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Supporting Online Material

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REPORTS

Late Pleistocene Demography and the Appearance of Modern Human Behavior

Adam Powell,^{1,3} Stephen Shennan,^{2,3} Mark G. Thomas^{1,3*}

The origins of modern human behavior are marked by increased symbolic and technological complexity in the archaeological record. In western Eurasia this transition, the Upper Paleolithic, occurred about 45,000 years ago, but many of its features appear transiently in southern Africa about 45,000 years earlier. We show that demography is a major determinant in the maintenance of cultural complexity and that variation in regional subpopulation density and/or migratory activity results in spatial structuring of cultural skill accumulation. Genetic estimates of regional population size over time show that densities in early Upper Paleolithic Europe were similar to those in sub-Saharan Africa when modern behavior first appeared. Demographic factors can thus explain geographic variation in the timing of the first appearance of modern behavior without invoking increased cognitive capacity.

The Upper Paleolithic (UP) transition, which occurred in Europe and western Asia about 45 thousand years ago (ka) (1, 2), and later in southern and eastern Asia (3, 4), Australia (5, 6), and Africa (7), is seen by many as marking the origins of modern human behavior. UP material culture, usually referred to as the Late Stone Age (LSA) in Africa, is characterized by a substantial increase in technological and cultural complexity, includ-

ing the first consistent presence of symbolic behavior, such as abstract and realistic art and body decoration (e.g., threaded shell beads, teeth, ivory, ostrich egg shells, ochre, and tattoo kits); systematically produced microlithic stone tools (especially blades and burins); functional and ritual bone, antler, and ivory artifacts; grinding and pounding stone tools; improved hunting and trapping technology (e.g., spear throwers, bows, boomerangs, and nets); an increase in the long-distance

transfer of raw materials; and musical instruments, in the form of bone pipes (1, 2, 5, 7–9).

In Europe and western Asia, the UP transition happened relatively rapidly, with most of the characteristic features listed above appearing (the “full package”), and is thought to coincide with the appearance of anatomically modern humans (AMH) in a region previously occupied by Neandertals (10). In southern Siberia and north-east Asia, microlithic technology appears between 43 and 27 ka (11), but a fuller UP package is not evident until ~22 ka (12). The evidence from south and southeast Asia and Australia also points to a more gradual accumulation of modern behavioral traits (ornamentation, use of ochre, and possibly rock art) (3–6). These are thought to first appear soon after the initial expansions of AMH into the regions but only become widespread later on, ~30 ka (4) and ~20 ka, if not later (5), in south Asia and Australia, respectively. In Africa, the idea of a single transition has been

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contested (9) because there is strong evidence for the sporadic appearance of many markers of modern behavior at multiple sites as early as 70 to 90 ka (2, 9, 13), and possibly as far back as 160 ka (14). The African Middle Stone Age (MSA) sites of Katanda, Democratic Republic of Congo (~90 ka) (9); Klasies River mouth (Howieson's Poort and Still Bay industries), South Africa (~65 to 70 ka) (9, 15); and, in particular, Blombos Cave, South Africa (~75 ka) (10, 13) present a striking array of modern traits, including the earliest evidence of abstract art (8, 13), as well as geometric blades, barbed bone harpoon points (9), bone awls, and marine shell personal ornaments (10). However, these markers are intermittent and disappear between ~75 and 60 ka before making a more stable and widespread reappearance in the LSA starting ~40 ka (7, 10, 13).

Notwithstanding the oversimplifications made in the above outline, any adequate account of the emergence of modern behavior would need to explain not only the transition itself but also its

heterogeneous spatial and temporal structuring (2) and earlier transient appearance in sub-Saharan Africa (9, 10, 13). It is now widely accepted that AMH evolved in Africa ~160 to 200 ka (9, 16–18) and expanded into most habitable parts of the Old World between 90 and 40 ka (19–21). If, as some have suggested (22–24), the main cause of behavioral modernity is heritable biological change just before the UP/LSA, then any such mutation(s) would have had to rise to substantial frequencies after human populations had dispersed out of Africa; implying either their rapid spread around the world in the past 45,000 years or, potentially, geographic structuring of cognitive capacity. Furthermore, it is difficult to account for the southern African evidence with a late, biologically determined cognitive advance. Many authors have argued that AMH (1, 9, 10, 17, 20), and possibly even Neandertals (8, 10), possessed the requisite capacities long before the UP/LSA. This raises the further question of why there was a delay of some 100,000 years between anatomical modernity and perceived behavioral modernity (1, 17). A number of mechanisms triggering the expression of modern behavior have been proposed, many of which invoke demo-

graphic change as a causal factor. These include expansion into new environments necessitating the invention of new technologies (25), increased subpopulation density escalating intergroup resource competition (1, 25) or social organization (1), increased intergroup interaction requiring various cultural signaling mechanisms (6, 25, 26), and increased stimulus for exoteric language (23, 27, 28). Two recent cultural evolutionary models (29, 30), which explicitly demonstrate the positive effect of increasing population size on the accumulation of beneficial culturally inherited skills, have been proposed as an integral explanatory component of the appearance of modern behavior [see also (17)]. Here, we adapt and extend Henrich's transmission model (30) into a more realistic structured metapopulation, which reflects plausible late Pleistocene conditions, to investigate the effects of demographic factors on the accumulation (or loss) of cultural complexity.

Henrich's model (30) demonstrates that under certain critical conditions, directly biased transmission can lead to cumulative adaptation of a culturally inherited skill, even when the transmission process is inaccurate. Each individual in a population of size N has a z value, z_i , that measures their level of ability at

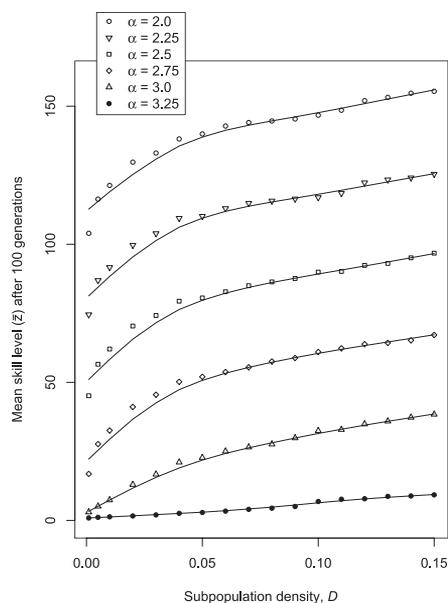


Fig. 1. Mean z values in the final (100th) generation, averaged over 100 iterations, for a range of values of skill complexity α and subpopulation density D .

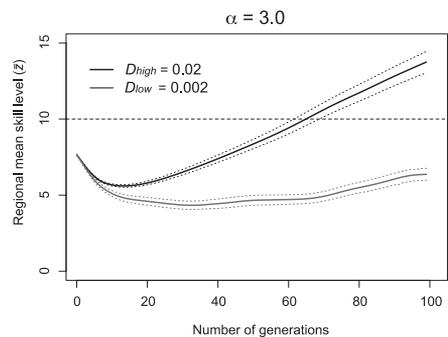


Fig. 2. Regional mean z values (averaged over 100 iterations) over 100 generations in a heterogeneous subpopulation density world. The 95% confidence intervals for each region are given as dotted lines.

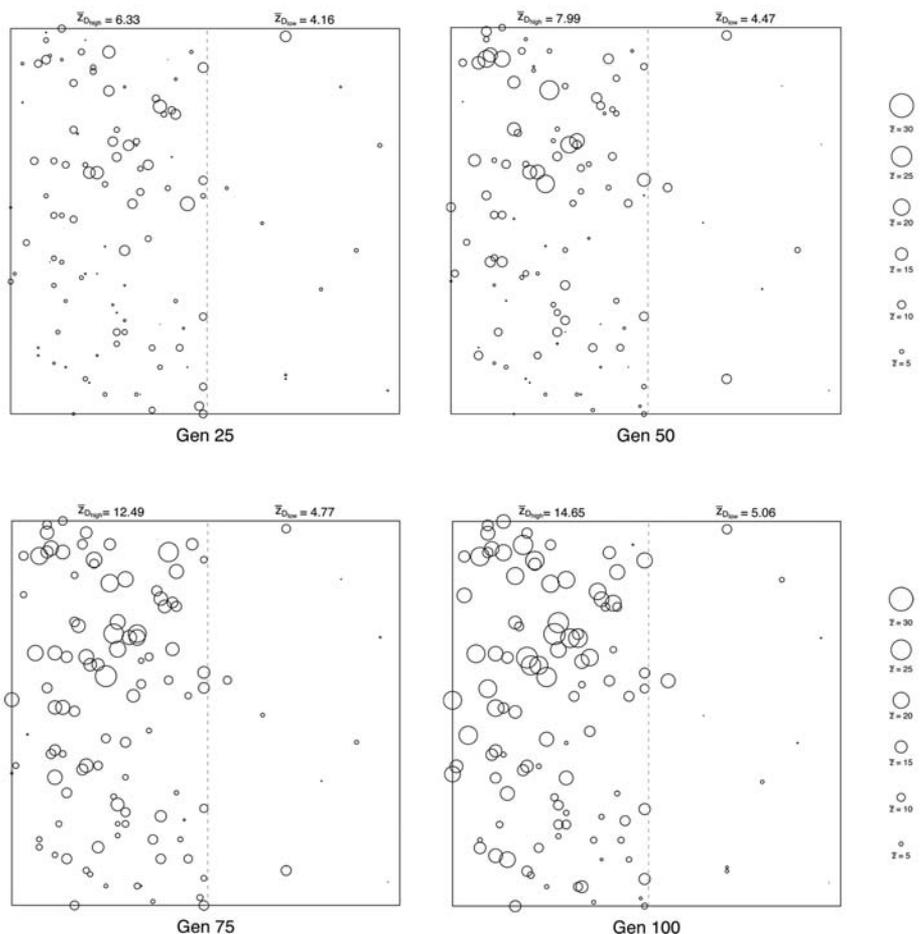


Fig. 3. An illustration, from a single iteration and shown at 25-generation intervals, of the spatial structuring of skill accumulation in a heterogeneous subpopulation density world. The left side of each subplot is populated at density D_{high} (0.02) and the right side at density D_{low} (0.002). Each subpopulation is marked by a circle, centered on the spatial location of the group and with diameter proportional to its mean z value. Regional mean z values are also given at the top of each subplot.

some cultural skill or in some cultural domain. Members of this population attempt to learn from the maximally skilled individual (i.e., direct bias), but an imperfect learning process leads on average to a loss of skill (a reduction in z value), determined by the parameter α . However, individual errors or “inaccurate inferences” during transmission (the extent of which are governed by a parameter β) occasionally allow some learners to acquire a z value greater than that of their model. Henrich shows that as population size, N , increases, the more likely it is that the positive combined effect of these occasional inaccurate inferences and the selective choice of cultural model to copy will outweigh the degrading effect of low-fidelity transmission. This results in an increase in the mean level of skill in the population, \bar{z} . He terms this “cumulative adaptive evolution” and derives the critical population size necessary, N^* , for this to occur for specific ratios of α and β (30, 31).

We introduce a stochastic transmission model analogous to the one presented by Henrich that incorporates both vertical and skill-level dependent oblique learning processes. We place individuals in G subpopulations, each of size N , in a simulated world at density D . These subpopulations are connected by Gaussian random-walk migratory activity, with standard deviation M_{SD} , such that the mean global migration rate approximates the subpopulation density D (31). Where possible, we use parameter values from ethnographic and comparative behavioral studies that approximate presumed late Pleistocene demography (31). We initialize simulations by giving all adults in all subpopulations a z value of 10.0 and run forward for 100 generations. The mean level of cultural skill accumulation, \bar{z} , is measured by averaging z values across all individuals in all subpopulations. If the mean z value in the final generation is greater than 10.0 (i.e., $\Delta\bar{z} > 0$), then the result was deemed “cumulatively adaptive.” To account for stochastic variation in simulation outcomes, we performed 100 iterations and averaged the results across these.

We first explored the effects of varying the number of subpopulations in our simulated world, G , on the mean level of cultural skill accumulated, \bar{z} . For values of $G > \sim 50$, the \bar{z} value did not increase much further across the entire range of subpopulation densities D and skill complexities α (fig. S1). Figure 1 illustrates that the degree of skill accumulation increased with increasing subpopulation density and decreasing skill complexity. These results indicate that the accumulation, or maintenance, of culturally inherited skill is not dependent on the absolute metapopulation size, but rather on the degree of interaction of the constituent subpopulations, given population substructure and that $G > \sim 50$. However, when $G < \sim 50$, skill accumulation will, to an extent, be dependent on G , and thus the size of the metapopulation. This result may have some bearing on debate concerning the erosion of cultural complexity in Holocene Tasmania (30, 32, 33). As a conservative measure, we fixed G at 100 in all subsequent simulations.

A key feature of the UP is the geographic heterogeneity in apparent onset times, despite different

regions being mutually accessible with modest migration activity. To investigate whether skill accumulation can be spatially structured as a result of different subpopulation densities, we partitioned our simulated world into two regions differing in density by an order of magnitude, D_{high} and D_{low} . We retained M_{SD} at 1.0, but as a proportion of the mean nearest neighbor distance, r_E , in the lower density region (31). This ensured that sufficient subpopulations were connected by migratory activity—including across the partition—for the migration rate to approximate the density in each region. We set $D_{high} = 0.02$ and $D_{low} = 0.002$ and simulated a range of α values (2.0 to 4.0). For all α values, we found that skill accumulation is consistently higher in the D_{high} region even though the two regions were contiguous. As an example, when we fixed $\alpha = 3.0$, this difference in mean regional z values, averaged over 100 iterations, was maintained over the entire duration of the simulation (Fig. 2). Figure 3 and movie S1 provide an illustration from a single iteration of the spatial structuring of skill accumulation.

We would also expect heterogeneity in migratory range during the late Pleistocene due to, for example, differing terrains, vegetation, or subsistence strategies (4). To investigate whether this could result in spatial structuring of skill accumulation, we populated the simulated world at a constant subpopulation density $D = 0.01$ and partitioned it into two regions with differing M_{SD} values (31); $M_{SD,high} = 1.0$ and $M_{SD,low} = 0.1$, allowing migratory activity across the partition. Similarly to the heterogeneous density world, we find that skill accumulation was consistently higher in the well-connected $M_{SD,high}$ region across all α values simulated (2.0 to 4.0). An example, with $D = 0.01$ and $\alpha = 2.9$, is given in fig.

S2, with mean regional z values averaged over 100 iterations. Fig. S3 and movie S2 provide a spatial illustration from a single iteration.

From the above results, it is clear that migratory activity among a set of subpopulations can have the same effect on skill accumulation as increasing the size of a single population (30). This is because it increases the within-group variance in skill levels, z_i , which feeds the selective directly biased transmission process and offsets the eroding effect of low-fidelity transmission. We therefore sought to quantify the effect of increasing migration activity in terms of the effective number of adult individuals available as transmission models within each subpopulation. To achieve this, we inverted the previous simulation process; for given values of α and D , we simulated widely over N to find the minimum number of adults, N_{min} , needed in each subpopulation for adaptive cumulative evolution to occur (Fig. 4). We repeated this process for the same range of α , but with no migratory process operating, to obtain the minimum number of adults required for skill accumulation in an isolated subpopulation, N_0 , for each value of α (Fig. 4) [this is directly equivalent to Henrich’s analytical result (30) but uses the extended transmission process presented in our study]. We then calculated the effective increase in N due to migratory activity by finding the difference between the N_{min} we expect for given values of α and D , and the N_0 we expect for the same value of α . As can be seen from Fig. 4, not only does increasing migratory activity have the same effect as increasing the size of an isolated population (30), but also this effect is greater for higher skill complexities, α .

Our simulation results demonstrate that the influence of demography on cultural transmission

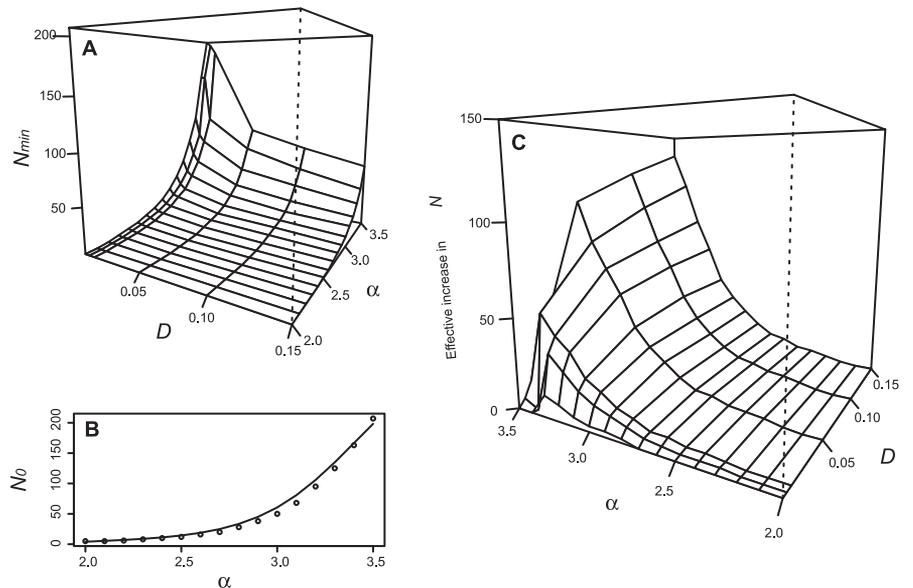


Fig. 4. The effective increase in adult subpopulation size due to migratory activity. (A) The minimum number of adults required for adaptive cumulative evolution to occur, N_{min} , for a range of values for subpopulation density D and skill complexity α . (B) The minimum number of adults needed in a single isolated population N_0 for the same range of α values. (C) The effective increase in adult subpopulation size N due to migratory activity for this range of D and α , calculated by subtracting surface (A) from curve (B) extended along the D axis. The axes of (C) have been rotated for display purposes.

processes provides a mechanism to explain three key features of the emergence of modern behavior in the archaeological record: the early appearance, and subsequent disappearance, of many modern traits in Southern Africa 90 to 70 ka; geographical heterogeneity in the timing of the UP outside Africa; and the delay between the emergence of AMH as a species and the material expression of modern behavioral traits. If, as proposed here, demographic factors are fundamental in shaping the evolution of human behavior, then well-supported estimates of late Pleistocene regional population densities will be crucial to understanding the UP/LSA. Recent estimates of population size changes in the late Pleistocene—based on a Bayesian coalescent inference method with a global data set of coding-region mitochondrial DNA (mtDNA) sequences (34)—permit some comparisons of relative effective population densities in different regions of the world and at different times.

By setting the UP transition in Europe at 45 ka (1, 2), we can infer the critical effective population size, and therefore density, necessary for the accumulation of markers of modern behavior. Although this transition is closely associated with the initial colonization by AMH, the rapid rise in skill levels under favorable demographic conditions that we observe in our simulations indicates that cultural intensification would be largely insensitive to the time since first occupation. We assume that the habitable area of Europe would not have included most of Scandinavia, resulting in an estimated area of 8.883 million km². The median effective population size estimate in Europe at ~45 ka is 2905 [with 95% highest posterior density interval of 280.4 to 15,933.9], giving an effective population density of ~3.2714 × 10⁻⁴ km⁻². The time at which this density would have been reached in sub-Saharan Africa (estimated area ~24.270 million km²) is ~101 ka. Although this is a relatively crude date estimate, and ignores the importance of the likely large heterogeneity in population densities at the local level, it does correspond well with the first appearance of modern behavioral traits in the region (9, 13). Furthermore, applying this estimation method to the Middle East and North Africa region (estimated area ~13.588 million km²) gives a date of ~40 ka at which the critical density is reached, relatively consistent with the first evidence of modern behavior in the Levant and northeast Africa (2, 7).

In southern Asia, our predicted time for the UP transition (~52 ka) considerably predates the first archaeological evidence for modern behavior at ~30 ka (3). Similarly, the date estimate for northern and central Asia (~40 ka) predates that of the first full UP site found at ~22 ka (12). One possible explanation lies in the choice of the regions used in the analysis presented by Atkinson *et al.* (34). An important assumption of the ancestral population size estimation method used is that samples are taken from unstructured (i.e., randomly mating) populations. Although multiple loci clustering analysis (35, 36) broadly supports this assumption for most of the other regions, it clearly does not for either the southern Asian or the north and central

Asian geographic regions (34). Performing Bayesian coalescent inference (34) on such structured data sets is likely to have resulted in an overestimation of the effective population size and the time at which population expansion took place. In addition, coalescence date estimates for major mtDNA haplogroups in southern Asia have been interpreted as reflecting an initial phase of population growth somewhat later (37). A second possible explanation for this anomalous result is that, although population density may have been sufficiently high for behaviorally modern traits to otherwise accumulate, the migratory range may have been insufficient to allow wide-scale interaction between subpopulations. This may have been the case in southern Asia during the later Pleistocene (4).

Although the inferred population densities (34) could account for the early appearance of behaviorally modern traits in sub-Saharan Africa and the Middle East—given our demographic model of cultural skill accumulation—they cannot explain the subsequent absence of these features between 70 and ~40 ka because no population size reduction during this period is inferred [see figure 1 in (34)]. However, the method of coalescent inference used (Bayesian skyline analysis) may be unable to accurately reconstruct more complex demographic histories when using sequences sampled from a single locus (38), so repeated bottlenecks and/or expansions, which would have an important bearing on the accumulation of culturally inherited skills (17), may not be recaptured. Paleoclimatic data does indicate worsening conditions during oxygen isotope stage 4 (~75 to 60 ka) (21)—possibly leading to population decline, fragmentation, and range contractions—during this period (20, 21). Lahr and Foley (20) suggest that continent-wide secondary population bottlenecks may have occurred ~70 ka, and there is some evidence that the sites of the South African Howieson's Poort industries became effectively depopulated by ~60 ka (15, 20).

We would expect a degree of positive feedback on population density after the accumulation of culturally inherited skills; the development of more advanced technologies, and possibly social organization, would likely lead to population growth. Furthermore, we would expect to see more artifactual evidence of behavioral modernity in higher population density contexts through increased deposition. Although the model we have presented does not accommodate these processes or explain the necessary cognitive developments that make possible the invention or improvement of complex behavioral traits, it does provide a demographic mechanism for limiting the degree to which early human populations would have accumulated these culturally inherited skills over time. Our model provides a plausible explanation for the spatial and temporal structuring of the markers of modern behavior in the paleoanthropological record, even if all AMH had the requisite biologically determined cognitive capacities from the time of origin some 160 to 200 ka.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/324/5932/1298/DC1

Materials and Methods

Figs. S1 to S3

Movies S1 and S2

References

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