not survive drier periods (Armitage et al., 2011; Delagnes et al., 2012;  
777 Jennings et al., 2016), suggesting either: 1) humans re-entered Arabia during MIS 4-  
778 3 (Mellars, 2006); or 2) some populations survived following the return to arid  
779 conditions during the MIS 5a-4 transition (e.g., Armitage et al., 2011). Absence of  
780 prolonged, wide-spread and intense climatic amelioration across Saharo-Arabia  
781 during MIS 4-3 (Fleitmann et al., 2011; Rosenberg et al., 2013; Grant et al., 2017;  
782 Tierney et al., 2017; Nicholson et al., 2020) means a large-scale dispersal and  
783 sustained occupation would be surprising from a palaeoclimatic perspective. Perhaps  
784 the MIS 3 evidence represents small-scale 'pulse' dispersals and short-lived  
785 occupations associated with brief wetter events? In the latter case, the low resource  
786 availability across much of the peninsula implies that these were probably outliers,  
787 which survived in temporary green spots and/or in the higher productivity areas of the  
788 southern Arabian highlands (Delagnes et al., 2012, 2013). Previous hints of different

land-use patterns between occupation phases have been witnessed in the Jebel Faya artefact assemblages (C: MIS 5e; B: late MIS 5 or MIS 3; and C: MIS 3), suggesting localised adaptations to changing environmental conditions (Armitage et al., 2011; Bretzke and Conard, 2017).

As outlined above, the debate on whether long-term refugia existed across Arabia have not produced clear results. So, whether or not *H. sapiens* populations survived within Arabia at varying scales and repopulated Arabia during the MIS 4-3 transition or were completely extirpated during returns to aridity (and the implications that might have for MIS 5d-5c and 5b-5a) is not clear. Others have considered that coastal regions may have provided suitable habitats for occupation following returns to aridity (e.g., Bailey et al., 2015; Erlandson and Braje, 2015). The expulsion of groundwater aquifers may have transformed exposed continental shelves into high resource areas (Faure et al., 2002; Rose, 2010; Erlandson and Braje, 2015). Yet there is currently insufficient data from Arabia to understand both their specific environmental character, spatio-temporal distribution and suitability to provide long-term habitats. Another potential issue is that where hominins have been present in coastal environments, productive inland environments were also available and exploited (e.g., Rector & Reed, 2010; Reynard & Henshilwood, 2019; Roberts et al., 2020). So, whether a long-term population could flourish whilst pinned to a narrow coastal strip in an otherwise barren landscape is not without uncertainty. Until further evidence for sustained coastal occupation and relevant sea-faring technologies becomes available, we suggest that populations dispersed primarily into inland habitats and occasionally exploited coastal environments. Further evidence of specific micro-environments, potential dispersal pathways and their suitability for occupation between wetter phases

are required to understand the resilience of human populations following transitions to aridity.

For now, our working model is that the Late Pleistocene saw repeated population expansions into Arabia, with the largest and most sustained dispersals occurring during warm substages. This was followed by regional extirpations and population retractions during returns to aridity (e.g., MIS 5d, 5b and 4) (Bretzke and Conard, 2017). This perhaps included retractions to retaining high-resource areas, as well as “pumped” dispersals out of Arabia and into the Levant and back into Africa (e.g., Groucutt et al., 2015a).

## **5. Summary and conclusion**

Overall, we highlight that dispersal likely occurred on different rates and scales. In the first instance, we stress that dispersal could have been a rather slow process on human and ecological timescales as a) populations need time to grow, and b) it is unlikely that there was specific directionality to dispersal. As precipitation and primary productivity rose in Saharo-Arabia, populations inflated, and competition pressure forced expansion into new patches with higher carrying capacities. In order to maintain successful populations, it is highly unlikely that societies were rapidly moving across these landscapes, with a single population traversing from Africa into Eurasia. Instead, multiple semi-connected mobile metapopulations (Scerri et al., 2019) were linked across semi-arid Arabia by palaeohydrological corridors (e.g., Scerri et al., 2014a; Breeze et al., 2016). Over time, this would have included expansion towards areas of higher primary productivity and following water courses into southern Arabia (Groucutt and Petraglia, 2012; Breeze et al., 2017) and also the Levant (Shea, 2008). As populations moved into southern Arabia, it is expected that, due to both distance and

ultimately due to separation, distinctive regional populations developed and came to vary from their parent populations (Fig. 5). This is potentially reflected by the localised characteristics of Middle Palaeolithic southern Arabian archaeological assemblages and autochthonous development of stone tool techno-cultures following green periods (Armitage et al., 2011; Delagnes et al., 2012). As precipitation declined and “green” environments retracted and dilapidated, reduced resources caused increased competition pressure, local extirpations (Bretzke and Conard, 2017), fragmentation, dispersal into remaining higher-resource areas (Delagnes et al., 2012), and group home-range size expansions. We relate these longer-term dispersals to the warm substages of MIS 5e, 5c and 5a, and perhaps MIS 3.

However, dispersal could have, at times, been rather rapid. Stochastic increases of precipitation and environmental amelioration could have facilitated very brief expansions into the now arid interiors of Arabia. These dispersals were perhaps more ephemeral and mobile in nature and perhaps subjected to local extirpations. Our current interpretation of these more ephemeral dispersals is that these were likely related to colder substages, such as MIS 5d and 5b, and perhaps MIS 4, 3 and 2. However, we emphasise that understanding these differences in environments, dispersal rates and dynamics will be key for moving away from simplistic narratives of *H. sapiens* dispersals.

## **6. Targets for future research**

The conclusions drawn from this paper are based on current and limited evidences which are partly linked to theoretical expectations. We acknowledge that substantial gaps remain in both archaeological and environmental datasets, which obscure our understanding of human-environment interactions in the past. Throughout this paper

we have identified challenges and targets for new research. Here, we briefly provide a few suggestions as to how these may be achieved:

1. Linking theoretical models with archaeological data can allow us to overcome simplistic narratives of how humans occupied and moved through Arabia. This includes considering macro-scale causes of dispersal, but also more micro-scale and immediate influences on human “lived” timescales. Yet, we must be cautious of interpreting archaeological data to fit our theoretical expectations: further analysis must also test expectations. For example:

a. It is not necessarily the case that past animal migration patterns matched the present (e.g., Henton et al., 2018). If past migration patterns of prey species altered from the present, this could alter our expectations of hominin migration and dispersal patterns. Detailed isotope (O, C and Sr) analysis of both animal and human remains could prove useful in discussions of home-range sizes and seasonal migration patterns (Pike et al., 2016; Henton et al., 2018).

b. Chemical analyses (X-Ray Fluorescence/electron probe microanalysis) of stone tool assemblages and local and distant raw material outcrops could provide information on the distance of raw material transfer (local sourcing versus imported material) (Blegen, 2017; Brooks et al., 2018). This could be used to determine how “connected” past populations may have been, and how far groups were moving.

c. Linking climate records, environmental parameters and population dynamics through numerical models (e.g., Beyer et al., 2020) could

provide an additional method to visualise and test dispersal models  
across the Arabian Peninsula.

2. Identification and mitigation of biases within both archaeological and  
environmental records must be achieved to understand the full suite of *H.*  
*sapiens* behaviours and human-environment interactions in Green Arabia.

For example:

- a. There are very few examples of material culture beyond stone  
artefacts in Arabia. Further surveys of caves and open-air sites,  
which are not raw material procurement localities, on the Arabian  
Peninsula should be conducted to identify evidence of more  
permanent residency and material culture beyond stone artefacts.
- b. Although it is not currently certain if a-DNA could preserve in Arabian  
speleothems, efforts to extract and analyse a-DNA could provide  
species level identification flora and fauna (e.g., Stahlschmidt et al.,  
2019) and improve the current environmental record of Arabia.  
Additionally, more detailed considerations of the Mutual Climatic  
Range (MCR) of fossil fauna, diatoms, ostracods and phytolith taxa  
could prove useful in characterising past environments.

3. Improved dating of archaeological contexts is crucial for linking these to  
other palaeoclimate datasets and understanding the dynamics of *H. sapiens*  
occupation and dispersal. Current methods favour Bayesian statistical  
modelling (e.g., Groucutt et al., 2018) or “wigggle-matching” with precisely  
dated records (such as stalagmites, e.g., Rosenberg et al., 2013). New  
methods must be developed, as well as development of current methods



910 (e.g., OSL and single amino acids for <sup>14</sup>C dating), to provide robust and  
911 independently dated archaeological records.

912 Here, we have synthesised palaeoclimate, environmental, archaeological and  
913 anthropological data – and combined these with theoretical models – to understand  
914 human-environment interactions and dispersal mechanism in Arabia during MIS 5.  
915 Current evidence has allowed us to create a working model that moves beyond an  
916 “arrows on a map linking Africa to Eurasia” approach to dispersal. We emphasise that  
917 macroscale as well as microscale population dynamics must be considered when  
918 explaining human dispersal across landscapes.

## 919 **Acknowledgments**

920 This work was supported by the AHRC South, West and Wales Doctoral Training  
921 Partnership (Grant AH/L503939/1). HSG thanks the Max Planck Society for funding.

## 922 **References**

- 923 Amies, J.D., Rohling, E.J., Grant, K.M., Rodríguez-Sanz, L., Marino, G., 2019.  
924 Quantification of African Monsoon Runoff During Last Interglacial Sapropel S5.  
925 *Paleoceanography and Paleoclimatology*. 34, 1487–1516.
- 926 Armitage, S.J., Jasim, S.A., Marks, A.E., Parker, A.G., Usik, V.I., Uerpmann, H.P.,  
927 2011. The southern route “out of Africa”: Evidence for an early expansion of  
928 modern humans into Arabia. *Science*. 331, 453–456.
- 929 Bae, C.J., Douka, K., Petraglia, M.D., 2017. On the origin of modern humans: Asian  
930 perspectives. *Science*. 358, eaai9067.
- 931 Bailey, G.N., Devès, M.H., Inglis, R.H., Meredith-Williams, M.G., Momber, G.,

932 Sakellariou, D., Sinclair, A.G.M., Rousakis, G., Al Ghamdi, S., Alsharekh, A.M.,  
 933 2015. Blue Arabia: Palaeolithic and underwater survey in SW Saudi Arabia and  
 934 the role of coasts in Pleistocene dispersals. *Quaternary International*. 382, 42–  
 935 57.

936 Bar-Matthews, M., Ayalon, A., Gilmour, M., Matthews, A., Hawkesworth, C.J., 2003.  
 937 Sea - land oxygen isotopic relationships from planktonic foraminifera and  
 938 speleothems in the Eastern Mediterranean region and their implication for  
 939 paleorainfall during interglacial intervals. *Geochimica et Cosmochimica Acta*. 67,  
 940 3181–3199.

941 Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million  
 942 years. *Quaternary Science Reviews*. 10, 297–317.

943 Bergström, A., McCarthy, S.A., Hui, R., Almarri, M.A., Ayub, Q., Danecek, P., Chen,  
 944 Y., Felkel, S., Hallast, P., Kamm, J., Blanché, H., Deleuze, J.-F., Cann, H.,  
 945 Mallick, S., Reich, D., Sandhu, M.S., Skoglund, P., Scally, A., Xue, Y., Durbin,  
 946 R., Tyler-Smith, C., 2020. Insights into human genetic variation and population  
 947 history from 929 diverse genomes. *Science*. 367, eaay5012.

948 Beyer, R.M., Krapp, M., Eriksson, A., Manica, A., 2020. Windows out of Africa: A  
 949 300,000-year chronology of climatically plausible human contact with Eurasia.  
 950 *bioRxiv*. 2020.01.12.901694.

951 Binford, L., 2001. *Constructing Frames of Reference. An analytical method for*  
 952 *archaeological theory building using ethnographic and environmental data.*  
 953 *University of California Press, London.*

954 Blegen, N., 2017. The earliest long-distance obsidian transport: Evidence from the

955 ~200 ka Middle Stone Age Sibilo School Road Site, Baringo, Kenya. *Journal of*  
956 *Human Evolution*. 103, 1–19.

957 Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal  
958 strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*.  
959 80, 205–225.

960 Breeze, P.S., Drake, N.A., Groucutt, H.S., Parton, A., Jennings, R.P., White, T.S.,  
961 Clark-Balzan, L., Shipton, C., Scerri, E.M.L., Stimpson, C.M., Crassard, R.,  
962 Hilbert, Y., Alsharekh, A., Al-Omari, A., Petraglia, M.D., 2015. Remote sensing  
963 and GIS techniques for reconstructing Arabian palaeohydrology and identifying  
964 archaeological sites. *Quaternary International*. 382, 98–119.

965 Breeze, P.S., Groucutt, H.S., Drake, N.A., Louys, J., Scerri, E.M.L., Armitage, S.J.,  
966 Zalmout, I.S.A., Memesh, A.M., Haptari, M.A., Soubhi, S.A., Matari, A.H., Zahir,  
967 M., Al-Omari, A., Alsharekh, A.M., Petraglia, M.D., 2017. Prehistory and  
968 palaeoenvironments of the western Nefud Desert, Saudi Arabia. *Archaeological*  
969 *Research in Asia*. 10, 1–16.

970 Breeze, P.S., Groucutt, H.S., Drake, N.A., White, T.S., Jennings, R.P., Petraglia,  
971 M.D., 2016. Palaeohydrological corridors for hominin dispersals in the Middle  
972 East ~250-70,000 years ago. *Quaternary Science Reviews*. 144, 155–185.

973 Bretzke, K., Armitage, S.J., Parker, A.G., Walkington, H., Uerpmann, H.P., 2013.  
974 The environmental context of Paleolithic settlement at Jebel Faya, Emirate  
975 Sharjah, UAE. *Quaternary International*. 300, 83–93.

976 Bretzke, K., Conard, N.J., 2017. Not just a crossroad population dynamics and  
977 changing material culture in southwestern asia during the late pleistocene.

978 Current Anthropology. 58, S449–S462.

979 Bretzke, K., Conard, N.J., Uerpmann, H.P., 2014. Excavations at jebel faya - the  
980 FAY-NE1 shelter sequence. Proceedings of the Seminar for Arabian Studies.  
981 44, 69–81.

982 Brooks, A.S., Yellen, J.E., Potts, R., Behrensmeyer, A.K., Deino, A.L., Leslie, D.E.,  
983 Ambrose, S.H., Ferguson, J.R., D’Errico, F., Zipkin, A.M., Whittaker, S., Post, J.,  
984 Veatch, E.G., Foecke, K., Clark, J.B., 2018. Long-distance stone transport and  
985 pigment use in the earliest Middle Stone Age. Science. 360, 90–94.

986 Burns, S.J., Fleitmann, D., Matter, A., Neff, U., Mangini, A., 2001. Speleothem  
987 evidence from Oman for continental pluvial events during interglacial periods.  
988 Geology. 29, 623–626.

989 Burns, S.J., Matter, A., Frank, N., Mangini, A., 1998. Speleothem-based  
990 paleoclimate record from northern Oman. Geology. 26, 499–502.

991 Clark-Balzan, L., Parton, A., Breeze, P.S., Groucutt, H.S., Petraglia, M.D., 2017.  
992 Resolving problematic luminescence chronologies for carbonate- and evaporite-  
993 rich sediments spanning multiple humid periods in the Jubbah Basin, Saudi  
994 Arabia. Quaternary Geochronology. 45, 50–73.

995 Crassard, R., Hilbert, Y.H., 2013. A Nubian Complex Site from Central Arabia:  
996 Implications for Levallois Taxonomy and Human Dispersals during the Upper  
997 Pleistocene. PLoS ONE. 8.

998 Crassard, R., Petraglia, M.D., Drake, N.A., Breeze, P., Gratuze, B., Alsharekh, A.,  
999 Arbach, M., Groucutt, H.S., Khalidi, L., Michelsen, N., Robin, C.J., Schiettecatte,  
1000 J., 2013. Middle Palaeolithic and Neolithic Occupations around Mundafan

1001 Palaeolake, Saudi Arabia: Implications for Climate Change and Human  
1002 Dispersals. PLoS ONE. 8, e69665.

1003 Delagnes, A., Crassard, R., Bertran, P., Sitzia, L., 2013. Cultural and human  
1004 dynamics in southern Arabia at the end of the Middle Paleolithic. Quaternary  
1005 International.

1006 Delagnes, A., Tribolo, C., Bertran, P., Brenet, M., Crassard, R., Jaubert, J., Khalidi,  
1007 L., Mercier, N., Nomade, S., Peigné, S., Sitzia, L., Tournepiche, J.F., Al-Halibi,  
1008 M., Al-Mosabi, A., MacChiarelli, R., 2012. Inland human settlement in southern  
1009 Arabia 55,000 years ago. New evidence from the Wadi Surdud Middle  
1010 Paleolithic site complex, western Yemen. Journal of Human Evolution. 63, 452–  
1011 474.

1012 deMenocal, P.B., 1995. Plio-Pleistocene African Climate. Science. 270, 53–59.

1013 Dennell, R., 2017. Human colonization of Asia in the late pleistocene the history of  
1014 an invasive species. Current Anthropology. 58, S383–S396.

1015 Dennell, R., Martínón-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin  
1016 variability, climatic instability and population demography in Middle Pleistocene  
1017 Europe. Quaternary Science Reviews. 30, 1511–1524.

1018 Dennell, R.W., 2018. Pleistocene hominin dispersals, naïve faunas and social  
1019 networks. In: Bovin, N., Crassard, R., Petraglia, M.D. (Eds.), Human Dispersal  
1020 and Species Movement: From Prehistory to the Present. Cambridge University  
1021 Press, Cambridge, pp. 62–89.

1022 Erlandson, J.M., Braje, T.J., 2015. Coasting out of Africa: The potential of mangrove  
1023 forests and marine habitats to facilitate human coastal expansion via the

- 1024 Southern Dispersal Route. *Quaternary International*. 382, 31–41.
- 1025 Faure, H., Walter, R.C., Grant, D.R., 2002. The coastal oasis: Ice age springs on  
1026 emerged continental shelves. *Global and Planetary Change*. 33, 47–56.
- 1027 Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate  
1028 surfaces for global land areas. *International Journal of Climatology*. 37, 4302–  
1029 4315.
- 1030 Fleitmann, D., 1997. Klastischer Eintrag in das Rote Meer und den Golf von Aden  
1031 durch den Arabischen Monsun-Untersuchungen an Kolbenlot-Kernen. Diplom-  
1032 Arbeit, Institut und Museum für Geologie und Paläontologie der Georg-August-  
1033 Universität zu Göttingen.
- 1034 Fleitmann, D., Burns, S.J., Mudelsee, M., Neff, U., Kramers, J., Mangini, A., Matter,  
1035 A., 2003a. Holocene forcing of the Indian monsoon recorded in a stalagmite  
1036 from Southern Oman. *Science*. 300, 1737–1739.
- 1037 Fleitmann, D., Burns, S.J., Neff, U., Mangini, A., Matter, A., 2003b. Changing  
1038 moisture sources over the last 330,000 years in Northern Oman from fluid-  
1039 inclusion evidence in speleothems. *Quaternary Research*. 60, 223–232.
- 1040 Fleitmann, D., Burns, S.J., Pekala, M., Mangini, A., Al-Subbary, A., Al-Aowah, M.,  
1041 Kramers, J., Matter, A., 2011. Holocene and Pleistocene pluvial periods in  
1042 Yemen, southern Arabia. *Quaternary Science Reviews*. 30, 783–787.
- 1043 Foley, R.A., 1987. Another Unique Species. *Patterns in human evolutionary ecology*.  
1044 Harlow.
- 1045 Gierz, P., Werner, M., Lohmann, G., 2017. Simulating climate and stable water

1046 isotopes during the Last Interglacial using a coupled climate-isotope model.  
 1047 Journal of Advances in Modeling Earth Systems. 9, 2027–2045.

1048 Glennie, K.W., Singhvi, A.K., 2002. Event stratigraphy, paleoenvironment and  
 1049 chronology of SE Arabian deserts. Quaternary Science Reviews. 21, 853–869.

1050 Gott, B., Murray, L., 1982. Ecology of root use by the Aborigines of southern  
 1051 Australia. Archeology of Oceania. 17, 59–67.

1052 Grant, K.M., Grimm, R., Mikolajewicz, U., Marino, G., Ziegler, M., Rohling, E.J.,  
 1053 2016. The timing of Mediterranean sapropel deposition relative to insolation,  
 1054 sea-level and African monsoon changes. Quaternary Science Reviews. 140,  
 1055 125–141.

1056 Grant, K.M., Rohling, E.J., Bar-Matthews, M., Ayalon, A., Medina-Elizalde, M.,  
 1057 Ramsey, C.B., Satow, C., Roberts, A.P., 2012. Rapid coupling between ice  
 1058 volume and polar temperature over the past 50,000 years. Nature. 491, 744–  
 1059 747.

1060 Grant, K.M., Rohling, E.J., Ramsey, C.B., Cheng, H., Edwards, R.L., Florindo, F.,  
 1061 Heslop, D., Marra, F., Roberts, A.P., Tamisiea, M.E., Williams, F., 2014. Sea-  
 1062 level variability over five glacial cycles. Nature Communications. 5, 5076.

1063 Grant, K.M., Rohling, E.J., Westerhold, T., Zabel, M., Heslop, D., Konijnendijk, T.,  
 1064 Lourens, L., 2017. A 3 million year index for North African humidity/aridity and  
 1065 the implication of potential pan-African Humid periods. Quaternary Science  
 1066 Reviews. 171, 100–118.

1067 Groucutt, H.S., 2020a. Volcanism and human prehistory in Arabia. Journal of  
 1068 Volcanology and Geothermal Research. 402, 107003.

1069 Groucutt, H.S., 2020b. Culture and Convergence: The Curious Case of the Nubian  
1070 Complex. In: Groucutt, H.S. (Ed.), Culture History and Convergent Evolution:  
1071 Can We Detect Populations in Prehistory? Springer, Cham, pp. 55–86.

1072 Groucutt, H.S., Breeze, P., Drake, N.A., Jennings, R.P., Parton, A., White, T.,  
1073 Shipton, C., Clark-Balzan, L., Al-Omari, A., Cuthbertson, P., Wedage, O.M.C.,  
1074 Bernal, M.A., Alsharekh, A., Petraglia, M.D., 2016. The middle palaeolithic of the  
1075 Nejd, Saudi Arabia. *Journal of Field Archaeology*. 41, 131–147.

1076 Groucutt, H.S., Breeze, P.S., Guagnin, M., Stewart, M., Drake, N., Shipton, C.,  
1077 Zahrani, B., Omarfi, A. Al, Alsharekh, A.M., Petraglia, M.D., 2020. Monumental  
1078 landscapes of the Holocene humid period in Northern Arabia: The mustatil  
1079 phenomenon. *The Holocene*. 30, 1767–1779.

1080 Groucutt, H.S., Grün, R., Zalmout, I.A.S., Drake, N.A., Armitage, S.J., Candy, I.,  
1081 Clark-Wilson, R., Louys, J., Breeze, P.S., Duval, M., Buck, L.T., Kivell, T.L.,  
1082 Pomeroy, E., Stephens, N.B., Stock, J.T., Stewart, M., Price, G.J., Kinsley, L.,  
1083 Sung, W.W., Alsharekh, A., Al-Omari, A., Zahir, M., Memesh, A.M.,  
1084 Abdulshakoor, A.J., Al-Masari, A.M., Bahameem, A.A., Al Murayyi, K.M.S.,  
1085 Zahrani, B., Scerri, E.M.L., Petraglia, M.D., 2018. Homo sapiens in Arabia by  
1086 85,000 years ago. *Nature Ecology & Evolution*. 2, 800–809.

1087 Groucutt, H.S., Petraglia, M.D., 2012. The prehistory of the Arabian peninsula:  
1088 Deserts, dispersals, and demography. *Evolutionary Anthropology*. 21, 113–125.

1089 Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M.L., Parton, A., Clark-Balzan,  
1090 L., Jennings, R.P., Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S., Inglis,  
1091 R.H., Devès, M.H., Meredith-Williams, M., Boivin, N., Thomas, M.G., Scally, A.,



1092        2015a. Rethinking the dispersal of *Homo sapiens* out of Africa. *Evolutionary*  
 1093        *Anthropology*. 24, 149–164.

1094        Groucutt, H.S., Scerri, E.M.L., Amor, K., Shipton, C., Jennings, R.P., Parton, A.,  
 1095        Clark-Balzan, L., Alsharekh, A., Petraglia, M.D., 2017. Middle Palaeolithic raw  
 1096        material procurement and early stage reduction at Jubbah, Saudi Arabia.  
 1097        *Archaeological Research in Asia*. 9, 44–62.

1098        Groucutt, H.S., Scerri, E.M.L., Lewis, L., Clark-Balzan, L., Blinkhorn, J., Jennings,  
 1099        R.P., Parton, A., Petraglia, M.D., 2015b. Stone tool assemblages and models for  
 1100        the dispersal of *Homo sapiens* out of Africa. *Quaternary International*. 382, 8–  
 1101        30.

1102        Groucutt, H.S., Scerri, E.M.L., Stringer, C., Petraglia, M.D., 2019. Skhul lithic  
 1103        technology and the dispersal of *Homo sapiens* into Southwest Asia. *Quaternary*  
 1104        *International*. 515, 30–52.

1105        Groucutt, H.S., Shipton, C., Alsharekh, A., Jennings, R.P., Scerri, E.M.L., Petraglia,  
 1106        M.D., 2015c. Late Pleistocene lakeshore settlement in northern Arabia: Middle  
 1107        Palaeolithic technology from Jebel Katefeh, Jubbah. *Quaternary International*.  
 1108        382, 215–236.

1109        Groucutt, H.S., White, T.S., Clark-Balzan, L., Parton, A., Crassard, R., Shipton, C.,  
 1110        Jennings, R.P., Parker, A.G., Breeze, P.S., Scerri, E.M.L., Alsharekh, A.,  
 1111        Petraglia, M.D., 2015d. Human occupation of the Arabian Empty Quarter during  
 1112        MIS 5: Evidence from Mundafan Al-Buhayrah, Saudi Arabia. *Quaternary*  
 1113        *Science Reviews*. 119, 116–135.

1114        Grove, M., 2009. Hunter-gatherer movement patterns: Causes and constraints.

1115 Journal of Anthropological Archaeology. 28, 222–233.

1116 Gurven, M.D., Davison, R.J., 2019. Periodic catastrophes over human evolutionary  
 1117 history are necessary to explain the forager population paradox. Proceedings of  
 1118 the National Academy of Sciences. 116, 12758–12766.

1119 Hartman, A., Torfstein, A., Almogi-Labin, A., 2020. Climate swings in the northern  
 1120 Red Sea over the last 150,000 years from  $\epsilon\text{Nd}$  and Mg/Ca of marine sediments.  
 1121 Quaternary Science Reviews. 231, 106205.

1122 Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C.,  
 1123 Karkanas, P., Thompson, N.C., Koutoulidis, V., Mouloupoulos, L.A., Gorgoulis,  
 1124 V.G., Kouloukoussa, M., 2019. Apidima Cave fossils provide earliest evidence of  
 1125 Homo sapiens in Eurasia. Nature. 571, 500–504.

1126 Henton, E., Ruben, I., Palmer, C., Martin, L., Garrard, A., Thirlwall, M., Jourdan, A.L.,  
 1127 2018. The Seasonal Mobility of Prehistoric Gazelle Herds in the Azraq Basin,  
 1128 Jordan: Modelling Alternative Strategies Using Stable Isotopes. Environmental  
 1129 Archaeology. 23, 187–199.

1130 Herold, M., Lohmann, G., 2009. Eemian tropical and subtropical African moisture  
 1131 transport: An isotope modelling study. Climate Dynamics. 33, 1075–1088.

1132 HersHKovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A.,  
 1133 Bar-Matthews, M., Valladas, H., Mercier, N., Arsuaga, J.L., Martín-Torres, M.,  
 1134 Bermúdez de Castro, J.M., Fornai, C., Martín-Francés, L., Sarig, R., May, H.,  
 1135 Krenn, V.A., Slon, V., Rodríguez, L., García, R., Lorenzo, C., Carretero, J.M.,  
 1136 Frumkin, A., Shahack-Gross, R., Bar-Yosef Mayer, D.E., Cui, Y., Wu, X., Peled,  
 1137 N., Groman-Yaroslavski, I., Weissbrod, L., Yeshurun, R., Tsatskin, A., Zaidner,

1138 Y., Weinstein-Evron, M., 2018. The earliest modern humans outside Africa.  
 1139 Science. 359, 456–459.

1140 Hervella, M., Svensson, E.M., Alberdi, A., Günther, T., Izagirre, N., Munters, A.R.,  
 1141 Alonso, S., Ioana, M., Ridiche, F., Soficaru, A., Jakobsson, M., Netea, M.G., De-  
 1142 La-Rua, C., 2016. The mitogenome of a 35,000-year-old Homo sapiens from  
 1143 Europe supports a Palaeolithic back-migration to Africa. Scientific Reports. 6, 1–  
 1144 5.

1145 Hitchcock, R.K., Crowell, A.L., Brooks, A.S., Yellen, J.E., Ebert, J.I., Osborn, A.J.,  
 1146 2019. The Ethnoarchaeology of Ambush Hunting: A Case Study of ‡Gi Pan,  
 1147 Western Ngamiland, Botswana. African Archaeological Review. 36, 119–144.

1148 Hosfield, R., 2016. Walking in a Winter Wonderland? Strategies for Early and Middle  
 1149 Pleistocene Survival in Midlatitude Europe. Current Anthropology. 57, 653–682.

1150 Jablonski, N.G., 2004. The hippo's tale: How the anatomy and physiology of Late  
 1151 Neogene Hexaprotodon shed light on Late Neogene environmental change.  
 1152 Quaternary International. 117, 119–123.

1153 Jagher, R., 2009. The Central Oman Paleolithic Survey: Recent Research in  
 1154 Southern Arabia and Reflection on the Prehistoric Evidence. In: Petraglia, M.D.,  
 1155 Rose, J.I. (Eds.), The Evolution of Human Populations in Arabia:  
 1156 Paleoenvironments, Prehistory and Genetics (Vertebrate Paleobiology and  
 1157 Paleoanthropology). Springer, Dordrecht, pp. 139–150.

1158 Jennings, R.P., Parton, A., Clark-Balzan, L., White, T.S., Groucutt, H.S., Breeze,  
 1159 P.S., Parker, A.G., Drake, N.A., Petraglia, M.D., 2016. Human occupation of the  
 1160 northern Arabian interior during early Marine Isotope Stage 3. Journal of

1161 Quaternary Science. 31, 953–966.

1162 Jennings, R.P., Singarayer, J., Stone, E.J., Krebs-Kanzow, U., Khon, V.,  
1163 Nisancioglu, K.H., Pfeiffer, M., Zhang, X., Parker, A., Parton, A., Groucutt, H.S.,  
1164 White, T.S., Drake, N.A., Petraglia, M.D., 2015. The greening of Arabia: Multiple  
1165 opportunities for human occupation of the Arabian Peninsula during the Late  
1166 Pleistocene inferred from an ensemble of climate model simulations. Quaternary  
1167 International. 382, 181–199.

1168 Kelly, R.L., 2013. The Lifeways of Hunter-Gatherers: The Foraging Spectrum.  
1169 Cambridge University Press, Cambridge.

1170 Klein, R.G., 2009. The Human Career: Human Biological and Cultural Origins, 3rd  
1171 ed. University of Chicago Press.

1172 Kuper, R., Kropelin, S., 2015. Holocene Occupation of the Sahara : Evolution. 313, 803–807.

1174 Larrasoana, J.C., Roberts, A.P., Rohling, E.J., 2013. Dynamics of Green Sahara  
1175 Periods and Their Role in Hominin Evolution. PLoS ONE. 8, e76514.

1176 Larrasoana, J.C., Roberts, A.P., Rohling, E.J., Winkler, M., Wehausen, R., 2003.  
1177 Three million years of monsoon variability over the northern Sahara. Climate  
1178 Dynamics. 21, 689–698.

1179 Lind, E.M., Morrison, M.E.S., 1974. East African Vegetation. Longman, London.

1180 Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally  
1181 distributed benthic  $\delta^{18}\text{O}$  records. Paleoceanography. 20, 1–17.

1182 Liu, W., Martín-Torres, M., Cai, Y.J., Xing, S., Tong, H.W., Pei, S.W., Sier, M.J.,

1183 Wu, X.H.X.J., Edwards, R.L., Cheng, H., Li, Y.Y., Yang, X.X., De Castro, J.M.B.,  
1184 Wu, X.H.X.J., 2015. The earliest unequivocally modern humans in southern  
1185 China. *Nature*. 526, 696–699.

1186 Marean, C.W., 1997. Hunter-Gatherer Foraging Strategies in Tropical Grasslands:  
1187 Model Building and Testing in the East African Middle and Later Stone Age.  
1188 *Journal of Anthropological Archaeology*. 16, 189–225.

1189 Maslin, M.A., Brierley, C.M., Milner, A.M., Shultz, S., Trauth, M.H., Wilson, K.E.,  
1190 2014. East African climate pulses and early human evolution. *Quaternary*  
1191 *Science Reviews*. 101, 1–17.

1192 Matter, A., Neubert, E., Preusser, F., Rosenberg, T., Al-Wagdani, K., 2015. Palaeo-  
1193 environmental implications derived from lake and sabkha deposits of the  
1194 southern Rub' al-Khali, Saudi Arabia and Oman. *Quaternary International*. 382,  
1195 120–131.

1196 Mcbrearty, S., Brooks, A.S., 2000. The revolution that wasn't: A new interpretation of  
1197 the origin of modern human behavior. *Journal of Human Evolution*. 39, 453–563.

1198 McClure, H.A., 1984. Late Quaternary palaeoenvironments of the Rub' Al Khali.  
1199 University College London.

1200 Mellars, P., 2006. Why did modern human populations disperse from Africa ca.  
1201 60,000 years ago? A new model. *Proceedings of the National Academy of*  
1202 *Sciences*. 103, 9381–9386.

1203 Mellars, P., Gori, K.C., Carr, M., Soares, P.A., Richards, M.B., 2013. Genetic and  
1204 archaeological perspectives on the initial modern human colonization of  
1205 southern Asia. *Proceedings of the National Academy of Sciences*. 110, 10699–

1206            10704.

1207    Miller, A.G., Cope, T.A., 1996. Flora of the Arabian Peninsula and Socotra.

1208            Edinburgh University Press, Edinburgh.

1209    Nicholson, S.L., Pike, A.W.G., Hosfield, R., Roberts, N., Sahy, D., Woodhead, J.,

1210            Cheng, H., Edwards, R.L., Affolter, S., Leuenberger, M., Burns, S.J., Matter, A.,

1211            Fleitmann, D., 2020. Pluvial periods in Southern Arabia over the last 1.1 million-

1212            years. Quaternary Science Reviews. 229, 106112.

1213    Orland, I.J., He, F., Bar-Matthews, M., Chen, G., Ayalon, A., Kutzbach, J.E., 2019.

1214            Resolving seasonal rainfall changes in the Middle East during the last

1215            interglacial period. Proceedings of the National Academy of Sciences. 116,

1216            24985–24990.

1217    Otto-Bliesner, B.L., 2006. Simulating Arctic Climate Warmth and Icefield Retreat in

1218            the Last Interglaciation. Science. 311, 1751–1753.

1219    Parker, A.G., Rose, J.I., 2008. Climate change and human origins in southern

1220            Arabia. Proceedings of the Seminar for Arabian Studies. 38, 25–42.

1221    Parton, A., Clark-Balzan, L., Parker, A.G., Preston, G.W., Sung, W.W., Breeze, P.S.,

1222            Leng, M.J., Groucutt, H.S., White, T.S., Alsharekh, A., Petraglia, M.D., 2018.

1223            Middle-late quaternary palaeoclimate variability from lake and wetland deposits

1224            in the Nefud Desert, Northern Arabia. Quaternary Science Reviews. 202, 78–97.

1225    Parton, A., Farrant, A.R., Leng, M.J., Telfer, M.W., Groucutt, H.S., Petraglia, M.D.,

1226            Parker, A.G., 2015a. Alluvial fan records from southeast Arabia reveal multiple

1227            windows for human dispersal. Geology. 43, 295–298.

1228 Parton, A., White, T.S., Parker, A.G., Breeze, P.S., Jennings, R., Groucutt, H.S.,  
 1229 Petraglia, M.D., 2015b. Orbital-scale climate variability in Arabia as a potential  
 1230 motor for human dispersals. *Quaternary International*. 382, 82–97.

1231 Petit-Maire, N., Carbonel, P., Reyss, J.L., Sanlaville, P., Abed, A.M., Bourrouilh, R.,  
 1232 Fontugne, M.R., Yasin, S., 2010. A vast Eemian palaeolake in Southern Jordan  
 1233 (29°N). *Global and Planetary Change*. 72, 368–373.

1234 Petraglia, M.D., Alsharekh, A., Breeze, P., Clarkson, C., Crassard, R., Drake, N.A.,  
 1235 Groucutt, H.S., Jennings, R.P., Parker, A.G., Parton, A., Roberts, R.G., Shipton,  
 1236 C., Matheson, C., Al-Omari, A., Veall, M.A., 2012. Hominin Dispersal into the  
 1237 Nefud Desert and Middle Palaeolithic Settlement along the Jubbah Palaeolake,  
 1238 Northern Arabia. *PLoS ONE*. 7, e49840.

1239 Petraglia, M.D., Alsharekh, A.M., Crassard, R., Drake, N.A., Groucutt, H., Parker,  
 1240 A.G., Roberts, R.G., 2011. Middle Paleolithic occupation on a Marine Isotope  
 1241 Stage 5 lakeshore in the Nefud Desert, Saudi Arabia. *Quaternary Science*  
 1242 *Reviews*. 30, 1555–1559.

1243 Petraglia, M.D., Groucutt, H.S., Guagnin, M., Breeze, P.S., Boivin, N., 2020. Human  
 1244 responses to climate and ecosystem change in ancient Arabia. *Proceedings of*  
 1245 *the National Academy of Sciences*. 117, 8263–8270.

1246 Petraglia, M.D., Korisettar, R., Boivin, N., Clarkson, C., Ditchfield, P., Jones, S.,  
 1247 Koshy, J., Lahr, M.M., Oppenheimer, C., Pyle, D., Roberts, R., Schwenninger,  
 1248 J.-L.J.-L., Arnold, L., White, K., 2007. Middle Paleolithic Assemblages from the  
 1249 Indian Subcontinent Before and After the Toba Super-Eruption. *Science*. 317,  
 1250 114–116.

1251 Pike, A.W.G., Angelucci, D.E., Cooper, M.J., Linscott, B., Matias, H., Zilhão, J.,  
 1252 2016. Reconstructing Neanderthal mobility and range at Gruta de Oliveira,  
 1253 Portugal, using high resolution laser ablation Sr isotope analysis. In:  
 1254 Proceedings of the European Society for the Study of Human Evolution 5. p.  
 1255 188.

1256 Rabett, R.J., 2018. The success of failed Homo sapiens dispersals out of Africa and  
 1257 into Asia. *Nature Ecology and Evolution*. 2, 212–219.

1258 Rector, A.L., Reed, K.E., 2010. Middle and late Pleistocene faunas of Pinnacle Point  
 1259 and their paleoecological implications. *Journal of Human Evolution*. 59, 340–  
 1260 357.

1261 Reynard, J.P., Henshilwood, C.S., 2019. Environment versus behaviour:  
 1262 Zooarchaeological and taphonomic analyses of fauna from the Still Bay layers at  
 1263 Blombos Cave, South Africa. *Quaternary International*. 500, 159–171.

1264 Roberts, P., Prendergast, M.E., Janzen, A., Shipton, C., Blinkhorn, J., Zech, J.,  
 1265 Crowther, A., Sawchuk, E.A., Stewart, M., Ndiema, E., Petraglia, M., Boivin, N.,  
 1266 2020. Late Pleistocene to Holocene human palaeoecology in the tropical  
 1267 environments of coastal eastern Africa. *Palaeogeography, Palaeoclimatology,*  
 1268 *Palaeoecology*. 537, 109438.

1269 Rohling, E.J., Grant, K.M., Roberts, A.P., Larrasoana, J.-C., 2013. Paleoclimate  
 1270 Variability in the Mediterranean and Red Sea Regions during the Last 500,000  
 1271 Years. *Current Anthropology*. 54, S183–S201.

1272 Rose, J.I., 2010. New light on human prehistory in the Arabo-Persian Gulf Oasis.  
 1273 *Current Anthropology*. 51, 849–883.



1274 Rose, J.I., Hilbert, Y.H., Usik, V.I., Marks, A.E., Jaboob, M.M.A., Černý, V.,  
 1275 Crassard, R., Preusser, F., 2019. 30,000-Year-Old Geometric Microliths Reveal  
 1276 Glacial Refugium in Dhofar, Southern Oman. *Journal of Paleolithic Archaeology*.  
 1277 2, 338–357.

1278 Rose, J.I., Usik, V.I., Marks, A.E., Hilbert, Y.H., Galletti, C.S., Parton, A., Geiling,  
 1279 J.M., Černý, V., Morley, M.W., Roberts, R.G., 2011. The Nubian complex of  
 1280 Dhofar, Oman: An African Middle Stone Age industry in Southern Arabia. *PLoS*  
 1281 *ONE*. 6, e28239.

1282 Rosenberg, T.M., Preusser, F., Blechschmidt, I., Fleitmann, D., Jagher, R., Matter,  
 1283 A., 2012. Late Pleistocene palaeolake in the interior of Oman: A potential key  
 1284 area for the dispersal of anatomically modern humans out-of-Africa? *Journal of*  
 1285 *Quaternary Science*. 27, 13–16.

1286 Rosenberg, T.M., Preusser, F., Fleitmann, D., Schwalb, A., Penkman, K.E.H.,  
 1287 Schmid, T.W., Al-Shanti, M.A., Kadi, K.A., Matter, A., 2011. Humid periods in  
 1288 southern Arabia: Windows of opportunity for modern human dispersal. *Geology*.  
 1289 39, 1115–1118.

1290 Rosenberg, T.M., Preusser, F., Risberg, J., Pliikk, A., Kadi, K.A., Matter, A.,  
 1291 Fleitmann, D., 2013. Middle and Late Pleistocene humid periods recorded in  
 1292 palaeolake deposits of the Nafud desert, Saudi Arabia. *Quaternary Science*  
 1293 *Reviews*. 70, 109–123.

1294 Scerri, E.M.L., 2017. The North African Middle Stone Age and its place in recent  
 1295 human evolution. *Evolutionary Anthropology*. 26, 119–135.

1296 Scerri, E.M.L., Breeze, P.S., Parton, A., Groucutt, H.S., White, T.S., Stimpson, C.,

1297 Clark-Balzan, L., Jennings, R.P., Alsharekh, A., Petraglia, M.D., 2015. Middle to  
 1298 Late Pleistocene human habitation in the western Nefud Desert, Saudi Arabia.  
 1299 Quaternary International. 382, 200–214.

1300 Scerri, E.M.L., Chikhi, L., Thomas, M.G., 2019. Beyond multiregional and simple out-  
 1301 of-Africa models of human evolution. Nature Ecology & Evolution. 3, 1370–  
 1302 1372.

1303 Scerri, E.M.L., Drake, N.A., Jennings, R.P., Groucutt, H.S., 2014a. Earliest evidence  
 1304 for the structure of Homo sapiens populations in Africa. Quaternary Science  
 1305 Reviews. 101, 207–216.

1306 Scerri, E.M.L., Groucutt, H.S., Jennings, R.P., Petraglia, M.D., 2014b. Unexpected  
 1307 technological heterogeneity in northern Arabia indicates complex Late  
 1308 Pleistocene demography at the gateway to Asia. Journal of Human Evolution.  
 1309 75, 125–142.

1310 Scerri, E.M.L., Shipton, C., Clark-Balzan, L., Frouin, M., Schwenninger, J.-L.,  
 1311 Groucutt, H.S., Breeze, P.S., Parton, A., Blinkhorn, J., Drake, N.A., Jennings,  
 1312 R.P., Cuthbertson, P., Omari, A. Al, Alsharekh, A.M., Petraglia, M.D., 2018a.  
 1313 The expansion of later Acheulean hominins into the Arabian Peninsula.  
 1314 Scientific Reports. 8, 17165.

1315 Scerri, E.M.L., Thomas, M.G., Manica, A., Gunz, P., Stock, J.T., Stringer, C., Grove,  
 1316 M., Groucutt, H.S., Timmermann, A., Rightmire, G.P., D'Errico, F., Tryon, C.A.,  
 1317 Drake, N.A., Brooks, A.S., Dennell, R.W., Durbin, R., Henn, B.M., Lee-Thorp, J.,  
 1318 DeMenocal, P., Petraglia, M.D., Thompson, J.C., Scally, A., Chikhi, L., 2018b.  
 1319 Did Our Species Evolve in Subdivided Populations across Africa, and Why Does

1320           It Matter? Trends in Ecology & Evolution. 33, 582–594.

1321   Sept, J.M., 1994. Beyond bones: Archaeological sites, early hominid subsistence,  
1322           and the costs and benefits of exploiting wild plant foods in east African riverine  
1323           landscapes. Journal of Human Evolution. 27, 295–320.

1324   Sharp, W.D., Paces, J.B., 2018. Comment on “The earliest modern humans outside  
1325           Africa.” Science. 362, eaat6598.

1326   Shea, J.J., 2008. Transitions or turnovers? Climatically-forced extinctions of Homo  
1327           sapiens and Neanderthals in the east Mediterranean Levant. Quaternary  
1328           Science Reviews. 27, 2253–2270.

1329   Shipton, C., Blinkhorn, J., Breeze, P.S., Cuthbertson, P., Drake, N., Groucutt, H.S.,  
1330           Jennings, R.P., Parton, A., Scerri, E.M.L., Alsharekh, A., Petraglia, M.D., 2018.  
1331           Acheulean technology and landscape use at Dawadmi , central Arabia. PLoS  
1332           ONE. 13, 1–36.

1333   Shultz, S., Maslin, M., 2013. Early Human Speciation, Brain Expansion and  
1334           Dispersal Influenced by African Climate Pulses. PLoS ONE. 8, e76750.

1335   Siddall, M., Rohling, E.J., Almogi-Labin, A., Hemleben, C., Meischner, D.,  
1336           Schmelzer, I., Smeed, D.A., 2003. Sea-level fluctuations during the last glacial  
1337           cycle. Nature. 423, 853–858.

1338   Smith, M., 2013. The Archaeology of Australia’s Deserts. Cambridge University  
1339           Press, Cambridge.

1340   Soares, P., Alshamali, F., Pereira, J.B., Fernandes, V., Silva, N.M., Afonso, C.,  
1341           Costa, M.D., Musilová, E., MacAulay, V., Richards, M.B., Černý, V., Pereira, L.,

1342 2012. The expansion of mtDNA haplogroup L3 within and out of Africa.  
 1343 Molecular Biology and Evolution. 29, 915–927.

1344 Stahlschmidt, M.C., Collin, T.C., Fernandes, D.M., Bar-Oz, G., Belfer-Cohen, A.,  
 1345 Gao, Z., Jakeli, N., Matskevich, Z., Meshveliani, T., Pritchard, J.K., McDermott,  
 1346 F., Pinhasi, R., 2019. Ancient Mammalian and Plant DNA from Late Quaternary  
 1347 Stalagmite Layers at Solkoto Cave, Georgia. Scientific Reports. 9, 6628.

1348 Stewart, B.A., Zhao, Y., Mitchell, P.J., Dewar, G., Gleason, J.D., Blum, J.D., 2020.  
 1349 Ostrich eggshell bead strontium isotopes reveal persistent macroscale social  
 1350 networking across late Quaternary southern Africa. Proceedings of the National  
 1351 Academy of Sciences. 201921037.

1352 Stewart, M., Clark-Wilson, R., Breeze, P.S., Janulis, K., Candy, I., Armitage, S.J.,  
 1353 Ryves, D.B., Louys, J., Duval, M., Price, G.J., Cuthbertson, P., Bernal, M.A.,  
 1354 Drake, N.A., Alsharekh, A.M., Zahrani, B., Al-Omari, A., Roberts, P., Groucutt,  
 1355 H.S., Petraglia, M.D., 2020a. Human footprints provide snapshot of last  
 1356 interglacial ecology in the Arabian interior. Science Advances. 6, eaba8940.

1357 Stewart, M., Louys, J., Breeze, P.S., Clark-Wilson, R., Drake, N.A., Scerri, E.M.L.,  
 1358 Zalmout, I.S., Al-Mufarreah, Y.S.A., Soubhi, S.A., Haptari, M.A., Alsharekh, A.M.,  
 1359 Groucutt, H.S., Petraglia, M.D., 2020b. A taxonomic and taphonomic study of  
 1360 Pleistocene fossil deposits from the western Nefud Desert, Saudi Arabia.  
 1361 Quaternary Research. 95, 1–22.

1362 Stewart, M., Louys, J., Price, G.J., Drake, N.A., Groucutt, H.S., Petraglia, M.D.,  
 1363 2019. Middle and Late Pleistocene mammal fossils of Arabia and surrounding  
 1364 regions: Implications for biogeography and hominin dispersals. Quaternary

1365 International. 515, 12–29.

1366 Tierney, J.E., deMenocal, P.B., Zander, P.D., 2017. A climatic context for the out-of-  
 1367 Africa migration. *Geology*. 45, 1023–1026.

1368 Torfstein, A., Goldstein, S.L., Kushnir, Y., Enzel, Y., Haug, G., Stein, M., 2015. Dead  
 1369 Sea drawdown and monsoonal impacts in the Levant during the last interglacial.  
 1370 *Earth and Planetary Science Letters*. 412, 235–244.

1371 Usik, V.I., Rose, J.I., Hilbert, Y.H., Van Peer, P., Marks, A.E., 2013. Nubian Complex  
 1372 reduction strategies in Dhofar, southern Oman. *Quaternary International*. 300,  
 1373 244–266.

1374 Vaks, A., Bar-Matthews, M., Matthews, A., Ayalon, A., Frumkin, A., 2010. Middle-  
 1375 Late Quaternary paleoclimate of northern margins of the Saharan-Arabian  
 1376 Desert: Reconstruction from speleothems of Negev Desert, Israel. *Quaternary  
 1377 Science Reviews*. 29, 2647–2662.

1378 Vincent, A.S., 1985. Plant foods in savanna environments: A preliminary report of  
 1379 tubers eaten by the Hadza of northern Tanzania. *World Archaeology*. 17, 131–  
 1380 148.

1381 Wadley, L., Backwell, L., D’Errico, F., Sievers, C., 2020. Cooked starchy rhizomes in  
 1382 Africa 170 thousand years ago. *Science*. 367, 87–91.

1383 Waldmann, N., Torfstein, A., Stein, M., 2010. Northward intrusions of low- and mid-  
 1384 latitude storms across the Saharo-Arabian belt during past interglacials.  
 1385 *Geology*. 38, 567–570.

1386 Weyhenmeyer, C.E., Burns, S.J., Waber, H.N., Macumber, P.G., Matter, A., 2002.

1387 Isotope study of moisture sources, recharge areas, and groundwater flow paths  
 1388 within the eastern Batinah coastal plain, Sultanate of Oman. Water Resources  
 1389 Research. 38, 2-1-2–22.

1390 White, M.J., 2006. Things to do in Doggerland when you're dead: Surviving OIS3 at  
 1391 the northwestern-most fringe of Middle Palaeolithic Europe. World Archaeology.  
 1392 38, 547–575.

1393 Williams, M.A.J., Duller, G.A.T., Williams, F.M., Woodward, J.C., Macklin, M.G., El  
 1394 Tom, O.A.M., Munro, R.N., El Hajaz, Y., Barrows, T.T., 2015. Causal links  
 1395 between Nile floods and eastern Mediterranean sapropel formation during the  
 1396 past 125 kyr confirmed by OSL and radiocarbon dating of Blue and White Nile  
 1397 sediments. Quaternary Science Reviews. 130, 89–108.

1398

1399

1400 *Fig. 1. (A) modern annual precipitation (1970-2000; Fick and Hijmans 2017) map of*  
 1401 *Arabia showing permanent lakes (>10 ha; black circles: HYRDOLakes dataset),*  
 1402 *permanent rivers (HYDROLakes dataset), endoreic basins (HYDROsheds) and major*  
 1403 *weather systems (Parton et al., 2015b). Hydrological data available at AQUASTAT.*  
 1404 *(B) map of terrestrial biomes (data available from WWF. Adapted using Miller and*  
 1405 *Cope, 1996), including rivers, lakes and endoreic basins.*

1406

Lake basin	Site/core	Method	Age	MIS	Note	Ref
------------	-----------	--------	-----	-----	------	-----

Mundafan (Saudi Arabia)	C	TT-OSL (sands underlying lake marls)	101 ± 6 ka	MIS 5c		Rosenberg et al. (2011)
Mundafan (Saudi Arabia)	MDF-61	OSL and TT-OSL	A Bayesian statistical model of multi-grain OSL and TT-OSL dates places site formation between 97-77 ka BP.	MIS 5c		Groucutt et al. (2015d)
Khujaymah (Saudi Arabia)	B	TT-OSL (sands underlying lake marl)	Top: 136 ± 14 ka Bottom: 120 ± 10 ka	MIS 5e	Punctuated lake/sand deposits between ages	Rosenberg et al. (2011)
Khujaymah (Saudi Arabia)	D	TT-OSL (sands underlying lake marl)	99 ± 11, 96 ± 8 and 88 ± 6 ka	MIS 5c/a		Rosenberg et al. (2011)
Saiwan (Oman)	11.2	TT-OSL	108 ± 8 ka	MIS 5c		Rosenberg et al. (2012)
Saiwan (Oman)	13.6	TT-OSL	125 ± 9 ka	MIS 5e		Rosenberg et al. (2012)
Saiwan (Oman)	11.3	TT-OSL	102 ± 9 ka	MIS 5c		Rosenberg et al. (2012)
Saiwan (Oman)	11.4	TT-OSL	119 ± 14 ka	MIS 5e		Rosenberg et al. (2012)
Saiwan (Oman)	12.1	TT-OSL	Top: 102 ± 8 ka	MIS 5c		Rosenberg et al. (2012)

			Bottom: 114 ± 9 ka			
<i>Saiwan (Oman)</i>	12.8	TT-OSL	97 ± 12 ka	MIS 5c		Rosenberg et al. (2012)
<i>Rub' al Khali (Saudi Arabia)</i>	14.3	OSL	122 ± 6, 111 ± 9 and 118 ± 10 ka	MIS 5e		Matter et al. (2015)
<i>Rub' al Khali (Saudi Arabia)</i>	15.1	OSL (aeolian sands underlying limestone)	107 ± 13 ka	MIS 5c		Matter et al. (2015)
<i>Rub' al Khali (Saudi Arabia)</i>	15.3	OSL (aeolian sands underlying gypsums)	96 ± 6 ka	MIS 5c/a		Matter et al. (2015)
<i>Rub' al Khali (Oman)</i>	b18.1	TT-OSL	Top: 115 ± 5 ka	MIS 5c/a	Sabkha	Matter et al. (2015)
			Bottom: 82 ± 4 ka			
<i>Al Sibetah (UAE)</i>		OSL	Phase IX: 88 ± 7.8 ka  Phase VII: 130 ± 6.4 ka	MIS 5e, 5c and 5a	Three phases of stream activation + grassland development between 130- 88 ka considered to represent MIS 5e, 5c and 5a	Parton et al. (2015)

1407 *Tab. 1. Ages of palaeolake formations in southern Arabia.*



<i>Lake basin</i>	<i>Site/core</i>	<i>Method</i>	<i>Age</i>	<i>MIS</i>	<i>Note</i>	<i>Ref</i>
<i>Jubbah (Saudi Arabia)</i>	JB1 (zone III and IV)	OSL	<135.8 ± 23.9 and >73.4 ± 6.8 ka	MIS 5e (zone III) and MIS 5a (zone IV)		Parton et al. (2018)
<i>Jubbah (Saudi Arabia)</i>	JB3 (zone III)	OSL	75.3 ± 8.1 ka	MIS 5a	Age reversal (100.5 ± 20.5 ka) above considered to fall within MIS 5a.	Parton et al. (2018)
<i>Jubbah (Saudi Arabia)</i>	JQ1	OSL	Calcrete: 75 ± 5 ka Palaeosol: 95 ± 7 ka	MIS 5a and MIS 5c		Petraglia et al. (2011)
<i>Khall Amayshan (Saudi Arabia)</i>	16.4	TT-OSL (sands overlying and underlying lake diatomites)	Top: 117 ± 8 ka Bottom: 99 ± 7 ka	MIS 5e-c		Rosenberg et al. (2013)
<i>Nafud (interdunal). Close to Khall Amayshan. (Saudi Arabia)</i>	16.3	TT-OSL (sands underlying lake diatomites).	99 ± 7 ka	MIS 5c-a	Interdunal palaeolake	Rosenberg et al. (2013)
<i>Nafud (interdunal). Close to B'r al Hayzan. (Saudi Arabia)</i>	16.5	TT-OSL (sands overlying and underlying lake diatomites).	Top: 128 ± 9 ka Bottom: 125 ± 10 ka	MIS 5e	Interdunal palaeolake	Rosenberg et al. (2013)

Nafud (interdunal). Close to B'r al Hayzan. (Saudi Arabia)	17.3	TT-OSL (sands underlying lake diatomites).	99 ± 7 ka	MIS 5c-a	Interdunal palaeolake	Rosenberg et al. (2013)
Nafud (interdunal). Close to Jubbah. (Saudi Arabia)	14.3	TT-OSL (sands overlying and underlying lake diatomites).	Top: 19 ± 1 ka Bottom: 122 ± 10 ka	MIS 5e	Interdunal palaeolake	Rosenberg et al. (2013)
Nafud (interdunal). Close to Jubbah. (Saudi Arabia)	13.2	TT-OSL (sands underlying lake diatomites).	109 ± 8 ka	MIS 5c	Interdunal palaeolake.	Rosenberg et al. (2013)
Al Wusta (Saudi Arabia).		OSL (sands overlying and underlying lake diatomite).  U-Series/ESR (palaeontological remains).	Top: 98.6 ± 7 ka Bottom: 85.3 ± 5.6, 92.0 ± 6.3 and 92.2 ± 6.8 ka  AW1 (U- series): 87.6 ± 2.5 ka  WU1601 (enamel U- series): 83.5 ± 8.1 ka  WU1601 (combined U-series	MIS late 5c/early 5a.	Baysian model assigned suggests underlying sands (unit 1) were stabilised at 93.1 ± 2.6ka and unit 2 and 3 were deposited between 92.2 ± 2.6 ka and 90.4 ± 3.9 ka.	Groucutt et al. (2018)

			ESR): 103 +10/-9 ka		
<i>Alathar (Saudi Arabia)</i>	OSL of diatomites overlying and underlying hominin footprints	112 ± 10 ka BP (PD62; unit 5) and 121 ± 11 ka BP (PD61; unit 2)	Early MIS 5, likely MIS 5e	M. Stewart et al. (2020a)	
<i>Mudawwara (Jordan).</i>	U-series (mollusc carbonate)	125 ± 5  121 ± 9  124 +10/-9  116 +5.5/- 5.2  95.4 +3.2/- 3/1  91.1 +3.4/- 3.3  135 ± 6  88 ± 5  77 ± 8	MIS 5e and 5c/a	Petit-Maire et al. (2010)	

1410 *Tab. 2. Ages of palaeolake activation in northern Arabia.*

1411

1412

1413 *Fig. 2. (A) Precipitation map of Arabia showing locations of palaeolakes (light blue*  
1414 *circles), speleothem cave sites (white circles), marine sediment (green circles) and*  
1415 *fluvial/alluvial (dark blue circles). (B) Late Pleistocene climate records from Arabia. (a)*

1416 ODP 967 sapropels (black rectangles) and wet/dry (blue/red line) index (Grant et al.,  
 1417 2017) vs. Soreq Cave stalagmite  $\delta^{18}\text{O}_{\text{ca}}$  (black line) (Bar-Matthews et al., 2003; Grant  
 1418 et al., 2014) and Negev desert stalagmite formation (black circles) (Vaks et al., 2010).  
 1419 (b) Lake activation (TT-)OSL ages in Northern Arabia vs. Southern Arabia (Rosenberg  
 1420 et al., 2011, 2012, 2013; Petraglia et al., 2012; Jennings et al., 2016; Parton et al.,  
 1421 2018). (c) Red Sea grain sizes (KL-11) (Fleitmann, 1997). (d) Stalagmite determined  
 1422 SAHPs (green bars) vs. Hoti Cave  $\delta^{18}\text{O}_{\text{ca}}$  values and Mukalla Cave  $\delta^{18}\text{O}_{\text{ca}}$  (box-  
 1423 whisker plot) and  $\delta^{13}\text{C}_{\text{ca}}$  (black circles) values (Nicholson et al., 2020). (e) Gulf of Aden  
 1424 grainsize data (KL-15) vs.  $\delta D_{\text{leaf-wax}}$  values (RC09-166) (Fleitmann, 1997; Tierney et  
 1425 al., 2017). (f) insolation at  $15^{\circ}\text{N}$  ( $\text{W m}^2$ ) vs. global ice-volume (LR04  $\delta^{18}\text{O}_{\text{benthic}}$ ) and  
 1426 Marine Isotope Stages (Berger and Loutre, 1991; Lisiecki and Raymo, 2005).

1427

1428

1429 Fig. 3. (A) map showing locations of key (dated to MIS 5: white circles; undated: black  
 1430 circles) Arabian Middle Palaeolithic archaeological sites and annual precipitation  
 1431 during MIS 5e. (B) Ages of key dated Arabian archaeological sites (Armitage et al.,  
 1432 2011; Petraglia et al., 2011, 2012; Rose et al., 2011; Delagnes et al., 2012; Groucutt  
 1433 et al., 2015d, 2018) compared to global ice-volume (LR04; Lisiecki and Raymo, 2005)  
 1434 and Marine Isotope Stages. Different methods of age calculation are represented by  
 1435 circles (OSL), triangles (TT-OSL) and U-Th/combined U-Th-ESR (squares). Arrows  
 1436 denote maximum or minimum ages. Assemblage/unit identifiers are given for Jebel  
 1437 Faya. The blue bar denotes tentative age assignment for Jebel Faya assemblage B.

1438

<i>Location and Assemblage Site</i>	<i>Age</i>	<i>Method</i>	<i>(Ref.)</i>
<i>Al Wusta (Nafud Desert, Saudi Arabia)</i>	Insolation peak at ~84 ka	Combined UTh-ESR, OSL and Bayesian age modelling	Groucutt et al. (2018)
<i>Jebel Katabah (Nafud Desert, Saudi Arabia)</i>	JKF-1; Unit H. ~90-50 ka	OSL	Petraglia et al. (2012)
<i>Jebel Qattar (Nafud desert, Saudi Arabia)</i>	JQ-1 75 ± 5 ka	OSL	Petraglia et al. (2011)
<i>Khall Amayshan</i>	KAM-1 ~120 ka	OSL	Scerri et al. (2015)
<i>Mundafan (Rub' al Khali, Saudi Arabia)</i>	MDF-61 ~100-80 ka	OSL and TT-OSL and Bayesian statistical modelling	Groucutt, White, et al. (2015)
<i>Jebel Faya (UAE)</i>	C 127 ± 16 123 ± 10 ka (± 1σ).  B Relatively assigned to ~50-1000 ka based on stratigraphic position.  C 40.2 ± 3.0 to 38.6 ± 3.1 ka (± 1σ)	OSL	Armitage et al. (2011)
<i>Aybut al Auwal (Dhofar, Oman)</i>	106 ± 9 ka (minimum age)	OSL	Rose et al. (2011)

1439 *Tab. 3. Ages of key MIS 5 archaeological sites in Arabia.*

1440

1441

1442 *Fig. 4. Cores, retouched tools and flakes from (A) Jebel Faya assemblage C, UAE,*  
1443 *~125 ka, (B) Aybut Al Auwal and Mundayy As Sodh, Oman, early MIS 5, (C) Mundafan,*  
1444 *southwest Saudi Arabia, MIS 5, (D) Jebel-Qattar 1, Nefud Desert, ~75 ka (Illustrations*  
1445 *modified from Armitage et al., 2011; Petraglia et al., 2011; Rose et al., 2011; Crassard*  
1446 *et al., 2013).*

1447

1448

1449 *Fig. 5. Conceptual model for the dispersal of H. sapiens into Arabia and Eurasia using*  
1450 *MIS 5e as an example. Circles denote hypothetical metapopulations, which are*  
1451 *comprised of numerous inter-connected populations. Metapopulations are also semi-*  
1452 *connected to other metapopulations at a much broader scale, with connectivity*  
1453 *denoted by colour. As populations expand, they begin to differ from initial*  
1454 *metapopulations as they adapt to new environments and develop new cultures.*  
1455 *Rainfall maps include simulations for 140-120 ka BP (wetter period: Otto-Bliesner,*  
1456 *2006) and modern day (drier periods: Fick and Hijmans, 2017) and tuned to the*  
1457 *chronology of sapropel S5.*

1458