Tenfold Population Increase in Western Europe at the Neandertal–Modern Human Transition

Paul Mellars* and Jennifer C. French

European Neandertals were replaced by modern human populations from Africa ~40,000 years ago. Archaeological evidence from the best-documented region of Europe shows that during this replacement human populations increased by one order of magnitude, suggesting that numerical supremacy alone may have been a critical factor in facilitating this replacement.

Neandertal populations were replaced by anatomically and genetically modern human populations across Europe, between ~45,000 and 35,000 years before the present (yr B.P.). The reasons for the success of modern humans and the associated issues of Neandertal extinction have been widely debated (1–11). Any process of population replacement and extinction reduces ultimately to a question of numbers: the increase of the incoming population versus the decline of the resident population (12, 13).

*To whom correspondence should be addressed. E-mail: pam59@cam.ac.uk

References

19. See supporting material on Science Online.

Acknowledgments: J. Briner and the Greenland Institute of Natural Resources kindly provided several stream and iceberg silt samples. E. Obbink, K. Winsor, B. Welke, S. Strano, and A. Leaf provided assistance in the field and laboratory. D. Kelly and C. Hillaire-Marcel supplied comments on this research and manuscript. A. de Vernal provided her pollen records. This research was supported by the Geological Society of America and American Association of Petroleum Geologists (E.J.C.), University of Wisconsin–Madison startup funds (A.E.C.), and the Arctic Natural Sciences Division of NSF, Arctic Natural Sciences grants 0902571 (A.E.C. and B.L.B.) and 0902751 (I.S.S.).
Until recently, it has been difficult to quantify the relative population numbers of indigenous Neandertal and intrusive modern populations in Europe. Recent mitochondrial DNA data from present-day European populations, combined with similar analyses of ancient DNA derived from a small sample of Neandertal skeletal remains, have suggested that population numbers increased substantially across the Neandertal–modern human transition in the study region (marked by superimposed rectangles) in relation to the overall distribution of (A) final Neandertal (Châtelperronian) and (B) initial modern human (Aurignacian) archaeological sites in France as a whole (see table S1). The sizes of the circles indicate the total numbers of occupied sites in the different locations (largest circle = 42 sites). The total area of the study region is ~75,000 km². Data from (42).

**Fig. 1.** The maps show the location of the study region (marked by superimposed rectangles) in relation to the overall distribution of (A) final Neandertal (Châtelperronian) and (B) initial modern human (Aurignacian) archaeological sites in France as a whole (see table S1). The sizes of the circles indicate the total numbers of occupied sites in the different locations (largest circle = 42 sites). The total area of the study region is ~75,000 km². Data from (42).

**Fig. 2.** Numbers of occupied sites and intensities of occupation in sites across the Neandertal–modern transition. (A) Numbers of occupations recorded in cave/rock-shelter and open-air locations for the three main archaeological and demographic periods (MTA, Châtelperronian, Aurignacian) of the Neandertal–modern human transition in the study region. (table S1). At present, no reliable data are available for numbers of MTA open-air sites. (B) Average values (and standard errors) of densities of retouched stone tools and estimated animal meat-weights in occupation levels of five successive stages of the Neandertal–modern humans transition in the study region, expressed in terms of densities per square meter of the excavated occupation levels per 1000 years of the estimated occupation sequences (see Fig. 3 and tables S2 to S7 for details of individual sites and data sources). As discussed in the SOM, the time ranges of the different periods are taken as ~5000 years each for the earlier (type A) and later (type B) stages of the MTA, ~4150 years for the Châtelperronian, and ~2500 years each for the earlier and later phases of the Aurignacian. The data for the early Aurignacian sites include two levels (Le Piage K and Saint-Césaire EGF) attributed to the Proto-Aurignacian. No reliable data are available for meat-weights in the MTA sites.
transition (14–16). However, the magnitude is impossible to quantify from these analyses, which involve a number of debatable assumptions (15, 17).

As a complementary approach, we analyzed the archaeological evidence bearing on population numbers and densities across the period of the Neandertal–modern human transition in one specific region of Europe: the classic Aquitaine region of southwestern France. This region is centered on the limestone-dominated region of the Dordogne and adjacent areas and covers ~75,000 km² (Fig. 1). This region has a long history of archaeological research and excavations, and it contains the highest density of Neandertal and early modern human sites recorded in Europe (13, 18).

We analyzed the archaeological evidence from three separate, successive, and well-defined archaeological periods that are known to span the period of the Neandertal–modern human transition in this region and that together cover the time range from ~55,000 to 35,000 yr B.P., in calibrated radiocarbon terms [see supporting online material (SOM) text and table S1] (19): (i) The later stages of the conventional Mousterian sequence, represented by the so-called Mousterian-of-Acheulian tradition (MTA) industries and defined by the presence of small, bifacially flaked hand-axe forms, usually combined with equally distinctive backed-knife forms, and a range of other typically Middle Palaeolithic tools. The period is subdivided into two stages (MTA types A and B) that are defined by changes in the relative frequencies of bifaces and backed knives (9, 20–22). (ii) The ensuing Châtelperronian industries, defined by the presence of highly distinctive Châtelperronian point forms manufactured on blades and associated with a mixture of both Mousterian and Upper Palaeolithic tool forms (9, 23–25). The Châtelperronian is widely agreed to show direct technological and demographic continuity with the preceding MTA (type B) industries (9, 20, 22, 25), combined with some new elements of Upper Palaeolithic technology probably derived by cultural diffusion from the expanding anatomically modern populations in central and southern Europe (9, 23, 26–29). (iii) The classic Upper Palaeolithic Aurignacian (and Proto-Aurignacian) industries defined by a further range of distinctive type-fossil forms (carinated and nosed scrapers, busqué burins, Dufour bladelets, and heavily edge-retouched Aurignacian blades), often combined with bone, antler, and ivory tools and a variety of art objects and decorative personal ornaments (24, 28, 30).

The age ranges of these three successive "techno complexes" have been defined on the basis of recent radiocarbon dating to ~35,000 to 40,250 yr B.P. for the Aurignacian industries, ~40,250 to 44,400 yr B.P. for the Châtelperronian, and (on the basis of less precise thermoluminescence and electron-spin-resonance measurements) to ~44,000 to 55,000 yr B.P. for the MTA industries (see SOM text and table S1) (9, 20, 21, 28, 31–34).

Collectively, these occupations span a period of oscillating climatic conditions represented by interstadials GIS 13 to 7 of the Greenland ice-core records (34, 35). It is widely believed that the MTA and Châtelperronian industries were manufactured by late Neandertal populations (21, 29, 36–38), whereas the Aurignacian represents the initial appearance of fully anatomically and genetically modern human populations in Western Europe (2, 3, 28–30, 36, 38, 39) [for a conflicting view, see (40)]. We used three archaeological proxies for population numbers and densities: (i) data on total numbers of occupied sites in the study region during the three main periods of the Neandertal–to–modern human transition, as defined above; (ii) the overall intensity of occupation in these sites, as reflected by the accumulation rates of two different forms of occupation residues (stone tools and animal food remains) in occupation levels of the three periods; and (iii) data on the overall spatial extent of the archaeological occupation levels, as a potential reflection of the sizes of the human groups who occupied the sites in the successive periods (see SOM for details).

We included all of the sites in the study region (Fig. 1) for which relatively full and apparently reliable quantitative data on the relevant parameters could be obtained from the published literature or other available sources. In view of the relatively small number of fully documented Châtelperronian sites in the Périgord region, we added two well-documented sites (Arcy-sur-Cure and Châtelperron) from the adjacent areas of central France.

As shown in Fig. 2A and table S1, total numbers of recorded archaeological sites increased

---

**Fig. 3.** Distributions of individual values of the three principal occupation parameters. The graphs display the individual values of (A) stone-tool densities, (B) meat-weight densities, and (C) minimum documented areas of occupation across the full range of sites and occupation levels employed in the study. Means and standard errors for the three principal archaeological/demographic periods are indicated by horizontal bars. For details of individual sites and calculations, see tables S3 to S12. As discussed in the text, the overall (original) areas of occupation in the sites could, in several cases, be substantially larger than the figures shown. No reliable data are available for meat-weight densities in the MTA sites. S.E., standard error.
substantially over the period of the Neandertal–modern human transition. The numbers of cave and rock-shelter sites (which account for more than 75% of the total recorded sites in our database) increase from ~26 for the MTA to ~30 in the Châtelperronian to ~108 in the Aurignacian. The numbers of recorded open-air sites increase from ~7 in the Châtelperronian to ~39 in the Aurignacian (41, 42); no reliable data are currently available for the numbers of open-air MTA sites. If these comparisons are adjusted to allow for the different time ranges spanned by the two main archaeological periods (~4150 years for the Châtelperronian versus ~5250 years for the Aurignacian), these statistics taken alone would suggest an overall increase by a factor of ~2.5 in relative human population numbers and densities over the period of the Neandertal–modern human transition. As shown in Fig. 1, A and B, similar increases are reflected equally in the data from France as a whole, suggesting that these comparisons are applicable on a broader geographical scale. The possibility that these increases in site numbers could reflect simply changing patterns of site mobility and associated logistical strategies between the Neandertal and early modern human populations is contradicted by the associated data on relative intensities of occupation in sites discussed below.

Data on the relative intensities of occupation based on both the overall accumulation rates of retouched stone tools and the quantities of associated animal food remains similarly point to a substantial increase in population densities over the transition period (Figs. 2 and 3 and Table S2). Despite some substantial variations between sites, average densities of stone tools increase from ~6.6 tools per m² per 1000 years in the combined earlier (type A) and later (type B) MTA levels to ~9.7 tools per m² per 1000 years in the Châtelperronian to ~17.6 tools per m² per 1000 years in the Aurignacian sites. The densities calculated separately for the MTA A and MTA B stages of the MTA sequence are broadly similar, and the same is true for the (much higher) values recorded for both the earlier and later stages of the Aurignacian (Fig. 3A and tables S2 to S5). Similar increases are apparent in the accumulation rates of animal food remains. Although few reliable faunal data are available for the MTA sites, the data for the Châtelperronian and Aurignacian periods show an increase in estimated meat-weight densities from ~84.6 kg per m² per 1000 years in the Châtelperronian to ~152.8 kg per m² per 1000 years in the Aurignacian (Figs. 2B and 3B and tables S6 and S7), in close agreement with that suggested by the accumulation rates of stone tools—that is, an increase of ~1.8 in overall occupational intensities over the Neandertal–modern human transition (see Table S4 for statistical significance tests). The effects of any individual (site-to-site or layer-to-layer) variations in our data could be due to a variety of local environmental, economic, and social factors and are probably averaged out by the inclusion of data from many different sites and individual occupation levels for each demographic period.

Data on the overall areas of occupation in sites across the different periods are more limited and methodologically problematic than those for the site totals and intensities of occupation. The data shown in Table 3C and tables S11 and S12 represent, in each case, the minimal overall areas of occupation documented in excavations on the sites. The available data (Fig. 3C and tables S11 and S12) show that the minimum occupied areas increased substantially between the Mousterian and Châtelperronian occupations on the one hand and those of the Aurignacian on the other, with overall occupation areas for at least four of the Aurignacian sites of between 500 and 600 m², as compared with areas of, at most, 100 to 250 m² for the preceding Mousterian and Châtelperronian occupations (Fig. 3C and tables S11 and S12). Clearly, we cannot reliably equate these areas of occupation with the sizes of the individual groups who successively occupied the sites, in that the precise zones of occupation could have shifted laterally within the sites during successive occupations. However, it is apparent that the total areas over which occupation material was distributed must relate to the total quantities of occupation material generated during the different periods of the occupation sequences, and should therefore be an additional, and essentially independent, dimension to the overall intensities of human occupation during the different archaeological periods under review. At face value, the areas of occupation suggest an increase in population numbers in the study region by a factor of ~9, and probably by a factor of 10 (or even more), if we took more realistic as opposed to minimalistic estimates of the individual parameters. An alternative way of viewing these comparisons would be in terms of the total quantities of occupation material generated per 1000-year interval in each demographic period, for which an appropriate mathematical formula would involve the total numbers of recorded sites, multiplied by the average densities of occupation residues documented in the sites, multiplied by the average recorded areas of the occupation deposits in the sites (Fig. 4). Applied to the data we have presented here, such a calculation would again lead to a comparison between the final Neandertal and modern human transition within the southwestern region of France and, by reasonable inference, probably other regions of western Europe. Site numbers increased by a factor of ~2.5, intensities of occupation by a factor of ~1.8, and the minimum areas of occupation on the sites by a factor of at least 2 (Fig. 4). Because these separate demographic proxies are independent of each other in quantitative and demographic terms, these metrics would point to an overall increase in population numbers in the study region by a factor of ~9, and probably by a factor of 10 (or even more).
initial modern populations of ~2.5 × 1.8 × 2.0—
that is, an approximate (and probably minimal)
overall increase of a factor of ~9. This estimate is—at least broadly consistent with other indi-
cations of changing population numbers and
densities between Neandertal and early modern
human populations derived from recent DNA
data (14–16) and the relative intensities of hu-
man and cave-bear occupations in Central Euro-
pean sites (43–45).

These data imply that numerical supremacy
alone must have been a powerful, if not over-
whelming, factor in direct demographic and ter-
ritorial competition between modern humans and
Neandertals (12, 13). The precise technological,
economic, social, biological, and other adaptive
mechanisms by which modern humans were able
to survive in much higher population densities
than the Neandertals within a broadly similar
range of environments is currently a matter of de-
bate (5–8, 35, 46). Improved hunting and food-
processing technology; food storage; enhanced
mobility and transportation technology; increased
social integration and cohesion; expanded ex-
change; mating and alliance networks between
different groups; potentially enhanced planning
capacities; and new social relationships involving
a proliferation of symbolic, artistic, and ceremo-
nial practices could all have had a dramatic effect
on the overall competitive and survival capacities
of the modern humans (7, 8, 11, 15, 44, 46, 47).
A range of climatic and associated environmen-
tal factors could have played a further, crit-
ical role in this demographic replacement and extinction process—above all, perhaps the
impact of the sudden climatic cooling associated
with Heinrich event 4 in the oceanic records at
~40,000 yr B.P., in calibrated radiocarbon terms
(1, 10, 35). We would advocate the use of simi-
lar approaches to these employed here to clarify
the nature and scale of demographic changes
over the Neandertal–to-modern human transi-
tion in other areas of Europe.

References and Notes

(2003).

2. S. E. Churchill, F. H. Smith, Yearb. Phys. Anthropol. 43,
61 (2000).


7. C. W. Marean, in From Tools to Symbols: From Early Homo
nids to Modern Humans, F. d’Errico, L. Blackwell, Eds.

8. I. O’Connell, in When Neandertals and Modern Humans
Met, N. J. Conard, Ed. (Kerns Verlag, Tübingen, Germany,
2006), pp. 43–64.

Perspective from Western Europe (Princeton Univ. Press,

10. P. Mellars, in Neandertals and Modern Humans in
Western Asia, T. Akazawa, K. Aoki, O. Bar-Yosef, Eds.


Bats Use Echo Harmonic Structure
to Distinguish Their Targets from Background Clutter

Mary E. Bates, James A. Simmons, Tengiz V. Zorikov

When echolocating big brown bats fly in complex surroundings, echoes arriving from irrelevant objects (clutter) located to the sides of their sonar beam can mask perception of relevant objects located to the front (targets), causing “blind spots.” Because the second harmonic is beam ed more weakly to the sides than the first harmonic, these clutter echoes have a weaker second harmonic. In psychophysical experiments, we found that electronically misaligning first and second harmonics in echoes (to mimic the misalignment of corresponding neural responses to harmonics in clutter echoes) disrupts the bat’s echo-delay perception but also prevents clutter masking. Electronically offsetting harmonics to realign their neural responses restores delay perception but also clutter interference. Thus, bats exploit harmonics to distinguish clutter echoes from target echoes, sacrificing delay acuity to suppress masking.

Echolocating big brown bats (Eptesicus fuscus) broadcast brief frequency-modulated (FM) sounds with two prominent acoustic harmonics—FM1 and FM2 (Fig. 1A) (1, 2). The principal perceptual dimension in bat sonar is target range, as determined from echo delay (3). Although these bats typically catch insects in the open, they also can capture prey near vegetation

www.sciencemag.org  SCIENCE VOL 333 29 JULY 2011 627

REPORTS