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Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers

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Present-day hunter-gatherers (HGs) live in multilevel social groups essential to sustain a population structure characterized by limited levels of within-band relatedness and inbreeding. When these wider social networks evolved among HGs is unknown. To investigate whether the contemporary HG strategy was already present in the Upper Paleolithic, we used complete genome sequences from Sunghir, a site dated to ~34,000 years before the present, containing multiple anatomically modern human individuals. We show that individuals at Sunghir derive from a population of small effective size, with limited kinship and levels of inbreeding similar to HG populations. Our findings suggest that Upper Paleolithic social organization was similar to that of living HGs, with limited relatedness within residential groups embedded in a larger mating network.

Opportunities to investigate the population dynamics of early anatomically modern human (AMH) populations are rare owing to a dearth of human remains, with wide variations in ancient population size estimates from ethnographic and archaeological data (1, 2). In the absence of evidence for true contemporaneity among individuals recovered archaeologically, the population structure of foraging groups is even harder to establish. Exceptions are cases of multiple Upper Paleolithic individuals buried simultaneously or originating from sufficiently close temporal and spatial proximity that they may represent a single social group. One such example of multiple burials is Sunghir, a site harboring two of the most extraordinary Upper Paleolithic burials known (3, 4) (figs. S1 and S2 and tables S1 to S4): one of an adult male [Sunghir 1 (SI)] and another of two subadults [Sunghir 2 and 3 (SII and SIII)], originally thought to be a boy and girl, interred head-to-head. All remains were covered in ochre and were accompanied by rich grave goods including ivory beads and spearheads, armbands, and carvings, as well as arctic fox canines. Adjacent to SII was the femoral diaphysis of an adult [Sunghir 4 (SIV)] that had been polished, hollowed out, and filled with red ochre. The site also yielded other less complete human remains, some of uncertain stratigraphic provenance (Sunghir 5 to 9 (SY to SDX)). Radiocarbon analyses place the age of SI to SIV between 33,600 and 34,600 years (5, 6). The homogeneity in morphological traits (e.g., metopism) among the remains, as well as signs of possible congenital pathologies in SIII, have been interpreted as evidence of inbreeding (3). Other Upper Paleolithic individuals with reported congenital or degenerative pathologies (e.g., at Barma Grande and Doinîi Vinston) (7) reinforce the view that Upper Paleolithic groups were small and susceptible to inbreeding, possibly as extensive as what has been reported for the Altai Neandertal (7). However, genomic data available for some of those individuals (8) were of insufficient coverage to infer population sizes or inbreeding levels.

We screened six of the Sunghir individuals (SI to SIV) to assess DNA preservation; five of them (all but SV) yielded sufficient endogenous DNA for genome sequencing. We sequenced these genomes to an average depth of coverage ranging from 11× to 107× (figs. S3 and S4 and tables S5 and S6) and compared them to panels of modern and ancient human genomes (4). All individuals were genetically male on the basis of the fraction of Y chromosome reads (table S7), including SII, who was previously identified as female (3). Contamination levels from X chromosome heterozygosity were low (0.33 to 0.90%; table S5), except for SIV (13.1%). Radiocarbon dates indicate that whereas SV is only slightly more recent than the other individuals, SIV is from ~900 years before the present (figs. S5 and S6 and tables S8 to S10). Together with mitochondrial DNA (mtDNA) and Y chromosome haplogroups (W3a1 and I2a1b2, respectively), these data indicate that SIV is not associated with the Upper Paleolithic burials at the site; SVI was therefore excluded from further analyses.

Analyses of mtDNA genomes place S1 to SIV in haplogroup U, consistent with West Eurasian and Siberian Paleolithic and Mesolithic genomes (9) (fig. S7 and table S6). S1 belongs to haplogroup U8c; the sequences for the three individuals from the double burial (SII to SIV) are identical and belong to haplogroup U2, which is closely related to the Upper Paleolithic Kostenki 12 (8) and Kostenki 14 (10) individuals. Phylogenetic analyses of the Y chromosome sequences place all Sunghir individuals in an early divergent lineage of haplogroup C1a2 (fig. S8 and tables S12 to S23). Y chromosome haplogroup C1, which is rare among contemporary Eurasians, has been found in other early European individuals, including the ~36,000-year-old Kostenki 14 (11).

We investigated the degree of relatedness among the Sunghir individuals with a method that allows relationship inferences up to the third degree but does not rely on allele frequencies (4). Surprisingly, none of them were found to be closely related (that is, third degree or closer), even though the SII to SIV individuals buried together share both mitochondrial Y chromosome lineages (Fig. 1 and tables S16 to S23). We then inferred genomic segments that were identical by descent (IBD) and homozygous by descent (HBD) from three higher-coverage Sunghir genomes (SII to SIV) and a panel of ancient and contemporary humans (4). We compared their distributions to those inferred from whole genomes obtained using coalescent simulations (12) of randomly mating populations with varying effective population sizes (\(N_e\) values) (fig. S9). The distributions of HBD/IBD were different between AMHs and archaic humans, indicating small effective population sizes and/or recent inbreeding in archaic...
Fig. 1. Relatedness among ancient Eurasians. Kinship coefficients and R1 ratios (4) were inferred from IBS counts. (A) Pairs of Upper Paleolithic individuals, using 1000 Genomes Phase 3 single-nucleotide polymorphism (SNP) sites. (B) Pairs of ancient Eurasians, using 1240K capture SNP sites. Within-group pairs of Sunghir are highlighted.

Fig. 2. Identity by descent and recent effective population sizes. (A and B) Distributions of the number and total length of HBD and IBD segments in modern, ancient, and archaic humans (Altai Neandertal and Denisovan). Ellipses indicate 95th percentile (dark gray) and 99th percentile (light gray) of the distributions inferred from simulated data of various NE values. Individuals with previously described close relatedness and their degree are indicated in (B). (C) Distributions of inferred recent effective population sizes for modern and ancient HGs with a minimum of three individuals, as well as simulated data sets of randomly mating populations with a range of NE values. For each population, a pair of symbols and box plots indicates the distributions of population sizes inferred from individual HBD (left) and pairwise IBD tracts (right).
individuals, particularly the Altai Neandertal (7, 13) (Fig. 2A and figs. S10 to S14).

Patterns of pairwise IBD sharing successfully detect close genetic relatives in modern individuals (Fig. 2B). However, the Sunghir pairs do not share sufficiently long IBD tracts to suggest relatedness at the first or second degree, consistent with the results from genome-wide identity-by-state (IBS) counts (Fig. 2B and fig. S15). Interestingly, the effective population sizes tended to be higher ($N_e \sim 500$) for two of three Sunghir pairs than those estimated from HBD segments ($N_e \sim 200$). $N_e$ from both HBD and IBD tracts ($\delta$) was within the range of, or slightly higher than, that of contemporary non-African HG populations (Fig. 2C), particularly from genetically isolated groups (14).

Genetic clustering of ancient individuals using outgroup-$f_3$ statistics ($f_3$(Mbuti; Ancient1, Ancient2)) indicates shared genetic drift and tight clustering of the Sunghir individuals, which form a clade to the exclusion of all other individuals (Fig. 3A, figs. S16 to S20, and tables S28 and S29). Furthermore, we find genetic affinities between the Sunghir individuals and those from Kostenki (12 and 14), as well as with the “Vêstonice cluster” (8) associated with the Upper Paleolithic Gravettian culture.

Individuals mapped onto a previously inferred admixture graph of early Eurasians (4, 8) placed the Sunghir cluster as a descendent of a lineage related to the Kostenki 14 individual, contributing the major fraction of the ancestry of the Vêstonice cluster (Fig. 3C and figs. S21 to S24). Adding the low-coverage Kostenki 12 individual suggests a closer relationship with the Sunghir group rather than with the earlier Kostenki 14 individual (Fig. S25). Kostenki 14 shows substantial population-specific drift after its divergence from the shared ancestor with Sunghir, allowing us to reject a direct ancestral relationship to both Sunghir and Kostenki 12 (fig. S26). These results suggest that the people at Kostenki were at least partially replaced by later groups related to Sunghir, which exhibit genetic affinities with individuals of the Gravettian culture, which extended to Western Europe.

Our high-coverage Sunghir individual (SIII) allows us to explore quantitative models of Eurasian demographic history. Using coalescent-based modeling of the site frequency spectrum (fig. S27), we estimate that SIII diverged $\sim 38,000$ years ago (95% confidence interval [CI], 35,000 to 43,000) from the lineage ancestral to contemporary Europeans, with a relatively small effective population size ($N_e = 297$; 95% CI, 158 to 901) (Fig. 4A, figs. S28 and S29, and tables S24 and S25). The Ust-Ishim genome, a 45,000-year-old Upper Paleolithic individual from Siberia (15) who diverged from the Asian lineage $\sim 48,000$ years ago (95% CI, 45,000 to 55,000) soon after the initial divergence among Eurasians $\sim 52,500$ years ago (95% CI, 49,000 to 57,000), indicates a comparably higher effective population size ($N_e = 1203$; 95% CI, 253 to 7098) (Fig. 4B, figs. S30 and S31, and tables S26 and S27). The best-fit models also suggest a common Neandertal admixture event shared by all Eurasians 55,000 years ago (95% CI, 52,000 to 63,000), consistent with previous estimates (11, 15). However, we also find evidence of multiple Neandertal admixture events in both SIII (36,000 years old; 95% CI, 34,000 to 42,000) and Ust-Ishim (47,000 years old; 95% CI, 44,000 to 51,000), the latter introgression providing an estimated 0.6% (95% CI, 0.002 to 1.53) of Neandertal ancestry to SIII. That excess may reflect either (i) further pulses of Neandertal introgression, or (ii) selection against Neandertal introgressed regions in AMHs, as previously suggested (8, 16–18). Analysis of putative archaic-introgressed genomic segments (4) confirms a higher level of Neandertal ancestry and a longer average Neandertal segment length among Upper Paleolithic individuals, in agreement with their closer proximity to the human-Neandertal admixture event than present-day Eurasians (fig. S36). Assuming that the Sunghir individuals are contemporaneous (4), we obtain a refined estimate of the time since admixture at 770 generations (95% CI, 755 to 786). Accounting for the uncertainty of both the admixture estimate and $^{14}C$ ages, this corresponds to an admixture date between the ancestors of Sunghir and Neandertals between 53,600 and 58,100 years ago (assuming 29 years per generation (19)), in agreement with the results obtained from coalescent modeling (fig. S37).
Fig. 4. Modeling of early Eurasian population history. (A and B) Best-fit demographic models for early Eurasian admixture including (A) SII and (B) Ust’-Ishim. Point estimates are shown in bold (kyr, thousands of years ago); 95% confidence intervals are shown within square brackets. Times of divergence in years are obtained assuming a generation time of 29 years and a mutation rate of $1.25 \times 10^{-8}$ per generation per site. N.R.E., Unsampled “ghost” population related to the Altai Neandertal used to model admixture contributing to Eurasians; N.R.A., Altai Neandertal–related ghost population contributing to ancient modern humans. Divergence of SII from proto-Europeans was supported in 100 of 100 bootstrap replicates, whereas divergence of Ust’-Ishim from proto-Asians was supported in 99 of 100 bootstrap replicates.

REFERENCES AND NOTES

4. See supplementary materials.

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SUPPLEMENTARY MATERIALS

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Supplementary Text

Figs. S1 to S37

Tables S1 to S29

References (20–159)

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How early human groups were organized

Sequencing ancient hominin remains has provided insights into the relatedness between individuals. However, it is not clear whether ancient humans bred among close relatives, as is common in some modern human cultures. Sikora et al. report genome sequences from four early humans buried close together in western Russia about 34,000 years ago (see the Perspective by Bergström and Tyler-Smith). The individuals clustered together genetically and came from a population with a small effective size, but they were not very closely related. Thus, these people may represent a single social group that was part of a larger mating network, similar to contemporary hunter-gatherers. The lack of close inbreeding might help to explain the survival advantage of anatomically modern humans.

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