Archaeogenomic evidence reveals prehistoric matrilineal dynasty

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For societies with writing systems, hereditary leadership is documented as one of the hallmarks of early political complexity and governance. In contrast, it is unknown whether hereditary succession played a role in the early formation of prehistoric complex societies that lacked writing. Here we use an archaeogenomic approach to identify an elite matriline that persisted between 800 and 1130 CE in Chaco Canyon, the centre of an expansive prehistoric complex society in the Southwestern United States. We show that nine individuals buried in an elite crypt at Pueblo Bonito, the largest structure in the canyon, have identical mitochondrial genomes. Analyses of nuclear genome data from six samples with the highest DNA preservation demonstrate mother–daughter and grandmother–grandson relationships, evidence for a multigenerational matrilineal descent group. Together, these results demonstrate the persistence of an elite matriline in Chaco for ~330 years.
Major advances in ancient DNA and genomic sequencing approaches have recently transformed our understanding of modern human and archaic hominin admixture\(^1^,\(^2\), dynamic population turnover in the European Upper Paleolithic and Neolithic\(^3^,\(^4\) and the peopling of the Americas\(^5^,\(^6\). Here we use these methods, in combination with high-precision accelerator mass spectrometry (AMS) \(^{14}\)C dating, to document the hereditary origins of a long-lasting elite lineage at Pueblo Bonito in Chaco Canyon, New Mexico (USA), the political and ritual centre of one of North America's earliest complex societies. Hereditary leadership formed the basis of the earliest historically recorded complex societies around the world\(^8\), but the cultural evolutionary foundations of these systems are unknown elsewhere because of the absence of writing in societies like Chaco.

Pueblo Bonito was the largest (~650 rooms, Fig. 1) of more than a dozen, multistoried masonry buildings, referred to as great houses, in Chaco Canyon. From 800 to 1130 CE, remarkable than a dozen, multistoried masonry buildings, referred to as mounds of domestic debris 11. The unusual burial pattern was unusual as otherwise most individuals were buried outside in earliest historically recorded complex societies around the world8, political and ritual centre of one of North America's earliest societies of some Eastern Pueblos13. In the latter, the highest-ranking members were chosen based more on ability and achievement rather than descent (whether patrilineal or matrilineal). The debate about the importance of kinship and unilineal descent groups in the evolution of complex society is a long-standing issue in anthropology (see, for example, refs 14,15) and has been central to much discussion of the evolution of Puebloan social organization\(^16^,\(^17\). Absent from this history of debate is the most direct method for studying descent in prehistoric populations, the analysis of ancient DNA data from skeletal material recovered during more than a century of excavation in the canyon.

Our effort to address these questions focusses on the extent of familial relationships among individuals interred in the most elaborate burial crypt in the Pueblo World. Pueblo Bonito Room 33 was part of the initial construction phase of this great house in the ninth century CE\(^11\). Intermittent inside Chacoan settlements was unusual as otherwise most individuals were buried outside in mounds of domestic debris\(^11\). The unusual burial pattern combined with an atypical, hatch-like entry in the eastern wall just below the roof of this small ~2 m × 2 m room suggests that room 33 was purposely constructed as a crypt for a high-status member of this nascent community (burial 14) and ultimately his lineal descendants.

Results

Results from previous osteological analysis indicate that burial 14 was a male in his 40s who died after a lethal blow to the head\(^15\). His body was placed in the centre of the burial crypt on a prepared floor of sand and wood ashes and adorned with thousands of turquoise (n > 11,200) and shell (n > 3,300) beads and pendants, originally part of necklaces, anklets and bracelets\(^19^,\(^20\). The abundance of turquoise alone makes this the richest burial known in the North American Southwest. Also placed on the right side of the individual were several other unusual offerings including multiple abalone (\(Haliotis\) spp.) shells from the Pacific Coast and a conch shell trumpet. The body was then entombed by a thick (70 cm) layer of clean sand devoid of artifacts except for two ceramic vessels. A second individual (burial 13), also associated with large amounts of turquoise (n > 5,800), was buried on top of this thick layer of sand and covered with a unique plank floor.

Twelve other individuals were then buried in this crypt above the wooden floor. When excavated in 1896, most burials above the floor were disarticulated and skeletal elements from different individuals were sometimes commingled, likely a result of disturbance as the bodies of deceased members of this elite lineage were periodically added to the small, dark room, as well as the methods used to excavate the room in 1896. These 12 interments were directly associated with offerings of ceramic bowls and pitchers and in some instances shell and turquoise. Nearby were caches of flutes in the northeastern corner and carved, wooden ceremonial staffs in the ceiling. Turquoise beads were placed around wooden posts in the room corners, a pattern consistent with ethnographic accounts of Puebloan cosmology\(^11\). Also noteworthy were the multiple caches of ritually important objects in adjacent rooms: hundreds of wooden ceremonial staffs; scores of cylindrical ceramic vessels; the remains of scarlet macaws (\(Ara\) \(macao\)) and jewelry\(^20^,\(^21\).

Here we use archaenogenomic methods, in combination with high-precision AMS \(^{14}\)C dating, to demonstrate that all nine of the successfully sampled individuals who were buried in this elaborate crypt have identical mitochondrial genomes. Analyses of nuclear genome data from the six individuals with the highest DNA preservation demonstrate mother–daughter and grandmother–grandson relationships consistent with matrilineal descent in this elite lineage. Together, these results indicate that hereditary inequality and societal complexity emerged in Chaco by the early ninth century CE and that this matrilineal dynasty persisted at the centre of this complex society for ~330 years until its rapid collapse in the early twelfth century CE.

Results

AMS \(^{14}\)C dating. We modelled the interment date for burials 14 and 13, and the placement of the split plank floor in room 33, using existing AMS \(^{14}\)C measurements obtained directly from the skeletal remains of these individuals\(^11\) in a phased Bayesian stratigraphic model (Fig. 2a and Supplementary Fig. 1). Bone collagen was extracted from the crania of nine additional individuals interred above the wooden floor and purified using ultrafiltration. Crude and ultrafiltered gelatin yields were excellent and stable isotope measurements are consistent with a population relying on maize agriculture (\(\delta^{15}\)N: 7 to ~9.5% VPDB; \(\delta^{13}\)N: 11.1 to 13.3% Atm N\(_2\), Supplementary Table 1). Burial 14 dates to the early ninth century (800–850 CE) and similar direct dates on abalone shells (\(Haliotis\) \(fulgens\)) from the southern California coast that were buried in association with this individual suggest that the burial remained intact and unaltered after this time (Supplementary Table 2). Persistent burial of the remaining individuals in this crypt occurred until ~1130 CE (Fig. 2a). Chronological simulations indicate interments occurred
continuously, rather than episodically, during this ~330-year period, suggesting persistent transgenerational use of the crypt throughout the growth and decline of Chaco as a regional political and religious centre (Supplementary Figs 2 and 3).

**Mitogenomic sequencing.** We next used archaeogenomic methods to reconstruct the complete or near complete mitochondrial DNA (mtDNA) genomes of nine room 33 individuals for whom ancient DNA preservation levels were sufficient for this analysis, including burials 13 and 14 (Fig. 2a). After sequence read quality and damage filtering (Supplementary Fig. 4), we called per-individual consensus sequences for nucleotide positions covered by a minimum of two independent reads. The resulting consensus sequences averaged 16,231 ± 455 bp, or 98.1% of the complete mitochondrial genome, with the average number of reads per nucleotide position (fold-sequence coverage) ranging from 7.4× to 117× among the 9 individuals (Supplementary Data 1). All nine room 33 mtDNA genome sequences were identical (Fig. 3 and Supplementary Fig. 5) and belonged to a B2y1 haplotype. The B2 haplogroup has been observed at low frequency among Southwest Native Americans based on hypervariable region sequences22. This observation is consistent with the hypothesis that the individuals buried in room 33 were members of a single, elite matriline that played a central leadership role in the Chacoan polity for ~330 years.

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**Figure 1 | Photographs and maps of Pueblo Bonito and surrounding Chacoan sites.** (a) Photograph and plan view map of Pueblo Bonito with the location of room 33 noted (photo: G. Perry). (b) Locations of the primary great houses in Chaco Canyon. (c) Locations of settlements of Chaco Canyon with great house-style architecture with inset showing North America. Maps and graphical layout: T. Harper. Each major element (other than the photograph, labels and legends) was produced in ArcGIS 10.4. All subsequent layout and design were performed in Photoshop CC 14.2.
Nuclear genome SNP genotyping and genetic relatedness. For six room 33 individuals, levels of ancient DNA (aDNA) preservation were sufficient to attempt genotyping a set of >1 million single-nucleotide polymorphisms (SNPs) from across the human nuclear genome. We successfully recovered sequence data for an average of 73,247 ± 46,843 SNPs per individual (range: 14,948–144,227; Supplementary Data 1) and used the intersecting SNPs for each pair of individuals to estimate the relatedness coefficient \( r \) (Supplementary Fig. 6 and Supplementary Table 3). We identified significant genetic relationships between two different pairs of individuals: individuals whose remains have been identified as crania 1 and 7 were likely first-degree relatives, and those identified as crania 8 and 10 were either first- or second-degree relatives (all 'lineal,' as opposed to 'collateral,' relations in the standard terminology of kinship-system analyses; Fig. 2b).

Genetic sex estimation and aDNA authenticity. Multiple lines of evidence support the authenticity of our room 33 aDNA results. First, among the sequenced reads we observe the expected patterns of aDNA damage that result from cytosine deamination at fragment ends (Supplementary Fig. 4). Second, for three individuals we generated mtDNA sequencing libraries separately in the ancient DNA laboratories at both Penn State University and the Harvard Medical School. The reconstructed mtDNA sequences were identical between the two labs. Third, for each individual with sufficient data we aligned the sequenced reads from our mtDNA analysis that did not align to the human mtDNA genome to the human reference nuclear genome in order to determine genetic sex from the ratio of chrY to chrX + Y mapped reads. Based on this analysis, three of the sequenced room 33 individuals were classified as female, three as male, and the sexes of the two oldest individuals in the sequence (burials 13 and 14) could not be determined confidently, but were likely male (Fig. 2c). These genetic sex estimates are 100% concordant with the most recent osteological sex determinations of the room 33 burials (Fig. 2c and Supplementary Data 1). These genetic sex estimates were additionally confirmed for six individuals (crania 1, 3, 5, 7, 10 and 12) using the nuclear genome SNP genotyping data described above (Supplementary Data 1).

Discussion

The use of room 33—constructed as an elaborate burial crypt in what became the largest great house in the region—provides...
evidence for the early hereditary basis of leadership in the Chaco World. Based on the combination of the relatedness estimates from the nuclear genome data, our high-precision AMS $^{14}$C dates, and osteological and genetic-based estimates of sex and ages of the room 33 individuals, we infer that two generations separated the individuals whose remains have been identified as cranium 8 (30–40-year-old female) and cranium 10 (30–35-year-old male), suggesting a grandmother–grandson relationship. Only one generation separated the individuals identified as cranium 1 (35–45-year-old female) and cranium 7 (23–27-year-old female), suggesting a mother–daughter relationship. Both of these observations are consistent with the importance of close matrilineal ties among those interred in the room (Fig. 4). Although hereditary relationships have been explored elsewhere in historic contexts using short-tandem repeat genotyping $^{26–28}$, to our knowledge this is the first study using genome-wide data to document hereditary relationships among individuals within an elite lineage using archaeogenomics, in the absence of a written record, anywhere in the world.

The extravagant grave goods and ritual objects associated with the lineage founder (burial 14) at the base of the room 33 crypt are clear status markers consistent with the elaboration evident in other early complex societies $^{11,15,29}$, an indication that a high degree of social differentiation and societal complexity existed in Chaco by the early ninth century. Our work demonstrates that institutionalized hereditary leadership was then passed through the female line until the early twelfth century CE. Matrilineal systems are present ethnographically in all the Western Pueblos (Hopi, Zuni, Acoma, Laguna), and the Rio Grande Pueblos (Cochiti, San Felipe, Santo Domingo and Zia) that speak the Keresan language (see Supplementary Note 1). Although the relationship between prehistoric people from Chaco and specific modern Native American groups remains uncertain, our finding is consistent with a widespread pattern reported for Pueblo social organization beginning with Spanish colonial records $^{12}$, and with Pueblo oral traditions recorded since the nineteenth century, especially among the Hopi and Zuni, that emphasize matrilineal clans as the founding social units and matrilineal leaders as key protagonists in social history $^{12}$.

Figure 3 | Heatmap distance matrix of pairwise mitogenome comparisons. The number of nucleotide sequence differences between all pairs of 39 Native American complete mtDNA genomes, representing the 9 prehistoric Pueblo Bonito room 33 mtDNA genomes and those previously published for 10 individuals each from North, Central and South America. Positions with missing data or deletions in any individuals were removed from all pairwise comparisons (bp analysed = 14,247). The non-Pueblo Bonito samples from each region were selected at random from an overall database of 171 complete mtDNA genomes (see Supplementary Fig. 5 for a pairwise distance matrix including all samples). (Graphical layout: T. Harper. All cartographic elements were produced in ArcGIS 10.4, with layout and design performed in Photoshop CC 14.2.)
Methods

We submitted a research proposal to the American Museum of Natural History (AMNH) requesting samples from Chaco Canyon burials classified as culturally unidentifiable following NAGPRA (Native American Graves Protection and Repatriation Act) criteria. The AMNH review committee approved our proposal in February 2012. We identified samples through a collaboration with the University of New Mexico’s Cultural and Biological Resource Management Laboratory. Samples were obtained for each room for which archaeogenetic data are available. We sampled skeletal remains from nine individuals: crania 6, 8, 10, 11, 13, 14; and the long bones from room 33 (Supplementary Data 1). The amelogenin PCR-amplification and sequencing success of one cranium (6) was 100% and 25% for the room 33 samples. We successfully amplified and sequenced 85% of the cranial and 21% of the long bone samples.

Calibration and modelling. AMS 14C dates below the split plank floor were calibrated with OxCal version 4.2.3 (ref. 34) within a stratigraphic model using the IntCal13 northern hemisphere curve48. The OxCal code used for the overall model is provided in Supplementary Table 1 and Supplementary Fig. 1. The OxCal code used for the overall model is provided in Supplementary Table 1 and Supplementary Fig. 1.

The abalone shells were modelled using the Marine13 curve49 and a reservoir (AR) correction of 234 ± 23 14C years assuming collection somewhere on the southern California coast in the vicinity of San Diego where this species is concentrated50.

Radiocarbon simulations. The apparent episodic structure in the calibrated ages for the room 33 crania (n = 11) could indicate several periods of interment or possibly continuous interment over the course of three centuries. When plotted against the IntCal13 curve48 (Supplementary Fig. 2), many of the dates fall on reversals and plateaus in the calibration curve between 900 and 1150 CE, similar to observed patterns for directly dated macaws remains from the Rio Grande region51. Conventional ages that occur within plateaus in the calibration curve cause the artificial stacking or over-representation of certain calibrated dates within certain intervals, whereas conventional dates falling on steeper parts of the curve tend to be under-represented.

The potential biases introduced by the calibration curve were explored by simulating radiocarbon ages from 750 to 1250 CE in OxCal v4.2.3 (refs 34,37). The model simulates a calibrated age and a maximum error that translates the age through the curve to generate a conventional age BD and then calibrates the conventional age. A model was made to simulate 10 dates with a precision of ± 20 14C years every 25 calendar years from 750 to 1250 CE for a total of 210 simulated dates. The conventional ages were extracted and frequencies plotted in 20 14C-year increments (Supplementary Fig. 3). Comparing the frequency of simulated 14C ages with the expected (40 per century), it was anticipated that even with more or less continuous (for example, generational) interment of individuals in room 33 that fluctuations in the calibration curve produce an apparent episodic structure on the conventional and calibrated ages. Although the model period (670–940 CE) is fairly small compared with the overall period of interment (~330 cal years), it is difficult to argue that certain periods are over- or under-represented, as was possible with the procurement of macaws over a shorter interval51. For room 33, we do observe that a few gaps in the 14C ages do correspond to periods where the calibration curve is relatively steep, and therefore are likely artefacts of the curve rather than pauses in interment. Overall, the simulations indicate the observed 14C ages of room 33 are consistent with continuous rather than episodic use of the crypt from the ninth through the twelfth century CE.

Ancient mtDNA capture and sequencing. Skeletal remains from nine individuals from room 33 (Supplementary Data 1) were successfully analysed at the ancient DNA facilities at Pennsylvania State University and Harvard Medical School. Eight of the nine room 33 samples for which archaeogenetic data are analysed in this study (excepting cranium 6) were processed initially in the Penn State Ancient DNA facility, with the mtDNA genome capture and sequencing performed as described in this section. The mtDNA genome sequences for three of these same individuals (crania 1, 3, and 7) were also determined at the Harvard Medical School ancient DNA facility, as part of the screening process for the nuclear genome SNP genotyping analyses that were performed there (see below). The mtDNA genome of one room 33 individual, cranium 6, was sequenced only at Harvard Medical School.

At Penn State, DNA extractions and pre-PCR library preparation steps were performed in a dedicated sterile laboratory with high-efficiency particulate air (HEPA) filter, arrestance-filtered air and positive air flow. Strict procedures were followed to prevent contamination and provide a sterile laboratory environment. All surfaces and workstations were sterilized using a concentrated bleach solution and 70% ethanol solution, before and after each use. Equipment and consumables were irradiated for 60 min under ultraviolet light before use. Dedicated reagents were only opened in a sterilized ultraviolet hood located within the clean laboratory. Negative control reactions were included alongside all DNA extractions and library preparations. DNA extractions and negative control reactions were prepared and processed in tandem.

Individual ancient samples were initially pretreated in 1% bleach solution in a separate nonmolecular laboratory before entering the dedicated sterile laboratory. To further reduce surface contamination, the surface layer of each sample was removed using a Dremel tool fitted with a disposable rotating disc that had been treated in 1% bleach solution, followed by multiple washes in molecular grade water to remove traces of bleach. After surface treatment, the samples were ground into a fine powder using a micro-dismembrator (Sartorius) ball mill with tungsten carbide balls. For each sample, we extracted DNA from 150 to 300 mg of bone

Figure 4 | Diagram of a hypothetical Chacoan matriline. The diagram illustrates the inferred relationships for at least two pairs of individuals interred in room 33. Matriline members and descent are highlighted in red. Lineal relationships (mother–daughter and mother–son) and sibling relationships are marked in blue. The asterisk shows the grandmother-grandson relationship suggested for crania 8 and 10 and the blue ** indicates the mother–daughter relationship suggested between crania 1 and 7.
powder exactly following a silica absorption/spin column method and eluted DNA twice in 50 μL TE buffer with 0.05% Tween 20.

Double-stranded barcodes with barcoded adapters were constructed with 50 μL of each ancient DNA extract based on the approach by Meyer and Kircher. Before the amplification step of this protocol, the libraries were split into two 10 μL aliquots, with different barcode indices added to each aliquot (Supplementary Data 1). Reactions were prepared in the ancient DNA facility, sealed, and then amplified in a separate lab. All libraries were amplified in a 50 μL reaction consisting of PCR buffer, 2 mM MgSO4, 200 μM each dNTP, 200 nM primer IS4 (5′-AATGA TACGGGCAACCAGCAGCTACTCTCTCTACGACGCTCT-3′), 200 nM barcoded p7 primer (5′-CAGCAGAACGGCAGATACGCTACGATxxxcccxxTGCxxxxCAGCAGxxxxxCTGACGCTCT-3′), where ‘x’ represented the unique sample-specific barcode) and 2.5 U Platinum High Fidelity DNA Polymerase (Thermo Scientific). Libraries were amplified as follows: 5 min at 94 °C; 24 cycles of 20 s at 94 °C, 15 s at 60 °C and 20 s at 68 °C; final extension 5 min at 60 °C. Indexed PCR products were purified using SPRI beads and eluted in 15 μL TET buffer.

Huck Institutes Genomics Core Facility on an Illumina HiSeq 2500 platform using the read. For this analysis we used two approaches. First, for the results shown in Fig. 2 we used the sequence reads obtained following the mitochondrial DNA capture enrichment that did not map to the human mtDNA genome (that is, ‘bleed-through’ reads, or those reads that were not removed from the library during the washing steps of the DNA capture protocol (DNA capture is not 100% efficient at reducing library representation). The sequence reads from each sample were aligned to the human reference sequence hg18 (NCBI36/hg18 human assembly). We used the BWA-backtrack algorithm in the Burrows-Wheeler Aligner, version 0.7.5 (ref. 42) and processed as above to remove potential PCR duplicate reads. Sequence alignments were restricted to those with a mapping quality score of at least 30. The genetic sexes of six samples could be estimated confidently, whereas for two other individuals our results were consistent with an assignment of male but the consensus DNA fragments52 to screen for samples with sufficient quality for nuclear genome SNP genotyping. We sequenced the enriched DNA libraries on an Illumina NextSeq500 instrument using 2 × 75 base pair reads. We used Segreg66 to identify paired sequences overlapping by at least 15 base pairs, and then mapped these reads to the mitochondrial DNA genome RS25 using BWA-0.6 (ref. 42).

We also compared the genetic sex estimates for the eight room 33 individuals with two previous osteological sex determinations14,65 showing 100% concordance with the more recent assessment67 and resolving the discrepancy for one individual between the two osteological studies (Supplementary Data 1).

Nuclear genome SNP genotyping. In a dedicated ancient DNA clean room at Harvard Medical School, we generated nine ancient DNA libraries, either from post-capture DNA that was treated with uracil-DNA-glycosylase5 for the recovery of ultra-short DNA fragments63 or using extracts made in the ancient DNA clean room at Penn State. We corrected the reads into sequencing libraries, most of which were treated with uracil-DNA-glycosylase53.

We first used in-solution capture method to enrich the DNA library for human mitochondrial DNA fragments52 to screen for samples with sufficient quality for nuclear genome SNP genotyping. We sequenced the enriched DNA libraries on an Illumina NextSeq500 instrument using 2 × 75 base pair reads. We used Segreg66 to identify paired sequences overlapping by at least 15 base pairs, and then mapped these reads to the mitochondrial DNA genome RS25 using BWA-0.6 (ref. 42). We used in-solution capture methodology to enrich and directly from the ancient DNA contamination. One accepted strategy for ancient DNA authentication in genome-wide ancient DNA analysis is to require at least 10% damage in the first nucleotide for a non-UDG-treated library and at least 3% in the first nucleotide for a UDG-treated library. The recovery of ancient DNA fragments and all libraries we took forward to genome-wide analysis met this requirement67.

We enriched the libraries taken forward to genome-wide analysis for 1,237,207 SNP targets (SNP panels 1 and 2 from Fu et al.67 that include all SNPs on the Affymetrix Human Origins, Illumina 610-Duo and Affymetrix 50k arrays). We sequenced the enriched products on a NextSeq500 instrument using 2 × 75 base pairs reads, and processed the sequences as we did for the mitochondrial DNA analysis except that we mapped instead to the human genome reference sequence hg19. We restricted our analysis to six samples for six distinct libraries passing our quality control. These samples had 14,948–144,227 SNPs covered by at least one sequence read.

Relatedness coefficient estimates. We extracted 856,473 SNPs on chromosomes 1–22 that are not in CpG dinucleotide context in order to avoid the potential influence of differences in postmortem damage rates among individuals. For each pair of individuals, we computed the average mismatch rate across all autosomal SNPs covered by at least one sequence read for both of the two individuals being compared (when > 1 sequence read was present for one individual at a given site, a random read was sampled for the analysis) and computed e.g. using a weighted block jackknife. There were too few X-chromosome SNPs with sequence data for high-confidence relatedness results.

We observed that the greatest mismatch rates x between pairs were ~21%, but several were significantly lower (x > 3), providing putative evidence of relatedness. To estimate the relatedness coefficient r, we need to account for the fact that we are downsampling the data to a single sequence at each position. Thus, if we were comparing two identical individuals, the mismatch rate would still be only half of the

Comparison with modern mtDNA genomes from the Americas. We curated a reference database of 171 modern complete mitochondrial DNA sequences from the Americas44–49, restricted to genomes with ethnicity or region of origin documented (Supplementary Data 2). The ancient mtDNA genome consensus sequences from the Chaco region that generated this study are aligned to the modern reference sequences using MAFFT54 and manually verified using Geneious v8.1.8.
that observed between unrelated individuals. We thus correct our estimate of \( r \) using the expected mismatch rate because of random sequence sampling \( b \). We choose \( b = 0.212 ± 0.105 \) based on the approximate maximum mismatch rates observed. Our estimator is thus

\[
 r = 1 - \frac{(x - b)}{b} 
\]

We also computed a 95% confidence interval using block jackknife standard errors.

**Data availability.** Sequence reads from the mtDNA capture experiments and all nuclear genome SNP genotyping BAM files have been deposited in the NCBI Sequence Read Archive. Accession no. SRP094965 (SRA BioProject no. PRJNA353635). All BAM and FASTA files of both the original and damaged read version consensus mtDNA sequence for each individual have been deposited in the Dryad Digital repository at http://dx.doi.org/10.5061/dryad.3344ld4. The multisequence alignment has been deposited in the Dryad Digital repository at http://dx.doi.org/10.5061/dryad.3344ld4.

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Author contributions
D.J.K., S.P., D.R. and G.H.P. designed research; S.P. performed archival research; R.J.G., B.J.C., N.R., K.S. and L.K. collected data; D.J.K., R.J.G., B.J.C., P.S., S.M., K.S., L.K., D.R. and G.H.P. analysed data, S.P., A.S.W., S.A.L. and P.M.W. provided archaeological and ethnographic interpretations of the results; D.J.K., S.P., R.J.G., B.J.C., D.R. and G.H.P. wrote the paper, with contributions from all authors.

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