**Climatic variability, plasticity, and dispersal: A case study from Lake Tana, Ethiopia**

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**Abstract**

The numerous dispersal events that have occurred during the prehistory of hominin lineages are the subject of longstanding and increasingly active debate in evolutionary anthropology. As well as research into the dating and geographic extent of such dispersals, there is an increasing focus on the factors that may have been responsible for dispersal. The growing body of detailed regional palaeoclimatic data is invaluable in demonstrating the often close relationship between changes in prehistoric environments and the movements of hominin populations. The scenarios constructed from such data are often overly simplistic, however, concentrating on the dynamics of cyclical contraction and expansion during severe and ameliorated conditions respectively. This contribution proposes a two-stage hypothesis of hominin dispersal in which populations (1) accumulate high levels of climatic tolerance during highly variable climatic phases, and (2) express such heightened tolerance via dispersal in subsequent low-variability phases. Likely dispersal phases are thus proposed to occur during stable climatic phases that immediately follow phases of high climatic variability. Employing high resolution palaeoclimatic data from Lake Tana, Ethiopia, the hypothesis is examined in relation to the early dispersal of *Homo sapiens* out of East Africa and into the Levant. A dispersal phase is identified in the Lake Tana record between c.112,550 and c.96,975 years ago, a date bracket that accords well with the dating evidence for *Homo sapiens* occupation at the sites of Qafzeh and Skhul. Results are discussed in relation to the complex pattern of *Homo sapiens* dispersal out of East Africa, with particular attention paid to the implications of recent genetic chronologies for the origin of non-African modern humans.

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**Introduction**

Hominin dispersals have become the focus of a steadily increasing body of research in evolutionary anthropology over the past two decades (e.g. Lahr and Foley 1994; Anton et al. 2002; Hazelwood and Steele 2004; Dennell and Roebroeks 2005; Mellars 2006; Shea 2007, 2010; Lycett and von Cramon-Taubadel 2008; Lycett 2009; Steele 2009; Koenig and Borries 2012). During this time the appreciation of the vital role played by climatic factors in hominin dispersals has greatly increased (e.g. Foley 2002; Mithen and Reed 2002; Nikitas and Nikitas 2005; Hughes et al. 2007; Gamble 2009; Petraglia et al. 2010; Müller et al. 2011), with the result that palaeoclimatic records have become indispensable to this field of study. Despite the growing literature on hominin dispersals, however, there is a generic lack of engagement with theoretical developments concerning dispersal dynamics in the parallel disciplines of zoology and evolutionary biology (e.g. Mayr 1965; Baker 1965; Vazquez 2006; Sol 2007). This contribution proposes a theory of hominin dispersals rooted in the evolutionary biology of fluctuating environments, and examines that hypothesis via a detailed analysis of the Late Pleistocene dispersal of *Homo sapiens* from East Africa into the Levant. Integral to the hypothesis are the findings that species subject to high levels of climatic variability can accumulate plastic adaptations, and that such adaptations are characteristic of successful dispersers. Utilising new high-resolution palaeoclimatic data from Lake Tana, Ethiopia, a chronology of dispersal from this area is developed and assessed against the chronologies of the extensively studied Levantine sites of Qafzeh and Skhul.

**Climatic variability, plasticity, and dispersal**

*The evolutionary biology of plasticity*

Plasticity has varying, complex definitions in evolutionary biology, but is understood in a broad sense here as “the ability of an individual organism to react to an environmental input with a change in form, state, movement, or rate of activity” (West-Eberhard 2003:34). Foundational research on evolutionary responses to climatic variability at a microevolutionary level was provided by geneticists focusing on the maintenance of polymorphisms (e.g. Levene 1953; Dempster 1955; Haldane and Jayakar 1963; Cohen 1966; Lewontin and Cohen 1969; Gillespie 1974). The principles derived by such research include the fact that, since reproduction is a multiplicative process, the overall fitness of a genotype across generations should be measured by the geometric rather than the arithmetic mean. As the geometric mean is more sensitive to variance than is the arithmetic mean, this principle has the corollary that temporal climatic variability can favour highly tolerant genotypes. Figure 1a shows the fitnesses of two genotypes over a continuum of climatic states; Genoytpe 2 is more tolerant than Genotype 1 by virtue of having non-zero fitness values across a greater range of climatic states. When subject to climatic change through time as plotted in Figure 1b, Genotype 2 thus has lower variance in fitness through time, as shown in Figure 1c. Genotype 1 has a higher *arithmetic* mean fitness over these ten generations, but Genotype 2 has a higher *geometric* mean fitness due primarily to its lower variance, and is therefore favoured by natural selection. To clarify, the point is not that increased tolerance of environmental variability is necessarily due to plasticity, but that plasticity will necessarily lead to increased tolerance of environmental variability, and will often be the most efficient way of doing so.

Although formulated at the microevolutionary level, there is abundant evidence that the ‘geometric mean principle’ is also plays a prevalent macroevolutionary role (Moran 1992; Simons 2002; Lee and Doughty 2003; Yoshimura et al. 2009; Grove submitted). In its macroevolutionary form, this basic logic strikes a chord with a number of more recent, palaeoanthropologically grounded hypotheses concerning the relationship between climatic variability and human evolution. The variability selection hypothesis (Potts, 1996, 1998, 2013; see also Grove 2011a, 2011b) suggests that, on geological timescales, hominin species accumulated adaptations that increased behavioural versatility in response to substantial climatic and environmental fluctuations. Kingston’s (Kingston, 2007; Kingston and Harrison, 2007; Kingston et al., 2007) shifting heterogeneity model couples the idea of versatile responses to “complex and dynamic adaptive landscapes” (Kingston 2007:48) with the observation that precession-driven shifts in seasonality in equatorial African environments would have affected vegetation physiognomy and faunal distribution patterns. The focus on latitudinal and altitudinal drift in hominin geographic ranges, with the resulting establishment of isolated refugia, recalls Vrba’s (1992, 1995) habitat theory and outlines expectations concerning vicariance and speciation (see also Grove 2012a). Extending the theme of precessional effects on low latitude hominin populations, Trauth and colleagues’ pulsed climate variability hypothesis (Trauth et al. 2007, 2010; Maslin and Trauth 2009) focuses on the semi-precessional pulses of wetter and more variable conditions evinced in East African lake records.

*Plasticity and dispersal*

Though a number of hypotheses have been advanced regarding the details of the relationship between climatic variability and hominin evolution within Africa and elsewhere, research into the interactions between climate and dispersal remains focused on the basic paradigm that glacials and interglacials led to population contraction and expansion respectively (though see Vrba 1995; Lahr and Foley 1998). A more refined picture can be obtained, however, by examining the strong and consistent relationship between high levels of plasticity and the successful colonisation of new environments. Mayr (1965) listed six characteristics of successful colonisers, including “considerable ecological flexibility” and the “ability to shift habitat preference” (Mayr 1965:40-41); the former is effectively a synonym for plasticity, whilst the latter is a likely result of it. Similarly, Baker (1965; see also 1974) postulated that successful dispersal was particularly likely in organisms possessing “general-purpose genotypes” (Baker 1965:166) or capacities for “wide environmental tolerance” (Baker 1974:6). Sol (2007; see also Sol et al. 2002) stresses the importance of behavioural flexibility *per se*, whilst dietary flexibility (Mclain et al. 1999), habitat breadth (Cassey et al. 2004), and niche breadth (Vazquez 2006) have all been cited as specific factors.

There is also direct evidence that experience of environmental fluctuation within a given region equips organisms to survive future dispersals beyond that region (Agrawal 2001; Donohue et al. 2001; Yeh and Price 2004), and that those species showing high levels of dispersal are more plastic than co-occurring, non-dispersing species (Davidson et al. 2011). Recent studies of organisms facing novel environments *in situ* due to anthropogenic climate change suggest that plastic species are more successful at doing so (e.g. Chown et al. 2007; Charmantier et al. 2008), with Ghalambor and colleagues (2007) suggesting that plasticity acts both as a short-term buffer and as a longer-term facilitator of directional selection towards the new optimum. A coherent theory of hominin dispersal, therefore, should take into account both the potential for temporal variability in the environment to lead to the evolution of plasticity and the finding that such plasticity is likely to facilitate successful dispersal.

**Hominin dispersal: A hypothesis**

The accumulated plasticity hypothesis (APH; Grove 2014) explicitly states that populations surviving phases of high climatic variability in a given region will be well equipped to disperse into neighbouring regions during subsequent low-variability phases. It is established above that high variability phases can lead to the accumulation of plastic adaptations, and that such adaptations can facilitate dispersal, but by additionally considering how and when this accumulated plasticity is expressed we can begin to make predictions about the timing of dispersal phases based on close examination of palaeoclimatic records. When environments fluctuate relatively slowly, the optimal response in hominin populations is likely involve gradual shifting of the geographic range such that the habitats encountered remain essentially the same; during rapid climatic fluctuations, however, populations will not be able to shift their geographic ranges fast enough to fulfil this strategy, and it is in such circumstances that geographically static and increasingly plastic populations will be favoured. Phases of high variability lead to the accumulation of levels of plasticity that are substantially higher than those required by subsequent low variability phases, and it is in the early stages of these latter phases that dispersal is most likely to occur.

Figure 2 shows the output of a simple evolutionary algorithm that models this process. The full details of this model are available elsewhere (Grove 2014), but the important finding for the purposes of the current paper concerns the timing of a potential dispersal phase relative to phases of high and low climatic variability. During the phase of high climatic variability plasticity accumulates, as one would expect given the foregoing arguments, but high climatic variability also leads to a fitness decline in a population that at the outset is not sufficiently plastic to accommodate it. When climatic variability abruptly declines, there is selection for reduced plasticity (as the population evolves towards the optimum level for a less variable environment), and fitness abruptly increases. The dispersal phase is predicted to occur during the lag between the decrease in environmental variability and the point at which the population attains a level of plasticity suited to that decrease. During this phase, fitness is increasing rapidly and the population is substantially more plastic than is required for survival in its native region.

Figures 3a and 3b show schematic examples of high and low variability environments. During the high variability phase, a population remaining in its native region (Figure 3c) will develop levels of plasticity that allow it to deal with habitats encountered during both the peaks and the troughs of the environment plotted in Figure 3a. During the subsequent low variability phase, it will no longer experience the habitats generated by these extreme peaks and troughs in its native region, but these habitats are likely to be precisely those now found in the surrounding regions. It will thus be well equipped to disperse into those surrounding regions during the low variability phase. Figure 3d shows this effect as a simple latitudinal expansion, but a more realistic example is shown in Figures 3e-g. In this latter example, the effect is altitudinal, with populations withstanding high variability in mid-altitude refugia (Figure 3f) developing sufficient plasticity to disperse into surrounding regions at both higher and lower altitudes during the low variability phase (Figure 3g). Note that this effect is not dependent upon a directional change in the mean of the climatic variable (such as climatic amelioration via increases in temperature or precipitation), but is due purely to the plasticity accumulated in response to the wide range of habitats experienced in the high variability phase being expressed via dispersal in the low variability phase. An important difference between the APH and analyses based purely on amelioration effects is that the APH predicts bilateral expansion; for example, plastic species can expand into regions that are both colder and warmer than their native region during periods of low variability. In contrast, amelioration-based analyses predict what are essentially habitat-tracking migrations that co-occur in line with expansions of the native habitat.

The formulation of the APH above leads to a series of predictions regarding the timing of dispersal phases in relation to particular sets of climatic events; such events are easily detected in palaeoclimatic records, and the timings thus suggested can be tested against the palaeoanthropological record. The major predictions are that:

1. Dispersal will occur in relatively stable climatic phases following phases of relatively high climatic variability;
2. Dispersal potential will be greatest when transitions between high and low variability phases are abrupt;
3. Populations will have greater dispersal potential immediately following such transitions, with this potential gradually decreasing thereafter;
4. Longer periods of high climatic variability will lead to greater accumulations of plasticity, and thus greater dispersal potential, though such values will eventually asymptote.

As per amelioration-based analyses, stability of favourable climates will be more likely to lead to dispersal than stability of unfavourable climates, but under the APH this factor is of secondary importance, as more plastic populations will automatically experience a greater range of climates as favourable. When examining palaeoclimatic records, we thus highlight as potential dispersal phases the initial stages of phases of climatic stability that abruptly follow relatively long phases of climatic variability, and look secondarily at whether the transition to stability is accompanied by any mean shift in the climatic variable analysed.

**The origin and early dispersal of *Homo sapiens***

As the current contribution examines the early dispersal of *Homo sapiens* out of East Africa and into the Levant, we here briefly summarise the dated fossil evidence for early members of our species in these two regions. For the sake of brevity, we do not discuss fossil material from other African regions, and mention only relatively well-dated fossils. An illustration of the pan-African *Homo sapiens* record over the last 400ka is given for comparison in Figure 4 (following Bräuer 2012).

*African origins*

The fossils from the Ethiopian sites of Omo Kibish and Herto have the strongest claims to being the earliest members of our species. The Herto remains, from the Upper Herto Member of the Bouri Formation, are remarkably well constrained to between 160±2ka and 154±7ka via argon-argon dates on pumice and obsidian clasts in the surrounding sandstone unit and the capping Waidedo Vitric Tuff (WAVT), respectively (Clark et al. 2003; White et al. 2003). Argon-argon dates on feldspar crystals from pumice clasts within the Nakaa’kire Tuff at Omo give a maximum weighted mean age of 196 ± 2ka for Omo I and II, whilst a lower age limit of 104 ± 1ka is provided via the same method of analysis on the overlying Aliyo Tuff (McDougall et al. 2008). Researchers working on the Omo material present detailed arguments concerning the stratigraphic position of Omo I and II immediately above the Nakaa’kire Tuff, correlation of the KHS Tuff with the Herto WAVT and the tuff dated by sample TA-55 at Konso, and correlation of Kibish Member IIa with Mediterranean Sapropel 6 (McDougall et al. 2005, 2008; Brown and Fuller 2008; Feibel 2008; Brown et al. 2012) that suggest the fossils lie towards the earlier end of this age bracket, perhaps >172ka (McDougall et al. 2008).

The Tanzanian early *Homo sapiens* sample includes three crania from Lake Eyasi, Tanzania, reported by Reck and Kohl-Larsen (1936) and Leakey (1936; see Mehlman 1984 for a thorough overview). The age and affinities of Eyasi Hominin 1 (EH01) have since been clarified somewhat by Mehlman (see particularly 1984 *contra* Protsch 1981, and 1987), Bräuer and Mabulla (1996), and Trinkaus (2004). Mehlman (1987:142) provides a minimal age for EH01 via a U-series date on the overlying Mumba Beds of 131ka. Re-analyses of the faunal remains, artefacts (Mehlman 1984, 1987), and geology of the Eyasi Beds, however, led Bräuer and Mabulla (1996) to conclude that Eyasi Hominins 1-3 are of Middle Pleistocene date, probably between 200 and 400ka. An additional hominin frontal from Lake Eyasi, EH06, was reported by Domínguez-Rodrigo and colleagues (2008). The authors take the outer bounds of four ESR and U-series dates to produce an interval of 88-132ka for the specimen (Domínguez-Rodrigo et al. 2008).

Just over 3km from Lake Eyasi, three isolated human molars designated Mumba XXI were recovered from Mumba Rock Shelter (Bräuer and Mehlman 1988). A pair of U-series dates give a thorium ratio equivalent in age to ka and a protactinium ratio equivalent in age to ka, with these dates both viewed as younger than the hominin sample (Bräuer and Mehlman 1988:71). The fossil skull from the Ngaloba Beds at Laetoli (LH18), reconstructed and analysed by Magori and Day (1983), is probably of a similar age to Mumba XXI and EH06. Correlation of a tuff in the Ngaloba Beds with a marker tuff in the lower unit of the Ndutu Beds at Olduvai led Hay (reported in Day et al. 1980:55) to estimate an age of 120 ± 30ka on stratigraphic grounds. Bones from the tuff in the Ngaloba Beds yielded a uranium-thorium date of 129 ± 4ka (Hay 1987).

From Kenya, the ES-11693 cranium, a surface find from near the Eliye Springs, West Turkana, is routinely assumed to date from 200-300ka, but this is a generic assignment, with Bräuer and Leakey (1986:289) reporting that “there is no basis for locating the cranium in a stratigraphic context”. Of similar age and also from Kenya are the KNM-ER 3884 cranium and KNM-ER 999 femur from Ileret, northeast of Lake Turkana, considered to be around 270ka and 300ka respectively (Bräuer et al. 1997). Finally, the calcrete enclosing the Sudanese Singa calvarium yielded a series of U-Th dates (McDermott et al. 1996), with a date of 133 ± 2ka considered most reliable. As the calcrete necessarily formed after deposition of the calvaria, this is regarded as a minimum age, and linear uptake ESR dates on an associated *Equus* tooth range from 140 ± 11ka to 159 ± 12ka (McDermott et al. 1996:511).

*Early moderns in the Levant*

The debate concerning the earliest members of our species to leave Africa centres primarily upon the Levantine sites of Qafzeh and Skhul. These sites have been subject to numerous dating efforts; these are briefly summarised here. Other early sites, such as those on the postulated ‘southern route’ out of Africa (e.g. Armitage et al. 2011; Rose et al. 2011; Boivin et al. 2013) lack fossil evidence, but provide an intriguing addition to the data on early *Homo sapiens* dispersals, and are considered further in the Discussion.

The cave of Qafzeh, Israel, was excavated by Neuville and Stekelis from 1932-5 and by Vandermeersh from 1965-79 (Vandermeersh 1981). Five burials, together with fragmentary remains of up to 11 other skeletons, all attributed to AMHS despite a few primitive features (Stringer and Trinkaus 1981), were excavated from Vandermeersh’s layers XV and XVII (Vandermeersh 1981). Valladas and colleagues (1988) provided thermoluminescence dates on 20 burnt flints from the cave. Overall, the dates on layers XVII to XXIII range from 82.4 ± 7.7ka to 109.9 ± 9.9ka, with those on layer XVII, from which hominins Q8-12 and Q14-17 were recovered, dating from 87.8 ± 7.2ka to 107.2 ± 8.8ka. Valladas and colleagues (1988) demonstrate that there are no systematic differences in the ages from different layers, and provide a weighted mean age of 92 ± 5ka for layers XVII to XXIII.

ESR dates on bovid tooth enamel from the odd-numbered layers from XV to XXI were given by Schwarcz and colleagues (1988), and range from 73.7ka to 119.0ka on the early uptake model and from 89.1ka to 145.0ka on the linear uptake model (no errors are given in the publication). These authors provide weighted means for the four levels of 96 ± 13ka and 115 ± 15ka on the early and linear uptake models respectively. Dates on two of Schwarcz and colleagues’ bovid tooth samples from layer XIX were also calculated by McDermott and colleagues (1993) using U-Th methods on dentine and enamel. These analyses yielded dates of ka on sample 371 (enamel) and ka on sample 368 (dentine), with the latter date being closer to the previous ESR dates on these samples (regardless of whether one assumes the early or linear uptake model for the ESR dates). Yokoyama et al. (1997) provide direct U-series dates on the cranium of Qafzeh 6 using non-destructive gamma-ray spectrometry, with U-Th giving ka and U-Pa giving ka; these authors regard the latter age as more reliable, primarily due to its closer agreement with the findings of Valladas et al. (1988) and Schwarcz et al. (1988). Finally, Millard’s (2008) Bayesian stratigraphic modelling of the Qafzeh dates (employing only the sample from Valladas et al. (1988)), estimates ages of 87.0 – 95.2ka for the layer XVII hominins, and 87.6 – 96.9ka for hominins Q3 and Q6, the stratigraphic positions of which are less well constrained. Figure 5 shows all published dates from Qafzeh, together with Millard’s (2008) estimates encompassing hominins Q3, 6, 8-12, and 14-17.

The site of Skhul was initially excavated by McCown as part of Garrod’s Mount Carmel project between 1929 and 1935 (Garrod and Bate 1937; McCown and Keith 1939). The stratigraphy involves three main layers (A-C), with all the hominin remains occurring in layer B; layer B itself is divided into an upper sub-layer B1 and a lower sub-layer B2, on the basis that the sediments in B1 are uniformly softer (McCown 1937). The majority of the 10 hominins, all of whom are anatomically modern, were intentionally buried (Stringer et al. 1989). Stringer and colleagues (1989) dated two well preserved bovid teeth from Skhul layer B via ESR. Seven samples from the two teeth yielded an age range of 54.6 ± 10.3ka to 101.0 ± 19.0ka on the early uptake model and 77.2 ± 15.7ka to 119.0 ± 25.1ka on the linear uptake model; the weighted means are respectively 81 ± 15ka and 101 ± 12ka. McDermott and colleagues (1993) dated bovid teeth 521 and 522 via U-series analysis, and additionally dated two rhinoceros teeth from layer B. While their date for 521 is only partially younger than that attained via EU-ESR at ka, their other dates range from ka to ka. Following McCown (1937), they suggest that the hominins could thus fall into two chronologically distinct assemblages; however, they also note that the younger dates, particularly for enamel from 522, could be indicative post-depositional uranium uptake (McDermott et al. 1993:254).

Mercier and colleagues (1993) provide six TL dates on burnt flints from layer B ranging from 99.5 ± 15.9ka to 166.8 ± 26.8ka, with a weighted mean of 119 ± 18ka.These dates are thus somewhat closer to the LU-ESR dates than the EU-ESR dates of Stringer and colleagues (1989), and thus represent some of the earliest dates for Skhul layer B. The combined ESR / U-series dates provided by Grün and colleagues (2005) – given here as combined LU-ESR / open system U-series weighted means, as favoured by the authors - range from ka to ka, though these oldest dates are on a sample within 2 to 5cm of the bedrock. Grün et al. (2005) again sampled bovid teeth 521 and 522, yielding ages of ka and ka respectively. Additionally, these authors dated two further bovid teeth (samples 854 and 856), a tooth from a bovid skull directly associated with Skhul IX (sample 1057), a tooth from a pig mandible found with Skhul V (sample 1058), a molar from the Skhul II skeleton (sample SKII), and fragments of bone from Skhul IX. The sample from Skhul IX gave a U-series age of 131 ± 2ka, but the authors regard this as potentially suspect (Grün et al. 2005:326). Samples 854, 856, 1057, and 1058 provided ages of ka, ka, ka, and ka respectively; importantly, Skhul II is directly dated to ka. The authors note that there are two possible scenarios related to the burials of Skhul II, V, and IX. The first of these is that all three burials took place over a relatively short period of time, sometime between 100 and 135ka (based on 2-σ age ranges of the relevant samples); the second is that Skhul IX, in line with its more primitive morphology and lower stratigraphic position, is genuinely close to the date of 131ka, and that Skhul II and V were buried later, with a depositional age of ka given by the weighted mean of the two average US-ESR results. Millard’s (2008) Bayesian stratigraphic models suggest EU ESR ranges for Skhul IX of 103-164ka and for Skhul V of 59-92ka, though such modelling cannot admit the combined U-series / ESR dates provided by Grün and colleagues (2005), so relies only upon their ESR dates. Figure 6 shows all published dates from Skhul, together with Millard’s (2008) estimate for Skhul V and Grün et al.’s (2005) estimate for Skhul II and V.

**Data and methods**

*Data*

Lake Tana, at 12°N, 37°15’E, and 1830 m elevation on the northern Ethiopian plateau, is 400 km northwest of the Herto hominin site, and 800 km north of the Omo Kibish fossil locality. The lake’s position near the northernmost (July) position of the Inter-Tropical Convergence Zone (ITCZ), which brings heavy summer rainfall that feeds the numerous perennial and ephemeral rivers entering the lake, makes it sensitive to inter-annual variations in summer monsoon rainfall. Similarly, it lies close to the easternmost position of the Congo Air Boundary, marking the divide between rain-bearing air masses from the Atlantic and Indian Oceans (Nicholson 1996; Camberlin 1997). The lake itself is large (3156 km2) but shallow, with a mean depth of only 9 m, and overlies a triple-graben junction in the Tertiary flood basalts that form the Ethiopian plateau (Chorowicz et al. 1998).

Core PT-07-2, penetrating to 92 m depth, was recovered 3 km from the lake’s northern shore (see Lamb et al. submitted). Core recovery averaged 80%, the missing intervals coinciding with diffuse-chaotic seismic facies interpreted as coarser sediments. The sediments below 12 m depth are composed almost entirely of smectite clays and silts, with no clear stratigraphic match to the detailed structure of the seismic data. The age model for the 92 m core is constructed using the B-chron model from 15 post IR IRSL ages on polyminerals in the 4–11 μm fine grain sediment fraction, combined with radiocarbon determinations on bulk sediment, the latter being indistinguishable from analytical background below 25 m depth (Lamb et al. submitted). The basal core sediments yielded an age of 250 ka, with the basin fill facies. Radiocarbon dates on bulk sediments in the upper 25 m are consistent with IRSL ages (Lamb et al. submitted). Elemental ratios were obtained by Itrax XRF core scanning at 2 mm intervals; here we use the Calcium/Titanium ratio as a proxy for lake evaporative status.

*Methods*

Since the raw data from the Lake Tana precipitation-evaporation proxy are not equally spaced in time, they were first interpolated to 25 year intervals across the period from 79ka to 146ka using Matlab’s symmetrical piecewise cubic hermite interpolating polynomial (PCHIP) interpolation algorithm. Since there is an average of one data point per 24.4 years in the raw data, with a standard deviation of 7.42 years, this interpolation procedure does not create additional data points. The 79-146ka bracket is partly determined by the presence of hiatuses in the data immediately before and after it, but is also an ideal period in which to look for the signatures of dispersal out of Africa and into the Levant given the dating evidence considered above. There are also two small hiatuses within this period, between 89,320 and 90,640 and between 94,200 and 95,220 years ago; since interpolation across such hiatuses is unreliable, the variability analyses reported below were run in three blocks separated by these two periods.

The variability analyses involve first smoothing the interpolated data using a Gaussian filter. This symmetrical filter has a window width of 41 interpolate data points, equivalent to a chronological period of 1025 years. Analyses with varying window widths over an order of magnitude from 11-101 data points, equivalent to chronological periods of 275-2525 years, did not appreciably alter the results, though windows smaller than ≈21 and larger than ≈51 data points noticeably under- and over-smooth the data respectively, making results hard to interpret. Following standard procedure, the sigma value of the Gaussian filter is chosen such that the window width is equal to 6 × sigma (i.e. ). Absolute residuals are then taken between the interpolated data and the Gaussian filtered data to give an index of variability at 25 year resolution. The index of variability plotted in the results section is thus , with an interpolated data point at date and the output of the Gaussian filter at date .

To characterise chronological periods of the data as being of greater or lower than average variability, the average of the index across the section of the data analysed (from 79ka to 146ka) is calculated, and each 25-year period is assigned a value of 1 if its value falls below that average, or zero if its value is equal to or greater than that average. A similar procedure is used to characterise chronological periods of the data as being of greater or lower than average aridity, using the 25-year interpolated data in place of the values and assigning a value of 1 if a given 25-year period is below that average or zero if it is equal to or greater than that average. Finally, chronological periods that receive scores of 1 in both analyses (i.e. those that have lower than average values of both variability and aridity) are assigned a final value of 1, and all other chronological periods are assigned a value of zero. The values of zero and 1 output by these analyses are then graphed as bars in register with the raw data to highlight low variability (and, secondarily, low aridity) phases that are considered most amenable to hominin dispersal given the hypothesis and predictions outlined above.

**Results**

The results of the above analyses are shown in Figures 7 and 8. Figure 7a shows the 25-year interpolated data and the characterisation of periods of below average aridity, with Figure 7b showing the variability index and the characterisation of periods of below average variability. A 41-point Gaussian filter is also fitted to the data in Figure 7b to make the figure directly comparable to Figure 7a and thus aid interpretation. Figure 7a demonstrates the existence of relatively moist phases from c.137.6-146ka (note that the latter date is the end of the core segment considered), c.133.1-136.2, and c.95.3-112.9ka (note that the former date is the end of a hiatus in the data). The data suggest that the area remains relatively moist after c.95.3ka, until c.86.4ka when aridity increases substantially. Correlation of these moist phases with the Eastern Mediterranean Sapropels is relatively weak (see Figure 7a), with Sapropel 5 (at c.127ka) not represented as a moist phase at Lake Tana, and Sapropel 3 (at c.82ka) represented as a fragmentary moist episode against a backdrop of increasing aridity. Sapropel 4 (at c.106ka), however, occurs in the midst of the longest moist phase documented in this section of the core. These correlations suggest that strong, regional moist conditions prevailed in the Lake Tana region during the formation of Sapropel 4, but that more localised conditions led to greater aridity in this particular area during the formations of Sapropels 3 and 5.

The variability index () plotted in Figure 7b demonstrates that periods of lower variability coincide broadly with periods of greater moisture, with the exception of the period from c.114ka to c.130ka, which is unique in being relatively stable but also relatively dry. The single longest period of low variability occurs between c.96.9ka and c.112.6ka; this period of low variability is broken only by a very short (50 years, at the resolution of the data), small peak in variability at c.108.8ka. The rest of the core demonstrates relatively rapid transitions between short (c.25-2500 year) periods of alternating lower and higher variability set within generally higher variability phases.

Figure 8 shows the raw data and the results of the final analysis, highlighting those periods that demonstrate lower than average values of both variability and aridity. This figure, and the analyses that accompany it, allow for the delineation of a very clear dispersal phase in line with the hypothesis outlined above. The period between c.96,975yr and c.112,550yr (at the 25-year resolution of the analysis) fulfils all the criteria set out above for a period during which a plastic population would be able to disperse beyond their native area. This phase (marked on Figure 8) is more stable than any other period shown by the analyses, and follows a sustained period of higher variability from 146ka onwards with very high peaks at c.120ka, c.132ka, and c.137ka. These high variability peaks, as noted above, are also highly arid. The transition to both lower variability and lower aridity at the start of the dispersal phase is abrupt, though the transition to lower aridity is more pronounced. In line with the APH, it is thus considered likely that climatic conditions would have been most favourable for dispersal from the Lake Tana region in the earlier stages of this dispersal phase, after c.112.55ka. This dispersal chronology is discussed below in relation to the origin of modern humans and their dispersal into the Levant.

**Discussion**

Anatomically modern *Homo sapiens* first appeared in East Africa sometime between 200ka and 150ka, with the specimens of *Homo sapiens idaltu* from Herto, dated to between 160±2ka and 154±7ka and described by the excavators as “on the verge of anatomical modernity” (White et al. 2003:745) being perhaps the best-dated yardstick of this emerging trajectory. The Herto specimens, and others of similar age, were members of small populations with limited geographic ranges, and were probably reproductively isolated from one another for substantial periods of their evolution. A series of constricted regional groups evolving piecemeal towards modernity rather than a widespread, homogenous population with a single trajectory is the most parsimonious scenario for *Homo sapiens* evolution during the severe climatic conditions of MIS 6 and during the intermittent dry periods of MIS 5. The mosaic morphology attributed to almost all of the modern and pseudo-modern crania surveyed above is indicative of reproductive isolation; Gunz et al. (2009:6095) have recently put this intuitive conclusion on a more secure footing, with their 3D geometric morphometric analyses suggesting that early modern humans were already divided into “multiple, temporarily isolated populations” in the African Pleistocene.

A corollary of this finding is that the postulation of a single ‘Out of Africa II’ dispersal is no longer feasible; instead, multiple dispersal events at varying times and from various sources are supported by the morphological data (Gunz et al. 2009). The analyses of the Lake Tana data reported above highlight one probable phase of dispersal from Ethiopia (and perhaps other, climatically synchronous areas of East Africa) between c.96,975yr and c.112,550yr, with the earlier stages of this phase being most conducive to dispersal. The review of the Levantine data presented above suggests that the Qafzeh modern human specimens were most likely deposited between 87 and 96.9ka (Millard 2008). The dates for Skhul form a rather wider bracket, albeit with a similar mean; Grün et al.’s (2005) US-ESR estimate for Skhul II and V of 88-117ka and Millard’s (2008) estimate of 71-115ka for Skhul V are the most carefully considered, and show a period of overlap centred around 102ka. These dates are perfectly consistent with, but insufficient to prove, a dispersal event originating in the Lake Tana region after 112.5ka. The plausibility of this scenario can be further assessed, however, by examining the distances between Ethiopia and the Levant and the timescales of dispersal involved.

Due to the uncertainty involved in the estimated dates for Skhul (with brackets of 29ka and 44ka suggested by Grün et al. (2005) and Millard (2008) respectively), and the fact that the earliest of these predate the Lake Tana dispersal phase, the calculations presented here focus on the more securely dated site of Qafzeh, with probable dates for modern human occupation between 87.0 and 96.9ka (Millard 2008). By subtracting each possible arrival date (in small increments) from each possible departure date (in equally small increments) and dividing the resulting figure by the distance between the two sites, we derive a probability distribution of dispersal speeds. This exercise was undertaken for potential dispersal routes both to the east and west of the Red Sea, with equivalent differences in distance, as indicated in Table 1. The median travel speed for the more widely cited western route is 0.27 km / year. Probability distributions of dispersal speed are shown in Figure 9a. Such calculations are approximate, but used in this probabilistic way they provide a useful range of likely dispersal speeds with which to assess the dispersal scenario. Diffusion speeds are notoriously difficult to estimate, especially for extinct taxa, but a pioneering effort by Anton et al. (2002) estimated the speed of *Homo erectus* dispersal from Africa to Indonesia at between 0.08 and 2.19km/year and between Africa and Dmanisi at between 0.10 and 1.34km/year (these figures are the square roots of their area/year estimates). In this context, the profile of speeds for the postulated Ethiopian-Levantine dispersal shown in Figure 9a is highly plausible.

Whilst there is clear evidence for the dispersal of *Homo sapiens* into the Levant following the Lake Tana dispersal phase, and more contested evidence of a similar movement into the Arabian peninsula, the palaeoclimatic sequences in these areas are not necessarily synchronous with those in Ethiopia (e.g. Bar-Matthews et al. 2003; Rosenberg et al. 2011; Groucutt and Petraglia 2012; Drake et al. 2013). A preliminary analysis of differences in moisture and moisture variability between Ethiopia and the Levant during the time period considered here is shown in Figure 10. This figure was produced by applying the techniques outlined in the Methods section above to data from the Soreq speleothem from Israel (Bar-Matthews et al. 2003), and comparing the output with that produced from the analysis of the Lake Tana data. Figure 10b shows that there is only periodic alignment of the humid phases indicated by the two records, whilst Figure 10c indicates that low variability periods are more likely to overlap. Combining the analyses of Figure 10b and 10c, Figure 10d shows that putative dispersal phases are rarely aligned. This preliminary analysis sheds a potentially interesting light on patterns of regional asynchrony, and has clear implications for the modelling of dispersal: if the palaeoclimatic conditions viewed as conducive to modern human habitation are regionally asynchronous, they should allow us to predict spatio-temporal movements of modern humans between regions.

The early dispersal of *Homo sapiens* into the Levant, as reflected at the sites of Qafzeh and Skhul, is widely considered to be a ‘failed dispersal’; the population represented at these sites is thought to have been an early incursion unrelated to the successful, global dispersal of modern humans beginning at c.60ka (e.g. Mellars 2006). Much of the genetic data relevant to the timing of modern human dispersal out of Africa supports this scenario. However, genetic studies have produced a series of surprisingly disparate dates for the start of this dispersal; a recent review of mtDNA studies by Boivin et al. (2013) found estimates varying between 85ka and 45ka. The variance in these dates is due to differing estimates of the timing of chimpanzee-human divergence and differences between the two methods used to infer mutation rates, with further problems caused by the assumption of constant mutation rates through evolutionary time (Cox 2008; Endicott et al. 2009). Though the date most frequently employed by genetic studies for the chimpanzee-human divergence is 6Ma, molecular estimates themselves give ages between 4Ma and 8Ma (Bradley 2008); furthermore, putative hominin fossils close to or even pre-dating 6Ma (e.g. *Orrorin tugenensis* (Senut et al. 2001), *Sahelanthropus tchadensis* (Brunet et al. 2002)) suggest that an earlier date is more likely. Mutation rates calculated via phylogenetic methods are considerably and consistently higher than those produced using pedigree-based methods, with Cox (2008) further demonstrating that estimates based on the widely used statistic have an inherent bias towards younger dates, have large asymmetric error variances, and show a considerable risk of type I error. Events such as bottlenecks and founder effects, which in turn govern variation in effective population size and structure, cannot be reflected in this statistic; although ancestral population structure is difficult to reconstruct, autosomal studies (e.g. Barreiro et al. 2005; Garrigan and Hammer 2006; Plagnol and Wall 2006) provide evidence that individual human populations were small and reproductively isolated. Finally, regarding the consistency of mutation rates, Kim et al. (2006) show clear evidence that such rates have slowed over time in the primates.

Two recent papers, however, despite producing quite different mean estimates for the start of the global *Homo sapiens* diaspora, do show some potential for reconciliation around a rather earlier date than that of c.60ka. Scally and Durbin (2012), using a high-resolution pedigree-based estimate of human mutation rate, recover nuclear genomic estimates of the split between the Yoruba and non-Africans (a proxy for the dispersal date) at between 90ka and 130ka. This date is in broad agreement with the date of 80-140ka for the first modern human bottleneck evident in SNP data from the HapMap Project (Keinan et al. 2007; Altshuler et al. 2005; Frazer et al. 2007). A second recent study (Fu et al. 2013) used mtDNA sequences from ten radiocarbon-dated prehistoric modern human specimens to estimate the upper bound on the dispersal at between 62.4ka and 94.9ka. Although half the specimens in the Fu et al. (2013) analysis come from just two sites (Dolni Vestonice and Oberkassel), and the authors are open about the biases of mtDNA analyses, their date of 94.9ka is a statistically valid upper bound. Thus juxtaposition of the Scally and Durbin (2012) and Fu et al. (2013) analyses results in a short period of overlap at between 90ka and 94.9ka. Since phylogenetic estimates of mutation rate are uniformly higher (and thus give ages that are uniformly younger), the discrepancy between the two estimates is in the direction expected; the existence of the period of overlap between these two methodologically very different studies, however, is highly encouraging. Furthermore, the 90.0-94.9ka overlap falls within the bounds of Millard’s (2008) Bayesian stratigraphic estimate for the occupation of Qafzeh, and within the bounds of both Millard’s (2008) and Grün et al.’s (2005) estimates for the occupation of Skhul. Genetic research will doubtless continue to move on apace, and further revision of dates is inevitable, but these recent developments force us to reconsider the conclusion that the populations represented at the sites of Qafzeh and Skhul are indicative of a ‘failed dispersal’. Indeed, in a recent review of advances in whole-genome sequencing, Veeramah and Hammer (2014:153) conclude that revised mutation rate estimates “open the possibility that ~90,000-year-old hominins at the Skhul and Qafzeh sites... represent ancestors of modern-day non-African populations rather than an evolutionary dead end”.

As well as considering the speed and timing of dispersal, it is useful to consider routes of *Homo sapiens* dispersal out of East Africa, particularly given the increasing interest in, and evidence for, a possible ‘southern route’ of dispersal into Arabia (Armitage et al. 2011; Boivin et al. 2013). Lake Tana, at 12°0’N, is just 35 latitudinal minutes south of the Bab al Mandab strait, and the dispersal chronology suggested by the above analyses is of particular interest given the dates of the Omani ‘Nubian’ complexes studied by Rose and colleagues (2011). The possibility of a *Homo sapiens* Bab al Mandab sea crossing has been discussed primarily in the context of southern coastal dispersal through present day Yemen and Oman, and thence via the Strait of Hormuz into present day Iran, Pakistan, and India (e.g. Petraglia et al. 2007; Groucutt and Petraglia 2012). The site of Aybut al Auwal, OSL dated to 106±9ka (Rose et al. 2011), is integral to the reconstruction of this dispersal route, and fits remarkably well with the Lake Tana dispersal chronology established above. The median speed estimate for this dispersal, assuming a coastal route of 2,400 km, is 0.52 km/year. Assuming a route through the Sinai before heading southwards via the eastern coast of the Red Sea, the median dispersal speed estimate is 1.70 km/year. Further details of these results are given in Table 1; probability distributions of dispersal speeds are shown in Figure 9b. The probability distribution for the Bab al Mandab route is remarkably similar to that for dispersal from the Lake Tana region to Qafzeh. A second site of interest in this context is Jebel Faya, in the United Arab Emirates (Armitage et al. 2011; Groucutt and Petraglia 2012). The oldest level at this site (Level C) has yielded three OSL dates, of 95±13 ka, 123±10 ka, and 127±16 ka. Of these three dates, however, two pre-date the postulated Lake Tana dispersal phase, and are therefore not consistent with dispersal in this context. Although the latest date of 95±13 ka *is* consistent with the Lake Tana dispersal phase, and the authors indicate that the earliest date may be problematic (Armitage et al. 2011), there is no justification for selecting just one of these three dates, and therefore dispersal to Jebel Faya is not modelled at this stage.

Reconstructions of sea levels and visible shorelines for the Red Sea by Lambeck et al. (2011) suggest that at c.110ka and again at c.96ka the distance across the Bab al Mandab straits would have been <5km, with the Arabian shoreline clearly visible from the northeastern shore of present day Djibouti. The timing of the Lake Tana dispersal phase, the dating of Aybut al Auwal and the associated complex of sites (Rose et al. 2011), and the periods of low Red Sea level thus combine to present a compelling scenario of southern route dispersal. It is also worthy of note at this juncture that the geographical position of the Lake Tana region allows for two approximately equidistant routes from Ethiopia to the Levant. The traditional view suggests a route through present day Sudan and Egypt along the west coast of the Red Sea, but an alternative exists to the east of the Red Sea, through present day Yemen and Saudi Arabia. It is possible, therefore, that a Bab al Mandab crossing during a low sea level phase could have provided modern humans leaving Africa not only with access to the Arabian peninsula, but also with an alternative route north towards the Mediterranean. Though Middle Palaeolithic finds in Arabia are abundant, they are primarily from unstratified surface contexts and are thus dated only typologically; furthermore, there are no fossil finds at present that would support this alternative route northwards (Groucutt and Petraglia 2012).

The accumulated plasticity hypothesis of hominin dispersal builds on research in evolutionary biology suggesting that temporal fluctuations in environments can result in the accumulation of plastic adaptations, and that such adaptations are characteristic of successful dispersers. Although the relationship between plasticity and successful dispersal is well documented (e.g. Mayr 1965; Baker 1965, 1974; Price et al. 2003; Vazquez 2006; Ghalambor et al. 2007; Sol 2007), it admits two possible explanations concerning the relationship between behavioural flexibility and evolutionary change. The behavioural drive hypothesis (Hardy 1965; Wyles et al. 1983) suggests that behavioural flexibility equips populations to spread into novel environments, where they are exposed to novel selection pressures. Behavioural flexibility thus accelerates the pace of evolution. The hypothesis of behavioural inhibition (Bogert 1949; Huey et al. 2003), however, suggests that because behavioural flexibility alone can enable populations to inhabit varied environments it reduces the need for genetic change, and thus slows evolutionary rates. The APH views the mechanisms behind these two hypotheses as operating sequentially rather than simultaneously, and thus removes at least part of this opposition. The phase of the APH in which plasticity accumulates is consistent with behavioural inhibition explanations, whilst that in which that plasticity is expressed in dispersal leads to a scenario in which behavioural drive is likely to become the predominant force.

The surprisingly low level of genetic diversity in modern humans (Jorde et al. 2000; Kaessmann et al. 2001) is consistent with the behavioural inhibition hypothesis, though this may also be partly the result of ancestral population structure (Harpending and Rogers 2000). Alternately, the existence of multiple pene-contemporary and geographically proximate morphs of late archaic and early modern *Homo sapiens* in Late Pleistocene Africa (see above) could be interpreted as supporting the behavioural drive hypothesis, in that increasing behavioural flexibility can lead to rapidly evolving, divergent morphological trajectories (Wyles et al. 1983). The aspect of *Homo sapiens* morphology most relevant to this debate, however, is brain size. Larger-brained mammals (Sol et al. 2008), birds (Sol et al. 2005), and reptiles (Amiel et al. 2011) are more successful at colonising novel environments, with more encephalised species showing greater rates of innovation in their native regions (Sol et al. 2005), expressed primarily through tool behaviour (Reader and Laland 2002; Overington et al. 2009). Given the evidence that environmental variability is at least partially responsible for hominin encephalisation (Ash and Gallup 2007; Grove 2012a), it seems highly likely that behavioural plasticity facilitated by brain expansion was a driver of hominin dispersal, if not of genetic change directly.

Finally, there is also a potential coupling between plasticity and dispersal in terms of their effects on lithic technology. In particular, Binford’s (1976) arguments regarding toolkit complexity and the length of logistical forays can be usefully adapted to the case of dispersing hominins. Binford (1976) suggested that lengthier logistical forays are likely to involve a greater array of tasks, necessitating either a larger toolkit of task-specific tools or a toolkit of constant size wherein each tool serves multiple functions. The latter solution, involving a smaller number of what can reasonably be referred to as functionally plastic tools, has the advantage of reducing carrying costs (Torrence 1983; Shott 1986). Shott (1986) has amply demonstrated that toolkit diversity (the number of different tool types) is indeed lower in more mobile groups, and we might expect this to be particularly so of groups moving into unfamiliar territory. Ambrose (2010:S141) echoes this sentiment with specific reference to the African MSA, noting that “mobile foragers would be excessively burdened if they had to carry the right tool for every possible task”. Thus small toolkits of what Ambrose (*ibid*.) refers to as “generalized, durable, and transformable tools” would seem ideally suited to dispersing hominins.

Two further basic factors should condition the nature of toolkits carried by highly mobile foragers moving into unfamiliar territory: the difficulty of predicting the subsistence base, and the lack of information regarding raw material sources. Both these factors ultimately reinforce the notion that dispersing hominins should be accompanied by relatively plastic tools, and a number of researchers have suggested that bifacial MSA points or similar bifacial tools would be ideally suited (e.g. Parry and Kelly 1987; Kelly and Todd 1988; Ambrose 2002, 2010; McCall 2006, 2007). The unpredictability of the resource base in novel territory requires that, despite carrying small toolkits, foragers should be equipped to process as many different types of potential foods as possible. Parry and Kelly (1987), writing about the first colonisation of the Americas, argue that bifacial reduction is a direct response to unpredictable environments, with Kelly and Todd (1988) noting that bifacial points in particular were designed to be used for multiple purposes. In the MSA, Ambrose (2002, 2010) has labelled both Levallois and Still Bay points ‘jack-of-all-trades’ artefacts. By contrast, blades tools are often “too narrow and thin to be transformed expediently for use in unanticipated tasks” (Ambrose 2010:S141).

The lack of information regarding lithic sources should lead to the conservation of raw materials, suggesting that tools in modifiable forms may be transported large distances. Again, bifaces are central to the debate. Kelly and Todd (1988:237) found that populations dispersing into the New World carried bifacial points, as these were capable of sustaining “long, variable use-lives”. Such points were transported over thousands of kilometres in many cases (Kelly and Todd 1988). The key to the success of bifacial tools in such cases again stems from their flexibility; they minimize the number of tools and hence the weight of stone carried whilst maximizing the number of functions that the toolkit can perform. More important still is the ease and frequency with which relatively thick, bifacial flake tools can be resharpened relative to blade forms. Valuable studies by Eren and colleagues (Eren et al. 2008) demonstrate that, contrary to prevailing opinion, the use-life of flake edges surpasses that of blades of equivalent mass because repeated retouch of blades leads to exhaustion or breakage of the material, whereas flakes are far more durable. These authors conclude that, when resharpening processes are taken into account, the usable cutting edge produced from flakes per unit mass of raw material “will outstrip that of blades” (Eren et al. 2008:957). As bifacial thinning flakes are light relative to the tool being retouched, minimal mass is lost during each resharpening episode, with Kelly & Todd (1988) further suggesting that thinning flakes can be expediently used as temporary tools themselves.

The dispersal phase highlighted by foregoing analyses of the Lake Tana data, the recent genetic research discussed above, and the considerations regarding the relationship between lithic technology and dispersal presented in the previous paragraphs are all potentially in conflict with some aspects of the prevailing model of the global *Homo sapiens* diaspora. This model, most cogently stated by Mellars (2006a, 2006b; Mellars et al. 2013), proposes that major technological, economic and social changes in south and east Africa after 80 ka ago led to dramatic population expansion between 70 and 60 ka, with resulting dispersals beginning shortly thereafter. Mellars and colleagues (2013) argue for an earliest arrival date for *Homo sapiens* in southern Asia between 50 and 60 thousand years ago, reaching Australia by between 50 and 45 thousand years ago, and for an equivalent pulse northwards into Europe to accord with the dates for the earliest European Upper Palaeolithic at between 48 and 45 ka (e.g. Richter et al. 2008, 2009; Kuhn et al. 2009). A substantial part of the model centres upon the development of Howiesons Poort industries in southern Africa between 71 and 59 ka and the appearance of their east African corollaries in the latter half of this date range (Brown et al. 2012; Gliganic et al. 2012; Skinner et al. 2003). The production of small blades, and the preponderance of backed pieces and geometric microliths lead to the suggestion that the Howiesons Poort is indicative of increased levels of technological efficiency and behavioural innovation that could have facilitated the expansion of *Homo sapiens* populations (Lombard 2005; Wurz 2002; Soriano et al. 2007). The presence of a blade component together with extensively shaped bone tools and various elements of symbolic material culture are also seen to directly presage the European Upper Palaeolithic, further strengthening the notion of a Howiesons Poort-inspired expansion of modern humans out of Africa.

Mellars (2006a, 2006b) explicitly recognises the earlier dispersal of modern humans into the Levant documented via the extensive dating evidence surveyed above, thus the points of debate concern only a) the technological affinities (and thus by inference the makers) of the southern route assemblages, b) the extent to which the appearance of modern humans in the Levant prior to 90 ka is ‘temporary’ given the archaeological and genetic evidence, and c) the nature of the lithic assemblages one might expect to accompany dispersing populations. There are other researchers far better placed to comment on a), and indeed a lively debate is ongoing (see Groucutt and Petraglia 2012; Boivin et al. 2013; Mellars 2013). Suffice to say that the timing of the dispersal phase identified at Lake Tana and the dispersal speed analyses provided above are consistent with the possibility that modern humans were responsible for the Aybut Auwal material, if not for the earliest levels at Jebel Faya. That the presence of modern humans in the specific region surrounding Qafzeh and Skhul is temporary is very clear; by around 70 ka Neanderthals are the sole hominin species in the region, as demonstrated by abundant skeletal material from Kebara, Tabun, Amud, and Shanidar (Shea 2003, 2008). However, the genetic data surveyed above are consistent with the Qafzeh and Skhul specimens forming part of the global diaspora of our species, so the more pertinent question concerns the fate of these early Levantine moderns. Whilst the traditional view centres upon the idea of a simple local extinction, other suggestions include migration into Arabia (e.g. Rose 2010) or a retreat towards North African coastal refugia (e.g. Ambrose 1998), driven in both cases by deteriorating climatic conditions in MIS 4. This question remains unresolved, and recent genetic data (e.g. Scally and Durbin 2012; Fu et al. 2013; Veeramah and Hammer 2014) attach increased importance to potential answers.

Finally, the outline of a plastic ‘technology of dispersal’ given above is not consistent with the view that dispersal was driven by the innovations found within the Howiesons Poort industry. Indeed, the transition from earlier MSA industries to the Howiesons Poort is viewed by Ambrose (2002) and McCall (2006, 2007) as a transition *away* from a flexible toolkit towards a more specialized one (see Figure 11). Employing the model of Dyson-Hudson and Smith (1978), and following the work of Ambrose and Lorenz (1990), McCall (2007) explicitly associates the Howiesons Poort with high resource predictability; resources in unfamiliar habitats, however, are expected to be anything but predictable. In contrast, the Levallois affinities of the Tabun C industries found with early *Homo sapiens* in the Levant and the widespread bifacial component present in the Arabian Middle Palaeolithic (Rose 2004; Groucutt and Petraglia 2012) are consistent with the views put forward by Kelly and colleagues (Parry and Kelly 1987; Kelly and Todd 1988), and developed above, that bifacial technology embodies the plasticity required to enable dispersal.

**Conclusions**

The accumulated plasticity hypothesis of hominin dispersal suggests that plastic adaptations accumulated during phases of relatively high environmental variability will facilitate dispersal during subsequent phases of relatively low environmental variability. Under this hypothesis, analyses of a precipitation-evaporation proxy from Lake Tana pinpoint a likely dispersal phase from Ethiopia dating to between c.112,550 and c.96,975 years ago. The dating of this dispersal phase is consistent with early *Homo sapiens* dispersal into the Levant, and also accords well with some dates for the ‘southern route’ out of Africa. Although the dates of the Lake Tana dispersal phase are well constrained, the dates of occupation at the Levantine sites are less so, and further testing of the hypothesis is required. Finally, recent genetic analyses require us to re-evaluate the standard assumption that the early *Homo sapiens* presence at the sites of Qafzeh and Skhul is indicative of a ‘failed dispersal’.

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**Table Caption**

**Table 1**. Routes, distances, medians, and 95% confidence intervals for dispersal speed analyses.

**Figure Captions**

**Figure 1**. a) shows the fitnesses of two genotypes over a continuum of climatic states, b) shows the oscillating climate they experience over time, and c) shows the variation in fitness over time experienced by each genotype.

**Figure 2**. The effects of varying amplitudes of climatic variability (a) on levels of plasticity (b) and fitness (c). The dispersal phase begins during an abrupt transition from higher to lower variability, with plasticity high but decreasing and fitness low but increasing. After Grove (submitted).

**Figure 3**. Schematic view of the APH, showing the transition from a high variability climate (a) to a lower variability climate (b). A latitudinally constricted population (c) expands immediately after this transition (d). (e), (f), and (g) show an altitudinal equivalent, with (e) showing an elevation model, (f) the area occupied during the high variability phase, and (g) the expanded area of occupation in the lower variability phase.

**Figure 4**. Dated Early Archaic, Late Archaic, and Anatomically Modern *Homo sapiens* in northern, eastern, and southern Africa over the past 400ka. After Bräuer (2012).

**Figure 5**. Radiometric dates for early *Homo sapiens* levels at the site of Qafzeh, Israel. Diamonds are electron spin resonance (ESR) dates from Schwarcz *et al*. (1988), with black indicating early uptake (EU) and grey indicating linear uptake (LU) models; squares are thermoluminescence dates from Valladas *et al*. (1988); triangles are ESR dates from McDermott *et al*. (1993), with EU-ESR and LU-ESR indicated as before; grey circles are uranium series dates from McDermott *et al*. (1993); black circles are U-series dates on the Qafzeh 6 cranium from Yokoyama *et al*. (1997). Error bars are shown where the relevant data were published. The vertical grey region 87.0-96.9ka BP is that indicated by Millard’s (2008) Bayesian stratigraphic model as encompassing the layers from which hominins 3, 6, 8-12, and 14-17 were recovered.

**Figure 6**. Radiometric dates for early *Homo sapiens* levels at the site of Skhul, Israel. Black diamonds are weighted means of combined open-system U-series and linear uptake ESR (henceforth US-ESR) dates from Grün *et al*. (2005), with black crosses indicating individual dates (confidence intervals are shown for the means only); squares are from McDermott *et al*. (1993), with grey being LU-ESR and black being U-series dates (note that the confidence intervals on the U-series dates are shown, but are negligible at this scale); triangles are LU-ESR dates from Stringer *et al*. (1989); circles are TL dates on burnt flint from Mercier *et al*. (1993). The vertical grey regions are those indicated by Millard’s (2008) LU-ESR Bayesian stratigraphic model for the burial of Skhul V (associated with sample 1058) and Grün *et al*.’s (2005) combined US-ESR analysis for the burials of Skhul II and V. The darker grey region is the period of overlap in these two estimates from 88 – 115ka BP.

**Figure 7**. Results of the variability analyses on the Lake Tana moisture proxy. (a) shows the 25-year interpolated data (grey circles) and the 1025-year Gaussian filter output (black line), with periods of below average aridity marked by light grey bars. The Eastern Mediterranean Sapropels are marked as black stars. (b) shows the variability index, (grey circles) and the 1025-year Gaussian filter output through this data (black line), with periods of below average variability marked by light grey bars.

**Figure 8**. 25-year symmetrically interpolated data from Lake Tana (black line) with grey bars marking periods that are of both below average variability *and* below average aridity. The dispersal phase between c.96,975yr and c.112,550yr is indicated. Eastern Mediterranean Sapropels are marked as black stars.

**Figure 9**. Profiles of required dispersal speeds from the Lake Tana region to a) Qafzeh and b) Aybut Auwal given the timing of the dispersal phase, the dates of likely occupation at the two sites, and their distances from Lake Tana. For details and distances of routes, see Table 1.

**Figure 10**. Comparison of aridity and variability at Lake Tana with an identical analysis performed on speleothem data from Soreq Cave. a) MI Stages, b) aridity comparison, c) variability comparison, d) putative dispersal phase comparison. Tana Ca / Ti and Soreq δ18O‰ rows: grey bars indicate periods of b) low aridity, c) low variability and d) putative dispersal phases (i.e. those marked by both low aridity *and* low variability). Comparison rows: grey bars indicate agreement over adverse conditions (e.g. both Tana and Soreq show b) high aridity, c) high variability, or d) low dispersal potential); black bars indicate agreement over beneficial conditions (e.g. both Tana and Soreq show b) low aridity, c) low variability, or d) high dispersal potential). Hiatuses (in the Lake Tana record) are shown as grey vertical bands marked ‘H’.

**Figure 11**. MSA technologies plotted according to degree of plasticity and extent of manufacture and repair costs (adapted from McCall 2007:1748). Dispersing hominins would be expected to carry technologies as close to the star (bottom right) as possible.

**Figure 1**

JHE Figure 1.tif

**Figure 2**

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**Figure 3**

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**Figure 4**

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**Figure 5**

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**Figure 6**

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**Figure 7**

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**Figure 9**

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**Figure 10**

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**Figure 11**

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