Climate change and evolving human diversity in Europe during the last glacial

Clive Gamble[1*], William Davies[1], Paul Pettitt[2] and Martin Richards[3]

[1]*Centre for the Archaeology of Human Origins, University of Southampton, Avenue Campus, Southampton SO17 1BF, UK*
[2]*Department of Archaeology, University of Sheffield, Northgate House, West Street, Sheffield S1 4ET, UK*
[3]*School of Biology, L. C. Miall Building, University of Leeds, Leeds LS2 9JT, UK*

A link between climate change and human evolution during the Pleistocene has often been assumed but rarely tested. At the macro-evolutionary level Foley showed for hominids that extinction, rather than speciation, correlates with environmental change as recorded in the deep sea record. Our aim is to examine this finding at a smaller scale and with high-resolution environmental and archaeological archives. Our interest is in changing patterns of human dispersal under shifting Pleistocene climates during the last glacial period in Europe. Selecting this time frame and region allows us to observe how two hominid taxa, Neanderthals and Crô-Magnons, adapted to climatic conditions during oxygen isotope stage 3. These taxa are representative of two hominid adaptive radiations, termed *terrestrial* and *aquatic*, which exhibited different habitat preferences but similar tolerances to climatic factors. Their response to changing ecological conditions was predicated upon their ability to extend their societies in space and time. We examine this difference further using a database of all available radiocarbon determinations from western Europe in the late glacial. These data act as proxies for population history, and in particular the expansion and contraction of regional populations as climate changed rapidly. Independent assessment of these processes is obtained from the genetic history of Europeans. The results indicate that climate affects population contraction rather than expansion. We discuss the consequences for genetic and cultural diversity which led to the legacy of the Ice Age: a single hominid species, globally distributed.

Keywords: radiation; stage 3; late glacial; Greenland ice-core project; radiocarbon; phylogeography

1. INTRODUCTION

Almost 20 years after Agassiz (1840) published his evidence for Ice Ages, Darwin (1859, p. 371) surmised that the evolution of geographically expansionist species took place in 'the larger areas and more efficient workshops of the north'. In those times before the recognition of continental drift, the evidence for repeated glaciations provided the force for change across an otherwise stable Earth. The importance of Ice Ages can be seen in Wallace's (1880) biogeography that drew heavily on Croll's (1875) calculations of the Earth's orbital geometry and which predicted that climate change leading to glaciation had been frequent and regular. For Wallace these continual 'mutations' of climate provided:

> a motive power well calculated to produce far more rapid organic changes than have hitherto been thought possible; while in the enormous amount of specific variation we have ample material for that power to act upon, so as to keep the organic world in a state of rapid change and development proportional to the comparatively rapid changes in the Earth's surface.
>
> (Wallace 1880, pp. 228–229)

However, Croll's insights were disputed and then forgotten. By 1909 the Alpine sequence of only four major

glaciations and three interglacials set the framework for the impact of climate as an evolutionary mechanism for the next 60 years; the Ice Ages accelerated processes from time to time. As expressed by Lull (1917, p. 693) 'changing environmental conditions stimulate the sluggish evolutionary stream to quickened movement'. Left to its own devices stasis would prevail, a rather different view from that of Wallace who saw change and speciation as the norm.

The idea of occasional stimulus fitted well with the preferred model of human evolution. The limited fossil record which had to be explained recorded change along a single unbranching lineage. Human palaeontologists were more interested in identifying the geographical location of the cradle for the human lineage (Gamble 1993, ch. 3). Consequently the main effect of the Ice Ages was to disperse our ancestors from Darwin's factory gates.

So much for the intellectual luggage. The past 30 years has transformed this picture. The hominid cradle has come to rest somewhere in Africa below the Sahara. The widespread discovery of discrete but contemporary hominid species now favours models of cladogenesis. Archaeological evidence, in the form of stone tools, extends back to 2.5 Ma (Semaw *et al.* 1997), well before the onset of significant glaciations in the Northern and Southern Hemispheres. Climate records are now continuous, and of increasingly high resolution, providing evidence for variability in both the long and short term which may have selective significance (Potts 1998). Dispersal out of Africa,

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not once but repeatedly (Lahr & Foley 1994), is supported by archaeological, genetic and anatomical evidence (Stringer & Mackie 1996).

But for all these advances, the impact of the Pleistocene Ice Ages remains curiously vague. Everyone acknowledges that climate played an important role but exactly what, and precisely how, is much less clear. In this contribution we will focus on the issues of what we want to know, and examine, by means of a case study, the response of humans to climate change in the last glacial cycle. Our aim is to move the discussion towards a scale of analysis where we can achieve resolution to the question, 'is there a link?'

2. EVOLUTION AND THE PALAEOLITHIC

Foley (2001*a*, p. 5) has pointed out that for the past 50 years much of palaeoanthropology has been untouched by evolutionary theory. New data and new methods, in particular absolute chronologies, led to the development of more complicated models. But the change, while significant, was effected by weight of evidence rather than a purposeful shift in thinking. The patterns that emerged happened to match developments elsewhere and, in particular, the debate over macro- and micro-evolutionary processes in the tempo and mode of evolution.

If palaeoanthropology as a field has remained outside the development of evolutionary theory then one of its component parts, Palaeolithic archaeology, is probably even further behind. The reasons for this are several. First, the Palaeolithic has never really escaped from an orthogenetic view of technological change. While a great deal of research has been directed at the adaptive context of tool manufacture and use, when it comes to piecing the site-by-site accounts together into an evolutionary sequence, uni- or multi-lineal does not matter, the only conclusion to emerge is one of change towards complexity (Clark 1961; Wymer 1982).

Second, the underlying principle of progress which still permeates the study of the Palaeolithic is often explained as the result of lack of evidence. Perishable objects are very rare. Moreover, evidence for camps, hearths, huts and burials is either very scarce or non-existent before *ca.* 70 ka despite excellent preservation in a number of locales on a worldwide scale (Gamble 1993).

Finally, the role of climate and the environment is the preferred approach to explain cultural variation in the Palaeolithic (Torrence 1983; Kelly 1995; Kuhn 1995; Binford 2001). For example, an adaptive model of technology and culture can be tested using modern mobile peoples distributed across latitudinal and ecological gradients (Oswalt 1976). The results are encouraging because a considerable proportion of the variance in cultural response can be causally linked to survival and to such measures as the mobility, aggregation, weight, density, nutrient and non-food opportunities presented by plant and animal resources. These models have been extended to consider settlement location and patterns of local and regional land use. Ultimately, in this approach, the choices and decisions made by mobile foragers are determined by reproductive success.

However, such environmentally correlated variation in technology and material culture is a very recent

phenomenon in hominid evolution. In Africa such a response may extend back to 300 ka (McBrearty & Brooks 2000, fig. 13) while throughout the rest of the world a more recent date of between 100–60 ka is considered appropriate. By contrast, and concentrating solely on the stone tools, the earlier Palaeolithic produced very similar technological outputs from the equator to latitudes of 60° N. The classic case is the biface-rich Acheulean assemblages (Gamble & Marshall 2001; Marshall *et al.* 2002), but equally the paradigm continued with the varieties of prepared core technologies that followed. The conclusions are stark for an adaptive approach. Either stone tool technology was relatively unimportant in hominid evolution, or we are failing to read the ecological variation it represents. But, either way, if environmental gradients occupied by hominids within the Old World were not selecting for technological variety, we have to ask why the Ice Ages should have had any special selective force over the development of material culture and technology.

3. TWO TECHNOLOGICAL PARADIGMS

Elsewhere Gamble (1997) has discussed these two technological paradigms of an earlier and later Palaeolithic in terms of hominid skills that were socially constructed and passed on (table 1).

The earlier paradigm represents generic, or readily transferable, skills and where technology and material culture accompanied ecological generalists as described by Vrba (1984) and Geist (1978). As Vrba *et al.* (1989, p. 148) point out, the hallmark of ecological generalists is their increasing independence from environmental conditions. They propose that this was a critical difference between the robust australopithecines and earliest *Homo*. At this more general level the expectation is that specialists are more likely than generalists to speciate and become extinct (Turner & Paterson 1991, p. 767). Furthermore, as these authors also point out, the response of ecological specialists to environmental change is to remain, if possible, within their usual, or what they term normal, habitats because these are critical to stability. What needs to be determined is whether, as climates and environments changed, hominids always responded with similar ebbs and flows as they sought to track their shifting normal habitats.

But we doubt that hominids always had the same ebb and flow response to habitat change. For example, in table 1, we identify two ways that hominids responded to environmental change by becoming specialists. In the period 5–2.5 Ma, during which there is currently no evidence for stone technology (hence pre-Palaeolithic), hominids were specialists with habitat-specific skills. They were adapted through an anatomy under ecological and social selection. In the later Palaeolithic, hominid technological skills were place-specific (i.e. socially and culturally constructed) and therefore also specialists in an ecological sense but with a different adaptive base.

An alternative response to environmental change was to become a generalist. This led to the significant expansion by hominids with generic skills into a much wider range of habitats in the Old World in the period 2.5–0.3 Ma. One way to express the differences between the generalist hominids and specialist hominid, *Homo sapiens*, who did

Table 1. A Palaeolithic perspective on the break-points in hominid evolution.

technological paradigm	pre-Palaeolithic (5–2.5 Ma)	earlier Palaeolithic (2.5–0.3/0.1 Ma)	later Palaeolithic (0.3/0.1 Ma to present)
ecological adaptation	specialists ecological/anatomical	generalists ecological/cultural	specialists cultural/ecological
skills	habitat specific	generic, transferable	place specific
geographical range	Africa	Old World	global

expand, first out of Africa and then out of the Old World, is to recognize the change in scale of the geographical range within which they are found in the two periods (table 1).

Thus the ultimate legacy of the Ice Ages was a single, globally distributed, hominid species (Gamble 1993). Technological evolution alone did not allow this to happen. Neither were we pushed into every global nook and cranny by higher-amplitude and more frequent climate changes. If either had been the case, global saturation by generalist hominids would have happened a long time before and not as recently as world prehistory now shows.

4. PALAEOLITHIC BREAK-POINTS IN HOMINID EVOLUTION

From a Palaeolithic perspective new break-points can be recognized in hominid evolution (table 1). Prior to 2.5 Ma hominid evolution on current evidence was a central and southern African affair. Thereafter until *ca.* 100 ka the area occupied, using stone tools as a marker, is a part of the Old World (Gamble 2001).

The finds from Dmanisi at the northernmost end of the Rift Valley, reliably dated to 1.8 Ma (Gabunia *et al.* 1999*a*,*b*), have *H. ergaster*/*H. erectus* associated with stone tools. Earlier evidence from Riwat, Pakistan (Dennell 1998) and the Solo river, Indonesia (Swisher *et al.* 1994), for tools and fossils respectively, indicates that Dmanisi, important as it is, will not be the oldest evidence. Other candidates in Israel (Ronen 1991) and southern Europe (Milliken 1997–1998; Gibert *et al.* 1998) also need to be considered.

What these finds suggest is that the Sahara was never the barrier to hominid dispersal that it was once thought to be. Many opportunities for settlement existed during frequent wetter phases that resulted in active drainage and mega-lakes where now there is desert (Szabo *et al.* 1989). At the large scale, the geographical range of the ecological generalists was therefore very broad (table 1). Part of their repertoire that allowed such an adaptive radiation must have included carnivory (Foley 2001*b*), essential for a northern species limited by growing seasons, and the use of fire (Aiello & Wheeler 1995).

Within this restricted Old World range, the boundaries were fixed, not so much by Pleistocene climates, as by the impact of ecological conditions at any stage of a glacial–interglacial cycle on the ability of hominids to socially reproduce. In this respect the permanent oceans acted as a barrier in that they imposed high social costs on re-integration following long-distance voyaging. The highly seasonal climates of interior Asia and Siberia similarly stretched resources and attenuated population densities so

that, in a manner comparable to ocean exploration, social costs climbed steeply, and the need for intensive integrating mechanisms arose if colonization was to occur.

5. ADAPTIVE RADIATIONS: EXTINCTION AND CLIMATE

To illustrate theoretical issues in palaeoanthropology, Foley (2002, fig. 3) has recently proposed seven adaptive radiations in hominid evolution (table 2). In his formulation, adaptive radiations are based on the process of diversification that stems from dispersal, and the adaptive basis of these dispersals, rather than on the process of speciation (Foley 2002, p. 34). Most importantly, dispersal is the mark of evolutionary success: the signature, if you like, that speciation has occurred owing to a combination of allopatry, local adaptation and drift.

These adaptive radiations were not produced by climate changes. Using two different temporal units Foley (1994) has shown that species appearance is not causally linked to climatic variables. However, his statistical study does show that species extinction is more likely to be climatically controlled (Foley 1994, p. 285).

Foley's observation is important in establishing what the link might be between climate change and hominid evolution on the large scale. The implication is that normal habitats are more easily and quickly lost than gained. Neither did the repeated extinction of hominid species in radiations 1 to 6 select for new cultural means to track such habitats more effectively. Instead the pattern was for repeated contraction and expansion within the different geographical ranges of specialists and generalists (table 2).

Taking dispersal as our cue, we reduce the number of radiations among *Homo* to two: terrestrial and aquatic (table 3). As discussed above (and in table 1) the *terrestrial* radiation probably started as early as 2.5 Ma. It was after this time that the geographical range of hominids became Africa and part of the Old World. Within this hominid continent (Gamble 2001), and for more than 2 Myr, there were many species, some of them contemporary and with adjacent normal habitats. On occasion normal habitats were shared between *Homo* and taxa from the megadont radiation (table 2).

The second radiation can be termed *aquatic* because relatively recently a single species, *Homo sapiens*, extended the geographical range of hominids to include all the Earth's habitats. The novelty of this second adaptive radiation was the release from social proximity that it achieved. In other words, social life was now extended to include participants who were not always living together and who might be physically absent from their immediate social networks for lengthy periods (Gamble 1998).

Table 2. Seven hominid adaptive radiations (after Foley 2002).
(The time-scale is approximate.)

suggested time-scale	adaptive radiation	adaptive pattern	grade	representative taxa
past 100 kyr	7	aquatic resources	anatomically modern humans	*Homo sapiens*
500 ka	6	projectiles, ?fire	larger-brained *Homo*	*H. neanderthalensis, H. heidelbergensis*
1 Ma	5		*Homo*	*H. ergaster*
2 Ma	4	carnivory	earliest *Homo*	*H. rudolfensis*
3 Ma	3	megadonty	*Paranthropus*	*Australopithecus boisei*
4 Ma	2	bipedalism	*Australopithecus*	*A. afarensis*
5 Ma	1	African apes		

Table 3. Aspects of the two *Homo* adaptive radiations.

	terrestrial	aquatic
global habitats occupied	25%	100%
duration	2–2.5 Ma	300–100 ka
biological diversity	multiple species, genera	geographical populations, races
technological skills	generic and transferable	place specific
social networks	local	continental
release from social proximity	limited	achieved
climate change response	retreat to refuge	track from refuge
representative taxa in *Homo*	*erectus/ergaster/heidelbergensis/helmei/neanderthalensis*	*sapiens*

'Aquatic' expresses the separation and social extension that ocean voyages achieve, rather than implying a diet of seal and sea-food.

How this change was achieved is easier to answer than why. Social extension depended on the creation of networks which in a cultural sense were hybrid because they now included objects and people in comparable relationships (Gosden & Marshall 1999). Society was no longer constructed solely through the daily routines that hominids followed in their normal habitats. With the aquatic radiation the emphasis now shifted to the construction of society over longer time-scales and distances. This release from proximity was achieved by connecting objects and places in an extended social network, so that as people moved along paths within their normal habitats they obtained the resources to reproduce their social lives (Gamble 1999). This development was not due to language, which now seems to have been present in some form during the earlier terrestrial radiation (Dunbar 1996; Deacon 1997). Rather, it was exapted in particular circumstances from existing uses of material culture, particularly stone tools. These hybrid networks solved the social costs of prolonged separation that inevitably occurred for tactically mobile, small-world societies, and especially when climate change adversely affected the preferred pattern of a locally concentrated resource base (Gamble 1993).

6. TOLERANCE TO CLIMATE CHANGE AND PREFERENCE FOR HABITAT

The outcomes of the two adaptive radiations shown in table 3 can be examined through the concepts of climatic tolerance and preference as applied to hominids (Davies &

Table 4. Tolerances and preferences for selected climatic parameters among Neanderthals (Mousterian) and Crô-Magnons (Aurignacian and Gravettian) in Europe during the variable conditions of OIS3 (59–26 ka) (Van Andel 2002). (Based on archaeological site maps plotted on simulations of temperature, wind-chill and snow cover (based on Davies & Gollop 2003, table 8.3).)

	Neanderthals	Crô-Magnons
tolerance (range)		
temperature, wind-chill, snow cover and depth	similar	similar
preference (habitat)		
winter temperature and wind chill	milder	colder
days of snow cover	< 60	< 120
depth of snow cover (cm)	< 5	< 20

Gollop 2003). Tolerance refers to the ranges of climatic parameters thought to be important for hominid adaptation, while preference implies the active selection of a particular combination of climate conditions. Davies & Gollop (2003) propose that preference can be demonstrated by the relative frequencies of sites within reconstructed climate isozones and illustrate this (table 4) by comparing the very different Neanderthal and Crô-Magnon distributions during OIS3.

7. CLIMATE FORCING OF POPULATION EXPANSION AND CONTRACTION IN THE LATE GLACIAL

Here, we concentrate on the high-resolution record from the subsequent late glacial in western Europe. The

Table 5. Late-glacial population history of western Europe as reconstructed from archaeological, radiocarbon and molecular evidence.

population event	settlement pattern	dominant settlement type	phylogeography	GRIP stratotype	GRIP (ka)
1. refugium	dispersed	rockshelter	bottleneck	LGM–GS-2c	25–19.5
2. initial demic expansion	pioneer	rockshelter and open	founder effect	GS-2b–GS-2a/	19.5–16
3.1 main demic expansion	residential	rockshelter	founder effect	/GS-2a	16–14.7
3.2 main demic expansion	residential	open		GI-1e	14.7–14
4. population stasis	nucleation	open		GI-1d–GS1	14–12.9
5. population contraction		open		GS2	12.9–11.5

focus is on tolerance of climatic conditions and the expression of habitat preference through regional settlement patterns, the identification of the glacial refugium and subsequent population expansion. In the light of the broader discussion above, we are particularly interested in whether there is evidence that climate is more significant in causing population contraction and extinction than population expansion and speciation. Moreover, is any response to climate change peculiar to the aquatic radiation (table 3)?

To explore these questions we use the frequency of radiocarbon dates by region and through time as proxies for the relative distribution of past populations. The late-glacial (15–11.5 ka)[1] of western Europe has a high-resolution climatic record matched by a large number of radiocarbon determinations recently compiled in a database referred to as S2AGES (Pettitt *et al.* 2003). These datasets allow us to examine how a later Palaeolithic specialist (table 1) dealt with abrupt climate change.

Two extracts from our S2AGES radiocarbon database are presented here. The first examines the expansion of population in western Europe during GS-2a from a southern refuge in Cantabria and Portugal. Of interest here is the reading of the GRIP record from Greenland as either time-locked or time-transgressive because this concerns the role of climate forcing in the process of population expansion. Hominid dispersals were earlier discussed in terms of speciation. Here, the spatial scale is much smaller and, instead of speciation, we are seeking evidence of increased genetic diversity among recent human populations. The process, however, provides us with a model of the larger-scale processes outlined by Foley (2002) and where diversity can be measured through both fossil and genetic records.

The second extract examines the impact of the GS-1 cold phase (Younger Dryas) on population contraction. Here, the outcome provides a high-resolution test of the impact of climate change on population contraction which could lead to the process of extinction. Furthermore, the processes involved in both studies shed light on the issues of human tolerances and preferences in the pattern of dispersal and contraction and their relevance to current human diversity.

8. POPULATION EVENTS IN THE LATE GLACIAL OF WESTERN EUROPE

The S2AGES database has over 2000 calibrated determinations from the period 25–8 ka in western Europe (Pettitt *et al.* 2003). When the frequencies of all calibrated

determinations are plotted, using the CALPAL program (Weninger & Jöris 2000), the potential of these data as proxies for regional population histories is apparent (figure 1). A simple division into three major regions reveals a marked difference between on the one hand Iberia and on the other hand France and northern Europe. The Iberian radiocarbon curve shows a consistent upward trend in the frequency of determinations while the curves from the two regions north of the Pyrenees and Alps have a marked rise in the frequency of determinations between 16–14 ka.

On the basis of these radiocarbon curves standing as a proxy for past populations history we have divided the period into five events (table 5; figure 1).

(a) *Refugium*

Iberia emerges as the principal southern refuge for human populations in this region as shown by the more consistent numbers of radiocarbon determinations through time. Within Iberia the majority of the determinations come from Cantabria and Portugal (Zilhão 1997; Straus *et al.* 2000). By contrast, the small number of dated assemblages in France and northern Europe older than 16 ka is confirmed by the distribution of sites and assemblages assigned to larger ATUs in France (Thévenin 1995, 1997; Demars 1996; Bocquet-Appel & Demars 2000), Germany (Street & Terberger 1999; Street *et al.* 2001), Belgium and The Netherlands (Rensink 1993; Charles 1996) and the British Isles (Barton *et al.* 1991; Housley *et al.* 1997; Barton 1999). These distributions show a northward attenuation of settlement. Aquitaine has an important regional record as does the lower Rhône, but the Loire and northern France were at best infrequently used during the LGM, as were the Rhine corridor and Germany. While earlier views that these northern areas were completely abandoned at the LGM (Weniger 1990) can no longer be supported (Terberger & Street 2002), there is consensus that significant re-population of these areas was from a southern refuge.

Further confirmation that Cantabria/Portugal was the major refugium in OIS2 is provided by a more detailed examination of the Solutrean. This is regarded as the ATU of the LGM refugium (Smith 1964, Straus 2000*a,b*) and forms a distinctive presence in Aquitaine (Smith 1966) north of the Pyrenees. When the frequencies of determinations for this ATU are compared by region, it confirms an earlier presence in Iberia (figure 2). We interpret this sequential phasing as a small population expansion *ca.* 23 ka from the south to the north of the Pyrenees. This was followed by population contraction back into the refugium and the appearance in Aquitaine of the Badegoulian
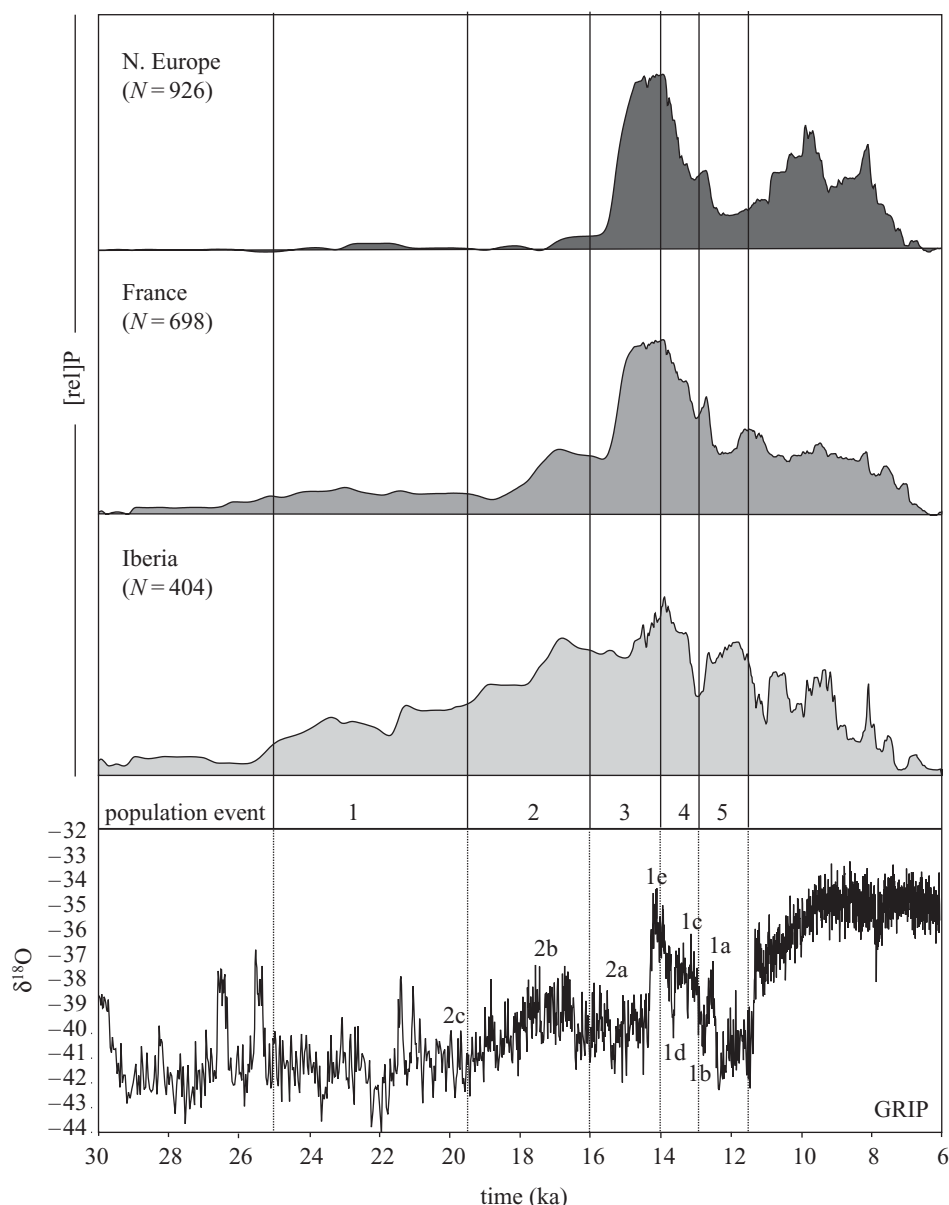
Figure 1. Population events 1–5 in western Europe (see table 5) using radiocarbon dates as a proxy for the process of demic expansion and contraction in three regions. The radiocarbon determinations are calibrated using CALPAL (Weninger & Jöris 2000) and their relative probabilities [rel]P presented by region. *N*, number of calibrated radiocarbon determinations in the [rel]P curves. The dates used in this figure are unaudited (see Pettitt *et al.* 2003). The sub-divisions of the GRIP stratotype are also shown for GI-1 and GS-2 (Björck *et al.* 1998; Walker 2001). This stratotype recognizes, after the LGM, two warm events, GIs 1 (12.7–14.7 ka, calendar BP) and 2 (21.2–21.8 ka, calendar BP), and two cold events, GSs 1 (11.5–12.7 ka, calendar BP) and 2 (14.7–21.2 ka, calendar BP). In conventional terms GS-1 broadly corresponds to the Younger Dryas, GI-1e to the Bølling and GI-1c–1a to the Allerød interstadials. Stratotype divisions are shown in figure 2.

ATU, which had its population focus in central Europe (Terberger & Street 2002), and a settlement pattern representing an extended use of distant territories.

(b) *Dispersal from south to north: genetic evidence and population size*

The eastern origins of the Badegoulian may be reflected in mtDNA haplogroups H and pre-V. These are inferred to have an origin *ca.* 20–30 ka either in eastern Europe or the Near East. Only later, *ca.* 16 ka, did they re-expand from southwest Europe (Torroni *et al.* 1998, 2001; Richards *et al.* 2000). The Y-chromosome cluster Eu18 shows a similar pattern (Semino *et al.* 2000).

The strong archaeological pattern of dispersal, from the south to the north, is confirmed by molecular studies using both mtDNA (Torroni *et al.* 1998) and Y-chromosomes (Semino *et al.* 2000). Moreover, a significant founder effect has been traced in the mtDNA haplotypes (Richards *et al.* 2000) which is dated, using the molecular clock model, to 16 ka. This estimate is in good agreement with dating of population events 2 and 3 (table 5) from the radiocarbon data.

Finally, demographic estimates for western Europe but excluding Iberia have been made by Bocquet-Appel & Demars (2000). Using a refugium based on the Dordogne, the metapopulation at maximum contraction is estimated
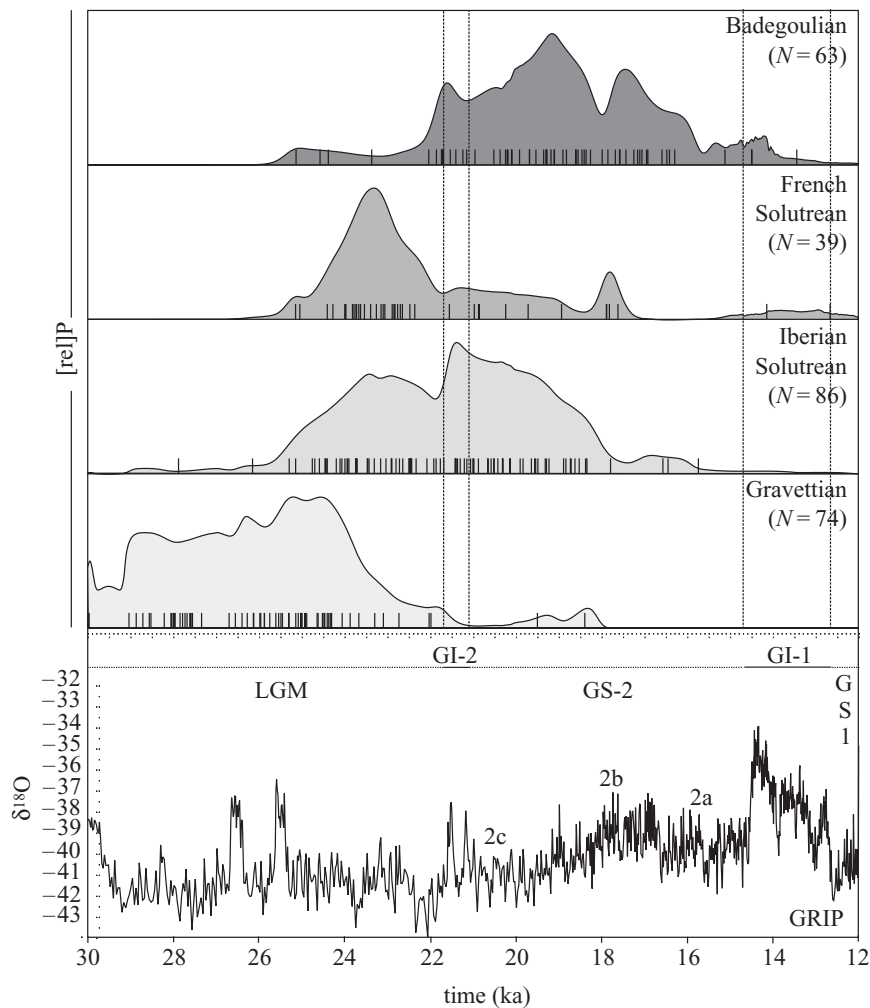
Figure 2. A comparison of the unaudited (Pettitt *et al.* 2003) radiocarbon frequency curves for the Solutrean ATU in Iberia and France. The bars below the curves are the means of each calibrated determination. The timing of the curves can be interpreted as a small population expansion from the Iberian refuge into southern France prior to GI-2.

Table 6. Population estimates for western Europe in a refugium and expansion phase.
(Adapted from Bocquet-Appel & Demars 2000.)

	Cantabria–Aquitaine	rest of France	rest of Iberia	rest of western Europe	total
expansion	18875	15271	15271	14860	64277
refugium	10246	3396	3396	0	17038

to have been 9000 people. This rises to 40 000 with the expansion into northern Europe. This represents a geographical range increasing from 0.55 million square kilometres to 1.22 million square kilometres. If these estimates are extended to the Iberian refuge, the total population of western Europe expanded from 17 000 (population event 1) to 64 000 (population events 3 and 4) (table 6).

(c) *Climate and population expansion in population event 3*

These data allow us further to examine the legacy of the Ice Ages. Was the population expansion after 16 ka climatically driven? It is now possible to examine this question using the GRIP stratotype (Björck *et al.* 1998) and high-resolution marine core data (de Abreu *et al.* 2003).

The archaeological model of major population expansion normally places it in the interstadials of Bølling and Allerød (Dolukhanov 1979; Otte 1997). As figure 1 shows, such a view is only possible if we accept a time-transgressive model between the Greenland ice core archives and the radiocarbon curve of archaeological settlement. The evidence is contained in multi-proxy climate records from the Atlantic edge of northern Europe (Walker *et al.* 2003) which point to warming commencing by 15.5 ka. The warming in GRIP between GS-2a and GI-1 is set at 14.7 ka (Björck *et al.* 1998; Renssen & Isarin 2001; Walker 2001). These multi-proxy records support the view that amelioration in such indicators as temperature and precipitation led to the migration north of key prey species, horse and reindeer, as suitable vegetation for
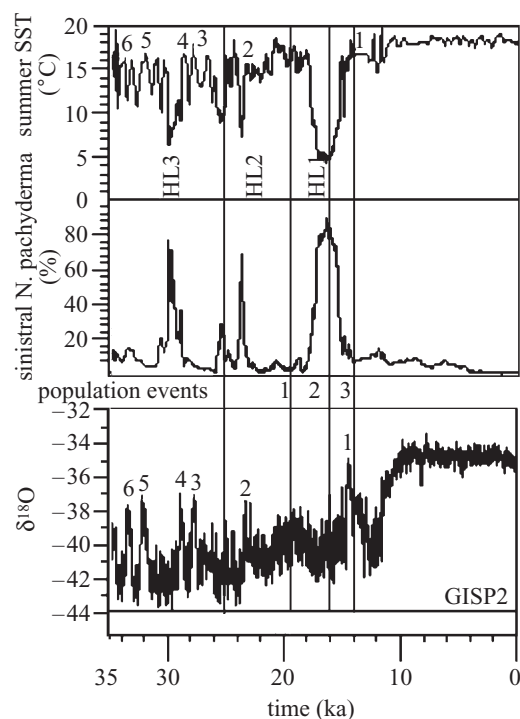
Figure 3. The late-glacial dispersal in western Europe during population events 2 and 3 compared with the GISP2 ice core and SST data from the deep sea core MD95-2040 on the Iberian shelf (adapted from de Abreu *et al.* 2003: fig. 5). 1–6, Dansgaard–Oeschger events.

grazing colonized the formerly polar deserts. These animals would have attracted population from the southern refugium. A cross-correlation of the radiocarbon and GRIP curves allows an estimate of the time-transgression to be made. Using the difference over the period 22–6 ka, the lag is of the order of 700 years.

Be this as it may, the record from ocean cores (figure 3) contradicts a time transgressive interpretation, suggesting that warming was not the catalyst that led to both the recovery of the environment and population expansion after 16 ka. High-resolution records of plankton and foraminifera from marine core MD95-2040 taken 125 km off the Portuguese coast indicate good temporal agreement with GRIP (de Abreu *et al.* 2003, p. 17), confirming earlier impressions of the close correlation between ice and ocean cores (Bond *et al.* 1993, p. 144). From these data the two archives appear to be time-locked rather than time-transgressive. As a result, population event 3 coincides with very low values for SSTs. In particular these are associated with HL1, which lasted from 17.6–14.9 ka. HLs are interpreted as the product of massive ice surging and calving and, during them, the polar foraminifer *Neogloboquadrina pachyderma* (sinistral) increases to over 95% of the faunal assemblage (de Abreu *et al.* 2003, fig. 5), indicating that summer SSTs fell to 5 °C compared with 18 °C today. SSTs drive the climate systems of western Europe (Renssen & Isarin 2001; Renssen *et al.* 2001), controlling such factors as permafrost, snow cover, precipitation and temperature. Low SST values in HL1 point to a context of cold climate for population expansion in events 2 and 3 (table 5).

The data point to extreme cold tolerance by human populations. Renssen *et al.* (2001, fig. 4) have simulated mean January temperatures for GS-2a which range from

0 °C to 5 °C for Iberia and −15 °C to −25 °C for northern Europe. These are comparable with those obtained from similar simulations for the Younger Dryas (Renssen *et al.* 2001), but temperature by itself was not a controlling factor. This is emphasized by that part of population event 3 which falls in the warm GI-1e (Bølling) when mean January temperatures ranged from −5 °C in northern Europe to 5 °C in Iberia (Renssen & Isarin 2001, fig. 4). One explanation of the early warming indicated by multi-proxy records in northern Europe (Walker *et al.* 2003) is the considerable effect that the location of sea and land ice had on local conditions (Renssen & Isarin 2001, p. 145).

(d) Greenland stadial 1: Younger Dryas

The Younger Dryas is widely regarded as one of the most significant climate changes in human prehistory. For example, it is implicated in the extinction of the North American megafauna (Haynes 1993) and the narrowing of subsistence options for populations in the Near East, already sedentary but forced to intensify subsistence through domestication (Bar-Yosef 2001). In western Europe we have identified it as population event 5 (figure 1).

In GRIP years GS-1 lasted for 1150 years between 12.7 ka and 11.5 ka. It is not associated with an HL although it has features in common with them such as an increase in *N. pachyderma* (sinistral), indicating lowered SSTs (Bond *et al.* 1993, p. 145). Mean January temperatures were between 20 °C and 30 °C lower than the present day in northern Europe (Renssen *et al.* 2001, fig. 9) but this should not have presented a problem, as we saw in the earlier GS-2a, to temperature-tolerant humans.

The abrupt increase in ice volume recorded in GRIP can be traced in local ice advances in Europe (Lowe & Walker 1997). It is also very closely phase-matched by a fall in the radiocarbon curve of archaeological assemblages (figure 4). The pattern in northern Europe is robust, archaeological assemblages now coming *predominantly* from open sites, whereas in population event 3 these had included caves and rockshelters as well as open locations. This shift in settlement pattern had started earlier, in population event 4, indicative of stability of human populations as larger, nucleated settlements replaced a more dispersed pattern of regional land use. The correspondence of the curves implies that, when climate was deteriorating, the impact on population was indeed more direct. Preference is here expressed in terms of settlement pattern with a move to aggregation in larger campsites. This pattern is in contrast to more scattered occupation across a larger region as shown by the habitual use of rockshelters in population events 2 and 3 in the northern part of western Europe. In this context it is interesting to note that the preferred settlement pattern for hunters and gatherers in the warmer and forested conditions of the Holocene was also for open locations (figure 4).

9. DISCUSSION

The high-resolution data from the late glacial allow us to evaluate the link between climate and hominid evolution. At this scale, expansion and contraction of the population are both well documented. The former is not strongly linked to climate change while the latter is, as the Younger Dryas case shows. However, the expansion
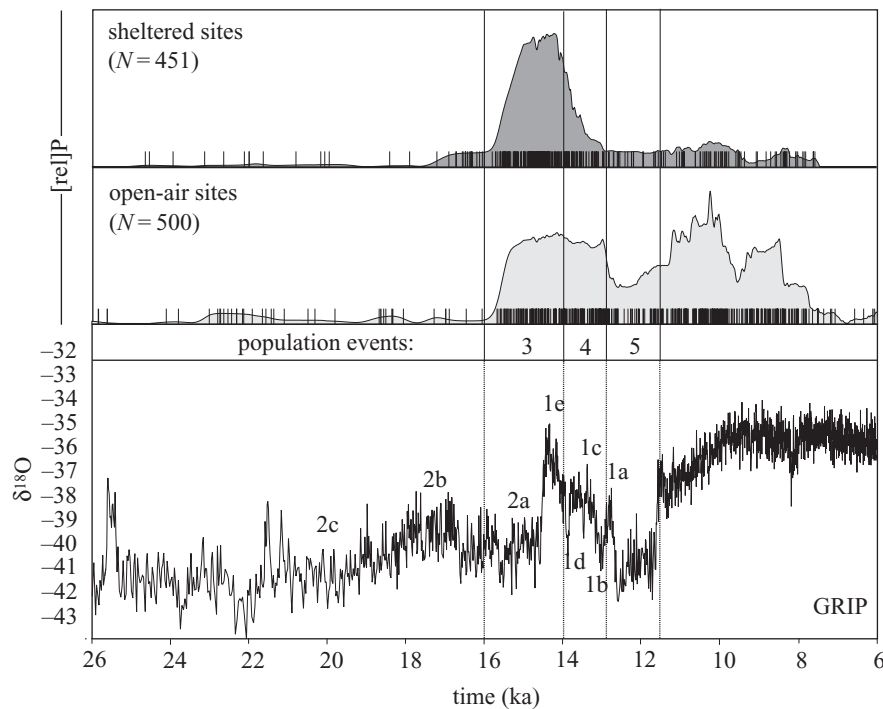
Figure 4. Open and sheltered sites from northern Europe in population events 3–5. For key see figures 1 and 2.

in population events 2 and 3 does result in changes in genetic diversity, as shown by founder effects involving some of the major European mitochondrial, and possible Y-chromosome, haplotypes. The situation in the Younger Dryas, population event 5, is much less clear (Richards *et al.* 2000) but it may have formed a constriction that was significant for further genetic diversity when the population grew in the Holocene. Full glacial refugia are important in temperate latitudes for understanding contemporary diversity (Willis & Whittaker 2000), but the dispersal mechanisms underpinning the aquatic radiation may be more important in forming those distinctive geographical populations (table 3).

Extrapolating further from this high-resolution late-glacial example confirms Foley's (1994) finding that climate change had more effect on extinction than on speciation. Our study also shows that dispersal took place within wide climatic tolerances so that explaining such events by general trends of warming or cooling is not possible. Dispersal is a search for those normal habitats that, once encountered, become preferred. The structure of the environment ahead of the leading population edge (Hewitt 1996) is therefore of key significance. For example, if cryptic refugia existed north of the European continental divide, and if early warming from multi-proxy indicators (Walker *et al.* 2003) were a local response to ice conditions, then saltation between patches of rapidly developing preferred habitats became possible.

However, saltation dispersal will occur only if the adaptive basis can exploit the conditions. Neanderthals, as representative of that basis associated with the earlier terrestrial radiation of *Homo*, clearly could not do so (table 4). In their preferred habitats they moved seasonally over short distances, maintained close social contact and were successfully adapted to local resource conditions (Finlayson *et al.* 2000*a,b*). By contrast the aquatic radiation had a different social basis. It promoted extension

from the refuge in time and space to places with acceptable conditions beyond the leading edge. Any changes in these places were tracked from the refuge by occasional visits whose purpose was to test the earliest opportunity for expansion. However, the Neanderthal response to climate change was to continue in the southern refuges and wait for a widespread change in conditions before re-expansion occurred. Therefore, in microcosm, we have an example of why the aquatic radiation of *Homo* was so successful and why its evolution and application to fluctuating environments, such as those of late-glacial western Europe, stands as paradigm for the legacy of the Ice Ages: a single hominid, released from social proximity and globally distributed.

ENDNOTE

[1]All dates in this paper are calibrated and presented as before present.

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Discussion

P. Forster (*McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, UK*). Your graph comparing ^{14}C dates with climate curves demonstrates a decrease of dates in the Younger Dryas for northern Europe and France, but an increase in Iberia. Your comment?

C. Gamble. It is interesting that in Iberia (figure 1) the radiocarbon determinations do not decline with GS-1

(Younger Dryas). This may be a reflection of the refugium status of the peninsula where, by comparison with regions north of the Pyrenees, there is generally less fluctuation in the frequency of determinations during the late glacial and hence less climate control over population. However, more work is needed on the regional patterns within the Peninsula and the balance in the samples from the three regions between open and sheltered sites (figure 4), because the latter dominate in Cantabria.

M. Jones (*Department of Archaeology, University of Cambridge, Cambridge, UK*). You have inferred from the European evidence that large-scale saltation is very much a feature of *H. sapiens*. If we turn to other hominids that have expanded from Africa, what implications do you think this might have on the kind of landscapes and their ecological texture between Asia and Europe?

C. Gamble. *H. sapiens* differs from other hominids in being able to exploit localized habitats that are far apart. This is what I mean by saltation and which others in the context of the colonization of the Americas refer to as a leap-frog model (Anderson & Gillam 2000). In this respect a cryptic refuge forms a patch for hunters and gatherers to jump onto as they disperse out of more traditional refugia. The expected ecological grain is therefore heterogeneous. Preferred habitats are localized and often of short duration, confirming *H. sapiens* as specialists (table 1). The ecological grain for earlier hominid dispersals in Asia and Europe was probably of two types as described by Guthrie (1984). His plaids and stripes fav- oured, respectively, high and low diversity in animal taxa. The former therefore favoured generalists and the latter specialists. I would also see earlier hominids as adapted to richer resource areas. A good example of a plaid ecology is provided by coastal environments. These may have facilitated, owing to their concentrated mosaic structure, the southern dispersal of hominids out of Africa and into Asia.

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GLOSSARY

ATU: archaeological taxonomic unit
GI: Greenland Interstadial
GRIP: Greenland ice-core project
GS: Greenland stadial
HL: Heinrich level
LGM: last glacial maximum
OIS: oxygen isotope stage
SST: sea surface temperature