

## Chapter 14

# Demography, Dispersal and Human Evolution in the Last Glacial Period

Marta Mirazón Lahr & Robert A. Foley

The Stage 3 Project represents a collaborative effort to unravel the complexities of European climate and environment during the long interstadial (~60,000 to 25,000 years) of the last glacial cycle. From interdisciplinary approaches and sophisticated climatic modelling, the main outcome of the project is the confirmation that Stage 3 was not just a slightly warmer phase of the last glaciation, but a climatically variable period that at moments approached nearly interglacial conditions, while at others experienced abrupt and profound changes towards glacial climates (van Andel 2002).

This focus on understanding Stage 3 — trends, variability, frequency of climatic change, the amplitude of those changes, and their effects on the fauna and flora of Europe — is important for the development of temporal biogeographic models of the Pleistocene, in particular the later part of the period. Such models tend to generalize change on the basis of the extremes within a glacial cycle — i.e. between interglacial and peak glacial conditions (Lahr & Foley 1998). Parameters derived from these models are important for interpreting the order and directionality of demographic change, both population expansion and contraction, and explaining such changes in the context of resource availability. These approaches have provided a general model for understanding the population history of Europe on a glacial-interglacial scale (Gamble 1993; Foley & Lahr in press).

However, from a phylogeographic perspective small-scale changes can have significant demographic and genetic effects. Recent research, such as that developed in other chapters of this book, highlights the degree of smaller-scale climatic changes between interglacials and peak glaciations (see Chapter 5: Barron *et al.* 2003; also Barron & Pollard 2002). This change largely reflects medium-term fluctuations in temperature and ice-sheet extent, but also short-term

abrupt changes identified as Dansgaard/Oeschger oscillations. The role of such interstadial fluctuations on evolutionary and biogeographic patterns is only just beginning to be explored.

These aspects are important at least partly because they provide the context for events following the emergence of modern humans. This period, encompassing approximately the last 160,000 years, witnessed the expansion of a small African population throughout the world and the subsequent disappearance of all other hominin species, leading to the existence of a single species of hominin throughout the world for the first time in five million years. How many other hominin species existed throughout the world in the early Upper Pleistocene is a matter of much controversy. However, for the focus of this book there is no doubt that the hominin species that had occupied Europe for a considerable period of time was replaced by expanding modern humans. This major demographic event, the extinction of the Neanderthals and the establishment of a modern human population in Europe, took place during Stage 3 (Stringer & Gamble 1993; Stringer 2002).

The fact that Stage 3 was the time when this happened is particularly significant. Modern humans evolved in Africa at some point during the previous glacial period (Stage 6) and experienced at least phases of moderate geographical expansion in the subsequent interglacial (Stage 5). However, these early modern human groups did not disperse further into Europe at that time. They did so later on, around, or soon after, approximately 60,000 years ago, before the peak of the last glaciation (Chapter 4: van Andel *et al.* 2003b; Lahr & Foley 1994; 1998). These two facts contradict predictions based on broad glacial-interglacial biogeographic models, and raise a major question — was the expansion of modern humans into Europe, the event that led to the extinc-

tion of Neanderthals, climatically driven?

In order to tackle this question, we will first discuss the broad biogeographical models of glacial–interglacial faunal exchange between Europe and Africa. Secondly, we will discuss the climatic context of Stage 3 and the implications for such biogeographic models. Thirdly, we will review the palaeoanthropological and genetic evidence for the timing and extent of modern human expansion during Stages 5, 4 and 3. Finally, we will explore analytically whether the fluctuating site demography of the Middle and Upper Palaeolithic in Europe during Stage 3 (using the Stage 3 Project Archaeological Data Base; see Chapter 3: van Andel *et al.* 2003a) can be linked to climatic change and discuss the implications of the findings.

### **Biogeographical models: evolutionary geography and climatic change**

#### *Evolutionary change in a dynamic climatic context*

While it is a truism that climatic and environmental change is a major influence on evolution, it is less clear exactly how this relationship operates. At one extreme it has been argued that climate is a necessary and sufficient cause of evolutionary change, and that in its absence speciation and directional changes are unlikely to occur (Vrba 1993; 1996). Under this model, often referred to as ‘pulse-turnover’, evolutionary change is expected to be synchronized with climatic change. At the other extreme, continuous co-evolutionary interactions have been seen as the main driver of change, and that this occurs independent of climatic shifts (van Valen 1973). Under this model, a tight relationship between evolution, such as the appearance of new species, and climatic change, is not expected. Between these two extremes lie a number of more intermediate positions, which recognize that while climate might prompt particular bursts of change, they occur in particular competitive contexts.

Elsewhere we have argued for one of those more intermediate positions, focusing on the role of geographical processes in shaping evolutionary patterns (Lahr & Foley 1998). In particular, we have argued that the populational response to climatic change is most directly distributional. When climates change, so does habitat distribution; this is the essence of the climatic simulations and reconstructions outlined in this book. In response to this, animal populations will either contract or disperse. It is these changed distributions that provide the new conditions under which selection may bring about evolu-

tionary change, or indeed extinction. However, the relationship between climate and these evolutionary processes is much less direct than is the case with dispersals or contractions (Foley 1999).

In terms of human evolution and Stage 3, one of the opportunities provided by the fine-grained analyses of climatic change is to see the extent to which changes in hominin distributions are a response to changes in habitat distribution, and whether this provides the microevolutionary basis for understanding later Pleistocene human evolution. We can consider this by first looking at how Pleistocene climatic change could provide the framework for understanding major dispersal patterns in a biogeographical context.

#### *Afro-European biogeography and glacial cycles*

Glacial cycles provide the primary framework for Pleistocene biogeography. Although cooling of the Earth’s climate began at the end of the Pliocene (Denys 1985; Loubere 1988), cyclical glacial fluctuations date from approximately 800 ka BP (Shackleton 1987). The first full glacial stage is recognized in the marine sequences as Stage 22, within the Matuyama subchron and before the Jaramillo event, and therefore between 900 and 790 ka BP. The succeeding glacial cycles each show the slow build-up of continental ice sheets, a rapid period of deglaciation, followed by a relatively short warm interglacial stage, although each cycle also shows unique aspects in terms of duration and extent (Shackleton 1987; 1996; Malatesta & Zarlenga 1988). These cyclical events influenced equatorial and northern latitudes in predictably different ways. Maximum cold in the north led to a southward shift of climatic belts, reduced temperatures globally, low sea-level stands, and aridity in many parts of the tropics. Warming is followed by the release of water trapped in the northern hemisphere glaciers, which is responsible for the global rise in sea level and for pluvial and high lake level short episodes in equatorial regions.

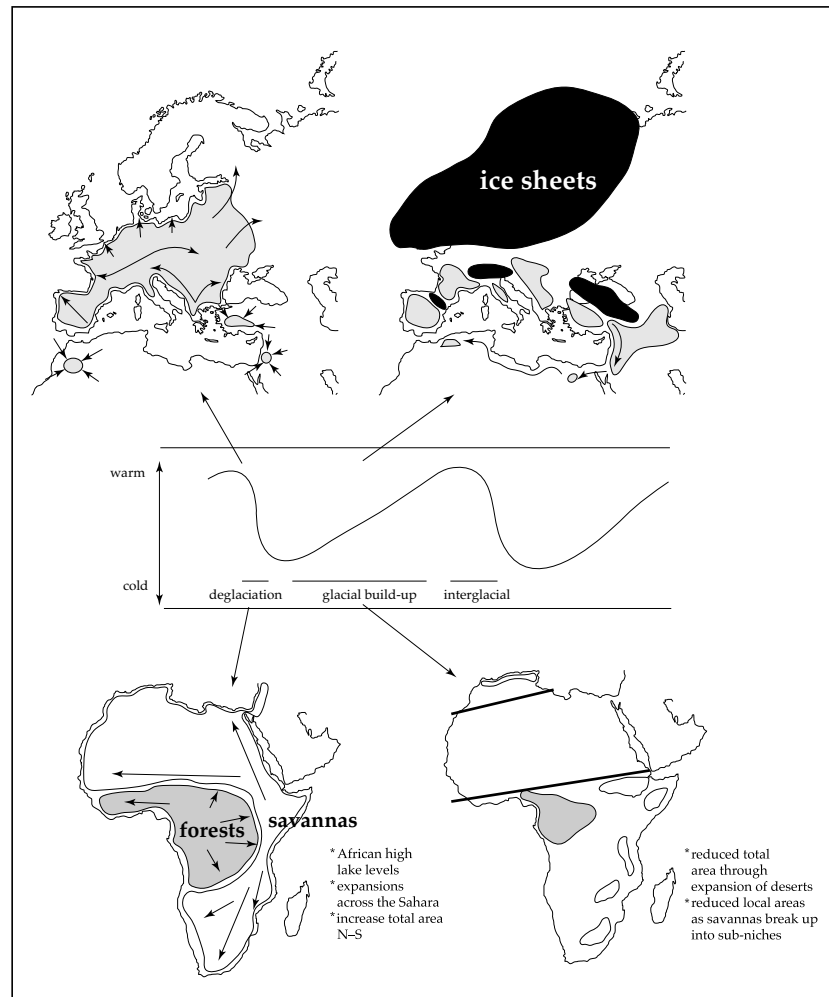
These changes have effects on African and Eurasian faunal distributions (Fig. 14.1) (Tchernov 1992a,b; Lahr & Foley 1998). Large mammalian faunas in both continents undergo periods of range expansion during early interglacials, while only Eurasian faunas seem to shift ranges during glacial build-up (in Africa extensive aridity causes the contraction of available ranges and a level of isolation and endemism). In the case of Europe, interglacial faunal expansions were associated with the retreat of ice and tundra along the Eurasiatic plains to the northeast, and occasionally towards the southeast, reaching the

Middle East (although the Taurus-Zagros mountain range and the interglacial forests of the Greek and Turkish peninsulas acted as important barriers to movement in this direction). During glacial periods, European animal ranges shifted southwards as continental areas became covered by ice sheets and permafrost terrain. At these times, the Middle East acted as a cul-de-sac, for these northern elements could not overcome the Saharan barrier at its maximum extent during glacial stages. Therefore, the main direction of Palaearctic expansions was East–West, as reflected by past and present animal distributions. In the case of Africa, population expansions were associated with increased moisture occurring particularly during the early phases of interglacials. These expansions were also directional, as forests expanded equatorially and savannas in a northerly direction across the Sahara. During these episodes, the Ethiopian faunal range also encompassed the Sahara, northern Africa and the Levant, which shows indications of savanna conditions, while movement into Europe would reflect a subsequent dispersal if the Taurus-Zagros barrier was transcended. Therefore, the main direction of non-forest Ethiopian expansions was north–south, reaching into the Middle East through the Sinai Peninsula.

#### *Hominin dispersals in relation to the climatic cycles*

The implication of this general model is that there should be a predictable relationship between climatic change and hominin dispersals between Africa and Europe. In particular, it can be expected that during periods of glacial tropical aridity, the Sahara would be a barrier to movements out of Africa, and European populations are likely to have experienced contractions as habitats become latitudinally compressed. Conversely, during early interglacials, the northward spread of savanna environments would open up routes of dispersal from Africa to Eurasia, while Eurasian populations are likely to have dispersed northwards in response to habitat expansion due to warmer climates.

This model fits well the pattern of dispersals



**Figure 14.1.** Schematic diagram of the effect of the glacial cycles on habitat distribution and biogeographical relationships between Europe and Africa. (From Lahr & Foley 1998.)

into Europe during the lower and middle Pleistocene, and the apparent depopulation that occurs in glacial stages. It also conforms to what is observed for the extra-African dispersals that occur in Stage 5, although they do not appear to have penetrated Europe at this time (Lahr & Foley 1998). However, this general dispersal model does not allow us to estimate the role of smaller-scale climatic change in promoting multiple or relatively few such dispersals, or what the outcomes of such dispersals could have been for the various hominin populations that lived during this time period.

#### *Flux & fragility as a demographic model for the Upper Pleistocene*

A further implication of the evolutionary model described here is that hominin populations may have

been highly unstable in numbers and distribution. The standard anthropological model of human demography has been one of overall stability, leading to a gradual increase in human population. Underlying this view, was the idea that as the human species — and its ancestral forms — became more sophisticated, intelligent or simply better adapted, they experienced population growth, or at least maintained local demographic stability. However, this stable model is inconsistent with the genetic evidence and the emerging archaeological evidence. This evidence suggests that human and hominin populations experienced major fluctuations in population size, and that rather than being characterized by stability, they were in fact in a permanent condition of flux and fragility (Foley & Lahr in press). The local level would be the starting point of this, as communities responded to immediate adverse challenges (or failed to), ranging from resource depletion, inter-group conflict, and disease. Where such factors extended regionally, then local effects would be amplified. The converse of this situation is expansion, leading to dispersals and geographical expansions of existing ranges; as resources recover, or alternatively, when new and successful adaptive strategies are developed, then populations may be expected to expand very rapidly. In the latter case, there may be interactive effects between population collapse and population expansion.

A 'flux and fragility' model of prehistoric demography has implications for human evolution, and the high resolution of the Stage 3 climatic and environmental data provides the context for testing some of these ideas.

### Stage 3 as a climatic context for human evolutionary: events and models

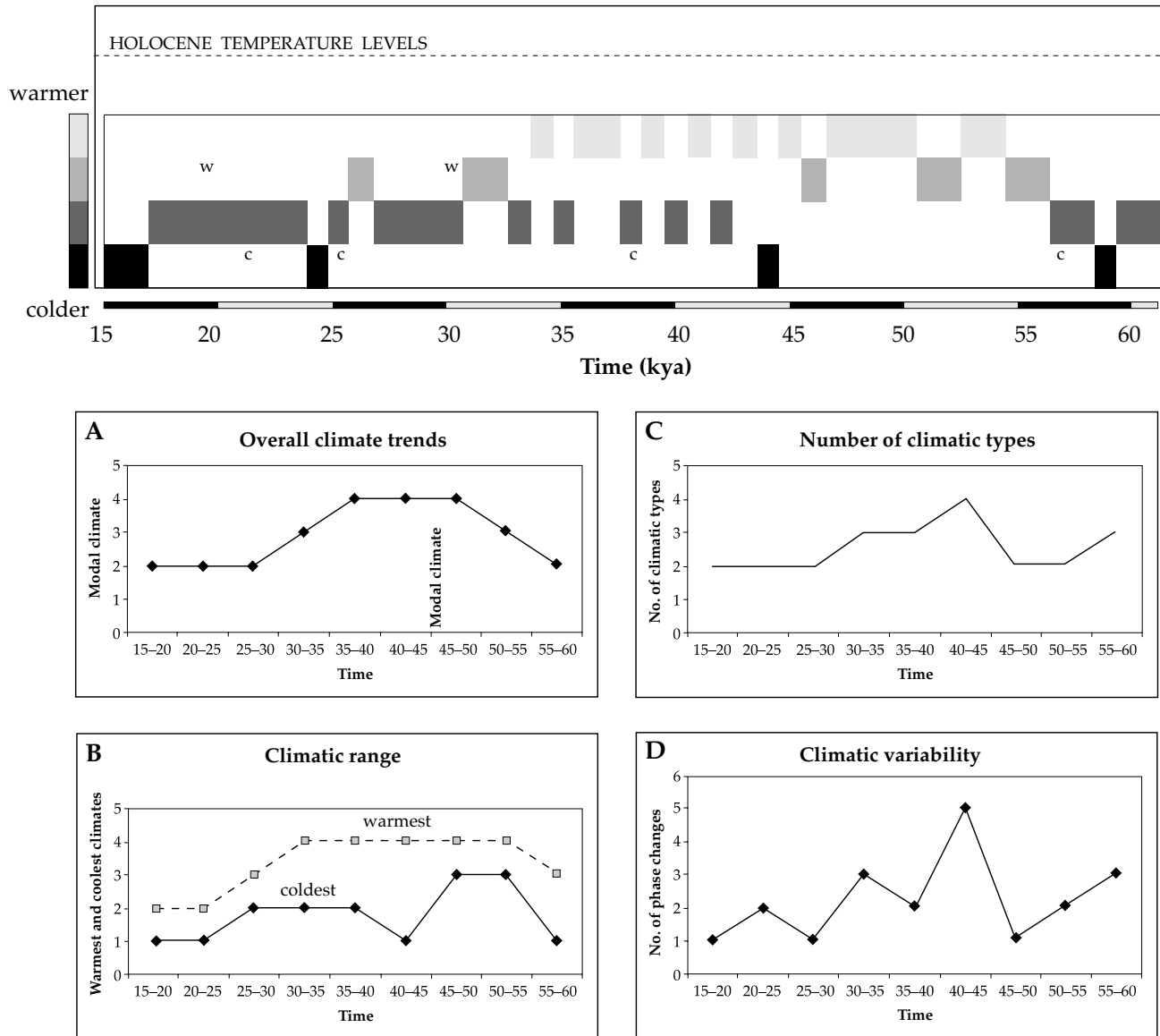
#### *The pattern of climatic change in Stage 3*

Figure 14.2 is a simplification and representation of the climatic sequence of the period from 64,000 to 15,000 years ago, based on the Atlantic Ocean core MD95-2042, using  $\delta^{18}\text{O}$  values derived from planktonic Foraminifera (Shackleton *et al.* 2000). The period has been divided into 1000-year units. Although this is more finely resolved than might be warranted, the purpose is to summarize the main climatic trends. The climate quality for each 1000-year period was estimated, using a four-level scale: a) extreme cold phases, when the planktonic values for  $\delta^{18}\text{O}$  were no more than 20 per cent less than during the last glacial maximum (LGM); b) cold phases, when  $\delta^{18}\text{O}$  values were between 20–40 per cent less than those

at the LGM; c) cool phases, when  $\delta^{18}\text{O}$  values were between 40–60 per cent less than LGM ones; and d) warm phases, when  $\delta^{18}\text{O}$  values were at least 60 per cent less than at the LGM. For the most part, each of the 1000-year units could be ascribed as having a modal value within each of these categories; where there were aberrant warm or cold surges or spikes, these are indicated in the figure.

A number of points can be made about the climate of the Stage 3 period (which are further elaborated in other chapters of this book: Chapter 2: van Andel 2003; Chapter 5: Barron *et al.* 2003 & Chapter 6: Huntley & Allen 2003):

1. *Comparison with LGM and Holocene:* Stage 3 is clearly considerably warmer than LGM (only two 1000-year blocks approach LGM inferred temperatures — 43–44 ka BP, and 63–64 ka BP). Although at no point does the temperature approach that of the Holocene, the period can be considered not just intermediate between extreme glacial and interglacial conditions, but composed of significant lengths of time of relatively warm temperatures. If we look at Stage 3 as a single period, 13,000 years of its 35,000 year length (37 per cent) are what we have defined here as warm (as opposed to extreme cold, cold, and cool); 8000 years (23 per cent) are cool; 12,000 years (34 per cent) are cold; and 2000 years (6 per cent) are extremely cold.
2. *Overall trends:* As can be seen in Figure 14.2A, there is a clear trend towards warming that stabilizes between 50–35 ka BP (i.e. the warming phase compared to Stage 4), followed by a general deterioration into the LGM. As noted elsewhere in this book, Stage 3 is really composed of two periods, an early warm phase and a colder late phase. After 33 ka BP, there are no further warm phases.
3. *Climatic variability:* However, these trends mask what is perhaps the most intriguing aspect of Stage 3, which is its high variability. Figure 14.2B shows the warmest and coldest phases for each 5000-year block of Stage 3. It clearly shows that the period from 40–45 ka BP has the widest range; it also has the largest number of different climatic phases (Fig. 14.2C), and the most changes (Fig. 14.2D). Although no other part of Stage 3 matches these 5000 years, the period between 40–30 ka BP is also relatively variable, certainly compared to Stage 2.
4. *Stability and change:* Beyond overall variability is the rate of change, and by inference the degree of stability. Using the simple classification of major shifts shown in Figure 14.2, there are 22 phase



**Figure 14.2.** Simplified scheme of climatic change across Stage 3. The vertical scale in the upper diagram shows a four-part categorization of temperatures derived from the oxygen isotope record of MD95-2042, in 1000-year units. The darker shading shows increasingly cold conditions (see text for details). A–D in the figure shows various parameters of Stage 3 by 5000-year units: A) overall climatic trends based on modal  $^{18}\text{O}$  values; B) climatic range based on maximum and minimum  $^{18}\text{O}$  values; C) the number of each of climatic category found in each 5000-year period; and D) climatic variability based on the number of changes occurring in each 5000-year period.

changes across the 35,000-year period; in other words, the climate seldom remains within a single phase for more than 1000 years. Indeed, the longest period of stability is 4000 years, which occurs with a warm phase between 46–50 ka BP, and a cold phase between 26–30 ka BP.

5. *Interactive effects:* One further point is that the period between 46–50 ka BP has been characterized by the most prolonged phase of climatic sta-

bility, while the following 5000 years (45–40 ka BP) have the greatest levels of instability. The interactive effect of this combination may have been of significance for human evolutionary patterns.

#### *Relationship between Stage 3 scale of climatic change and the glacial–interglacial cycle*

The question is how can these characteristics of an interstadial, in this case Stage 3, be integrated into

the biogeographic model described before so as to provide more sophisticated or detailed predictions of hominin demographic change?

Some simple expectations can be outlined. First, if full interglacial conditions are necessary to prompt 'out of Africa' hominin dispersals, then these do not occur in Stage 3, even though it is a relatively warm period. Stage 3 might thus offer a test for aridity/humidity thresholds for hominin dispersals across the Sahara. Second, it is clear, as shown elsewhere in this book, that the earlier part of Stage 3 is considerably warmer than the later part. If contractions and extinctions are an expectation of colder conditions, then the slide into more glacial conditions during the course of Stage 3 might provide insights into how sensitive to such changes hominin populations are. Third, the high level of variability and oscillation between relatively warm and relatively cold conditions, particularly in the middle parts of Stage 3, should provide an indication of the sensitivity of hominin populations to such changes — for example, whether they respond on a scale of 40 generations (i.e. a thousand years), or whether they are sufficiently buffered to damp out the effects of such rapid change. These general questions will be addressed in the remainder of this chapter, first by considering the overall evidence for hominin dispersals and demography, and then by considering the quantitative approaches that might indicate the effect of climate on later human evolution.

### **Palaeoanthropological and genetic evidence for modern human expansion: tracing early modern human demographic change**

#### *Evidence for the pattern of later human evolution*

The fossil evidence suggests that the evolutionary lineage leading to modern humans is a uniquely African one, and that although the fossil record is relatively poor, it is possible to trace a trajectory from larger brained archaic forms such as Florisbad or Ngaloba (which we would refer to as *Homo helmei*) to early modern forms represented by the Idaltu and Omo Kibbish fossils from Ethiopia (Stringer & Andrews 1988; Lahr & Foley 1994; Stringer 2002; White *et al.* 2003). Although the date of the transition between archaic and morphologically modern forms continues to be a matter of debate, it is likely, on the basis of the Ethiopian material, that it took place before 150–160 ka BP, during Stage 6. No similar evidence for such a transitional process is found elsewhere in the world, and this is supported by abundant palaeoanthropological and genetic evidence.

Two observations about the genetic evidence are paramount. The first is that humans display relatively little genetic variation in fast-mutating loci, giving rise to the model that human diversity is a recent phenomenon derived from a very small population. Chronological estimates for when this occurred vary, but there is general consensus, based on a number of gene systems, that it was approximately 150,000 years ago. This accords well with the first evidence for generalized anatomically modern humans. The second is that there is greater genetic diversity in African populations than in non-African ones, and that the latter are a subset of the former. This, together with the directionality of genetic change observed in uniquely African lineages, supports the hypothesis that modern human origins lie in Africa, on the basis that the amount of diversity in populations is, in part, a reflection of the time over which they have persisted. This conclusion is derived from both unique phylogenies of particular loci, such as the Y chromosome and the mitochondrial genome, as well as by the geographical distribution of such genes in particular populations (Watson *et al.* 1997; Quintana-Murci *et al.* 1999; Ingman *et al.* 2000; Underhill *et al.* 2001).

During Stage 5 there is more widespread evidence for modern humans (Foley & Lahr 1997; Klein 2000). Within Africa, the fossil evidence from Klasies River Mouth shows that if the original population was in northeastern Africa, by this time descendent groups had expanded to the Cape. Archaeological evidence in the form of the MSA industries scattered over much of Africa would perhaps support this view. Furthermore, the presence of modern humans from at least 100,000 years ago in the Levant shows that dispersals across the Sahara or through the Nile had also occurred, as predicted by the biogeographical model for inter-glacial conditions. However, at that time, no evidence for modern humans beyond what can be considered an essentially African biogeographical zone has been found (Lahr & Foley 1998).

This is consistent with the genetic data. The rare and yet widespread distribution of Y-chromosome haplogroups I and II in Africa has been interpreted as evidence for these early dispersals. Today, these lineages are found mostly in small, outlier populations of hunter-gatherers throughout Africa (Underhill *et al.* 2001). The mtDNA evidence also reflects this pattern (Quintana-Murci *et al.* 1999).

From the perspective of demographic change, it is clear that African hominin groups consisted of small, isolated populations, and that these were sub-

jected to stresses that caused significant demographic contractions. Estimates of the size of the ancestral population of anatomically modern humans in Africa at the end of the Middle Pleistocene have been of the order of tens of thousands of individuals. If the populations were sub-structured, as is likely, then total numbers may have been even smaller. Fluctuating demographies are thus a key element in the process of late human evolution, as implied by the general evolutionary models discussed above. Archaeological and chronological evidence, and even ancient DNA results, increasingly suggest that such fluctuating demographies probably characterized all Pleistocene hominin groups.

#### *Major human dispersals beyond Africa*

While the earlier phases of modern human origins and dispersal seem to fit the general models presented earlier, it is clear that expansion beyond the African biogeographic zone had not occurred prior to the onset of Stage 4. Neither genetic evidence based on coalescence estimates, nor archaeological evidence, would suggest a greater geographical range for the earliest modern humans. Some caution has to be expressed on this point, as it is possible that later extinctions of modern human populations outside Africa may have erased the genetic evidence, and little work has been done in key areas such as Saudi Arabia and India to provide good dated sequences for the Middle Stone Age.

The earliest evidence for modern humans beyond Africa and the Levant comes from Australia. Although there is some controversy concerning dates, most researchers accept that humans reached Australia by at least 50,000 years ago, and possibly more than 60,000 years ago. We have argued elsewhere that this evidence, in conjunction with genetic data, shows that there was a separate 'Southern Dispersal' independent of the Upper Palaeolithic dispersals into and across Eurasia (Lahr & Foley 1994; 1998; Foley & Lahr 1997). Depending on a more precise chronology of such a Southern Dispersal, it may have taken place during the warming phase associated with the onset of Stage 3. If this is the case, then such dispersals would fit the general expectations of the biogeographical model, and would suggest that the conditions were sufficiently ameliorated to allow extra-Africa population expansion, presumably through the Horn of Africa. This would have been a coastal, sub-tropical expansion, in turn suggesting that it may have been either too cold to allow hominin populations to spread to higher latitudes, or too dry to allow crossing the Sahara. On the other hand, if

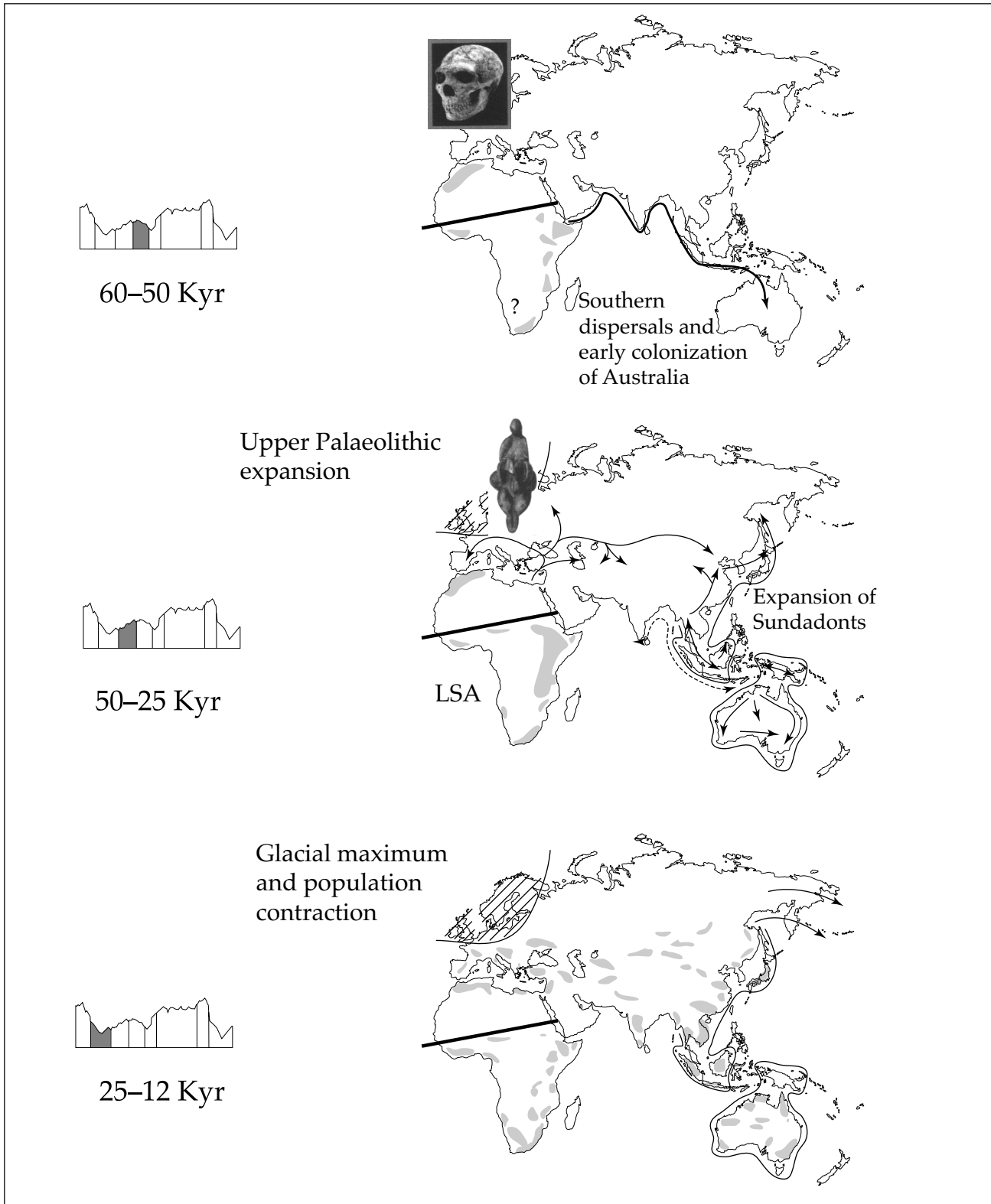
the very earliest proposed Australian dates prove to be correct (Roberts *et al.* 1994), then it would mean that the Southern Dispersal occurred against the directionality of the model. As we shall discuss later, this contrast between biogeographical expectation and archaeological evidence may indicate over-riding human behavioural capacities.

The spread of modern humans into Eurasia (Fig. 14.3) is generally associated with the Upper Palaeolithic. Although there are some indications of sites with Upper Palaeolithic industries occurring very early, most of the evidence suggests that major expansion occurred after 45,000 years ago, with dispersal across Europe taking place up to 30,000 years ago, and across central and eastern Asia somewhat later (Torrioni *et al.* 2000; Ke *et al.* 2001; Underhill *et al.* 2001).

The key point to stress is that these dispersals occur against the trend of climatic change. Although the period concerned is relatively warm compared to the LGM, nonetheless the overall direction of climatic change is towards colder conditions. In other words, as noticed by many before, the Upper Palaeolithic dispersals do not conform to the predictions of the general biogeographical model.

It is possible that the apparent lack of fit between the evidence for human Eurasian dispersals and the climatic evidence is the result of a mismatch of scale. As mentioned before, Stage 3 was characterized by high variability, with periods of relative warmth oscillating with colder phases on a scale of one thousand years or even less. It could therefore be that modern human behaviour allows Upper Palaeolithic populations to respond sufficiently fast to allow geographical expansion after very short-term climatic amelioration, and thus to disperse into Europe in a more interrupted manner, with bursts of expansion during the short warmer phases, interrupted by colder contractions or even extinctions. The alternative to this model is that the pattern of modern human dispersal into Europe is not influenced by climate, but either by the behavioural characteristics of modern humans, or the nature of the competitive interactions with the local European Neanderthals.

In the next section we will consider these possibilities by using the archaeological evidence compiled by William Davies as part of the Stage 3 Project (Chapters 3 & 4: van Andel *et al.* 2003a,b) as a proxy for human dispersals at a fine-grained chronological level, and by exploring whether it is possible to measure the interaction between human demography and climate during Stage 3.



**Figure 14.3.** Multiple dispersals and contractions of early modern humans. The top figure shows the early southern dispersals in Stage 4; the middle figure shows the Stage 3 Eurasian dispersals; in Stage 2 (bottom figure) the contraction and fragmentation of the human population is shown. See text for full discussion.

### Measuring the impact of climate on human dispersals

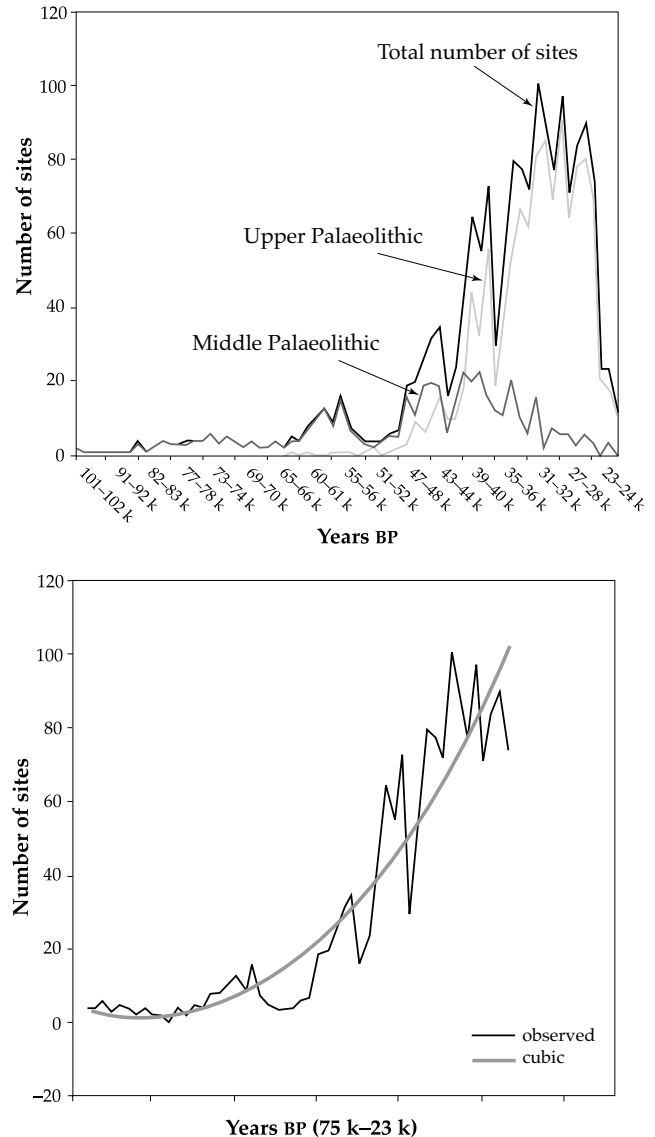
In order to examine the relationship between climatic variables and the number of Middle and Upper Palaeolithic sites in Europe, the raw  $\delta^{18}\text{O}$  data from the marine core MD95-2042 (Shackleton *et al.* 2000) were used.

Although the Stage 3 Archaeological Data Base contains dated occurrences of Upper Palaeolithic (UPal) sites in Europe as early as between 65–60 ka BP, the first clear evidence of UPal sites occurs after a period of stable and relatively warm climate (between 55 and 48 ka BP), when the number of Middle Palaeolithic (MPal) sites decreases considerably. The following period, between 45–40 ka BP, witnesses the growth of UPal sites, but also of MPal ones (Chapters 3, 4: van Andel *et al.* 2003a,b & Chapter 8: Davies & Gollop 2003) (Fig. 14.4).

The extent to which European hominin populations were sensitive to some aspect of climatic conditions (temperature, variability, etc.) was addressed at three levels: 1) through the overall number of sites, regardless of whether they were Middle or Upper Palaeolithic; 2) Middle Palaeolithic (and presumably Neanderthal); and c) Upper Palaeolithic (and presumably modern human). The Châtelperronian and other 'intermediate' sites were treated as Middle Palaeolithic. A number of climatic variables were generated from the  $\delta^{18}\text{O}$  data, namely: average  $\delta^{18}\text{O}$  values for 1000-, 3000- and 5000-year periods; maximum and minimum, as well as amplitude of  $\delta^{18}\text{O}$  values in the same periods; absolute and relative difference of  $\delta^{18}\text{O}$  values between units (1000-, 3000- or 5000-year long); or transformed into categorical measures of relative climatic quality, or stability of rate of change. Available evidence from Stage 4 (as existent in the Stage 3 Archaeological Data Base) was included in the analyses. The approach we adopted was to treat the archaeological and climatic data statistically rather than historically, and thus explore hypotheses relating to the measurable influence of climate on hominin populations.

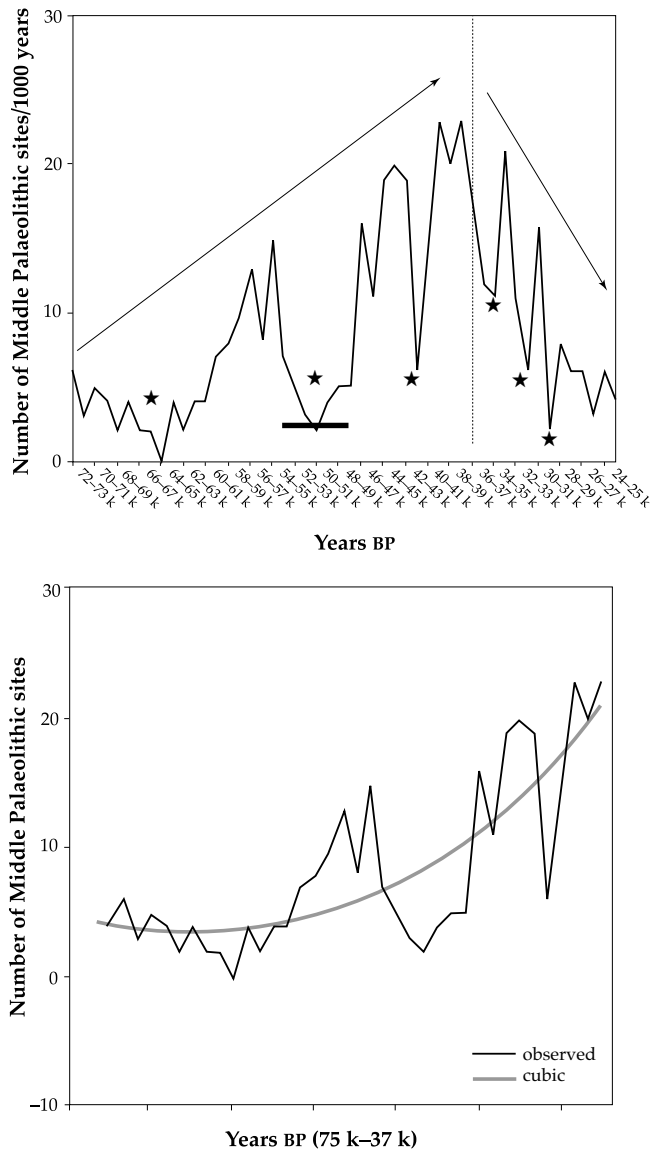
#### *Middle and Upper Palaeolithic sites in Europe during Stage 3*

Average  $^{18}\text{O}$  values/1000 years, extreme negative and positive  $\delta^{18}\text{O}$  values/1000 years, or amplitude of  $^{18}\text{O}$  values/1000 years do not account for the variation in the number of archaeological sites in Europe between 73 and 23 ka BP (insignificant cubic regressions). However, a cubic regression of number of archaeological sites through time is extremely sig-



**Figure 14.4.** Number of archaeological sites from the end of Stage 5 to the beginnings of Stage 2. The number of sites attributable to Middle and Upper Palaeolithic are also shown (top). Number of sites over time, and the cubic regression derived from these data are shown in the bottom graph.

nificant ( $F = 181.19936$ ,  $p < 0.001$ ), with an  $r^2$  of 0.88089 (Fig. 14.4). In other words, the main predictor of the number of archaeological sites is time itself; between 73–23 ka BP, one can predict with 88 per cent accuracy the number of archaeological sites in Europe (both Middle and Upper Palaeolithic) for each 1000 year time period. At this time scale, there is no relationship between climate and number of archaeological sites.



**Figure 14.5.** Number of Middle Palaeolithic sites over time (top). There is a marked trend towards increased numbers prior to 38 ka BP, and a decline after that time. Major departures from that trend are indicated by stars. The pattern indicates that Neanderthal populations may have been subject to fluctuations within the general trends. The increase in number of sites prior to 38 ka BP is best described by a cubic relationship (shown in bottom graph, see text for details).

The role of time in explaining the number of archaeological sites highlights the historical nature of the observed change — there is a cumulative addition of sites. However, it could be that climate is affecting the rate of accumulation, and that the 12 per cent variation not explained by time itself can be

accounted for by climatic change. In order to test this, the residuals of the cubic regression between number of sites and time were tested against the climatic variables. No significant relationship or pattern was found between these, i.e. climate does not seem to explain the overall increase in number of archaeological sites in Stage 3 Europe, nor the observed fluctuations in numbers relative to the general trend over time.

#### *Middle and Upper Palaeolithic sites in Europe during Stage 3*

It may be that the observed relationship with time conflates different patterns for the Middle and Upper Palaeolithic. The number of Middle Palaeolithic sites in Europe during Stage 3 is very variable, but can be described overall as progressively larger up to ~37 ka BP, and declining subsequently (Fig. 14.5). These generalizations, however, are marked by pronounced departures, particularly in the intervals of 66–65 ka BP, 54–49 ka BP, 44–43 ka BP, 38–36 ka BP, 34–33 ka BP, and 32–31 ka BP. The most significant of these periods in terms of the duration of the effect is clearly the 54–49 ka BP interval.

However, again, no strong statistical relationship between climatic variables and Middle Palaeolithic sites can be demonstrated. An analysis of the number of Middle Palaeolithic sites in Europe between 73–37 ka BP shows a strong relationship with time (Fig. 14.5) ( $F = 29.74072$ ,  $p < 0.001$ ,  $r^2 = 0.60839$  (cubic regression)). In other words, the more recent the period (between 73 and 37 ka BP), the larger the number of Middle Palaeolithic sites that can be expected (with a 61 per cent accuracy).

We also considered whether, once time was taken into account, there was a relationship between the number of Middle Palaeolithic sites and climatic variables. Using the same approach as above, the residuals of the cubic regression were tested against the climatic variables. The results obtained show that there is no relationship between  $\delta^{18}\text{O}$  values (1000-year averages, maximum or minimum). There is, however, a weak relationship between amplitude of  $^{18}\text{O}$  values in 1000-year intervals and whether there are too few or too many Middle Palaeolithic sites in 1000-year intervals as predicted by age (between 73 and 37 ka BP). The smaller the amplitude of climatic change, the smaller the residual values (i.e. the closer to expected by age). In other words, the greater the degree of climatic variability in 1000-year periods, the greater the probability of affecting the historical trend of increase in number of sites ( $r^2 = 0.17214$ ,  $F = 3.64$ ,  $p < 0.05$ ). These data therefore show some evi-

dence that Neanderthal populations were adversely affected by the amount of climatic change.

In the period between 37 and 23 ka BP, the temporal distribution of Middle Palaeolithic sites is best described by a linear decrease ( $F = 9.83$ ,  $p < 0.01$ ;  $r^2 = 0.472$ ). Although this historical trend can only account for 47 per cent of the variation in number of Middle Palaeolithic sites observed (and indeed, the majority of 1000-year periods have either too many or too few sites in relation to the number predicted by the historical trend), none of the climatic variables correlates significantly with the residual data (with  $\delta^{18}\text{O}$ :  $r^2 = 0.392$ ,  $p > 0.05$ ;  $\text{neg}\delta^{18}\text{O}$ :  $r^2 = 0.293$ ,  $p > 0.05$ ;  $\text{pos}\delta^{18}\text{O}$ :  $r^2 = 0.422$ ,  $p > 0.05$ ;  $\text{amp}^{18}\text{O}$ :  $r^2 = -0.133$ ,  $p > 0.05$ ).

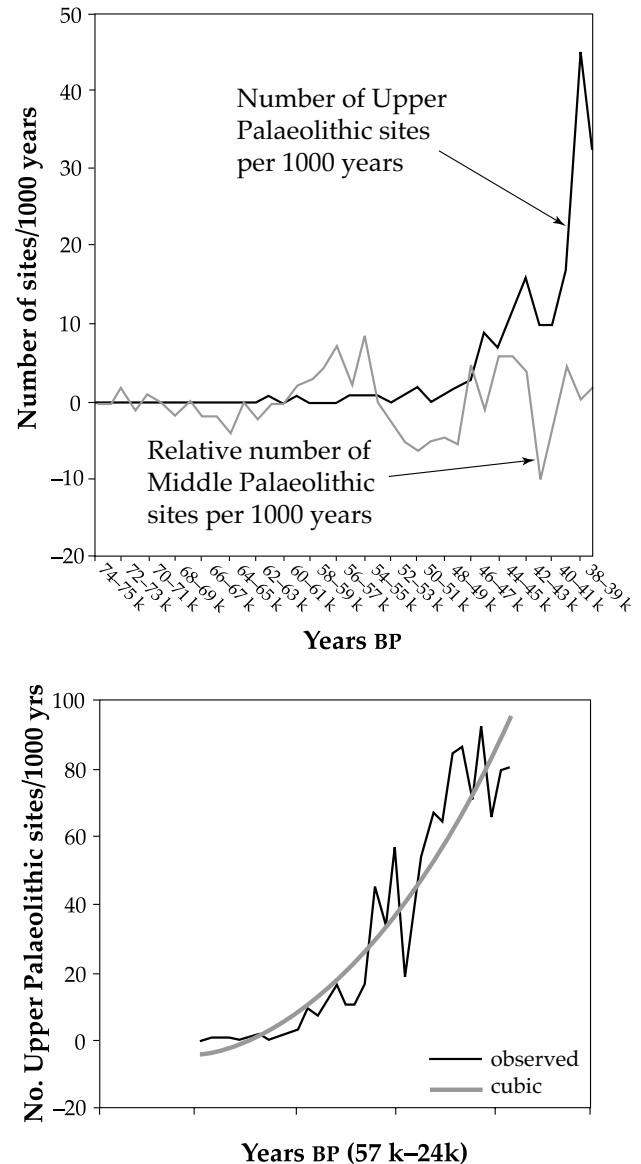
We also examined whether the residual variance in number of sites during this period was related to the increase in the number of Upper Palaeolithic sites, but no such relationship was found ( $r^2 = 0.088$ ,  $p > 0.05$ ). Multiple regression analyses including both climatic variables and number of Upper Palaeolithic sites also failed to explain residual Middle Palaeolithic temporal distributions

#### *Upper Palaeolithic sites in Europe during Stage 3*

We carried out the same set of analyses on the Upper Palaeolithic data set. As mentioned before, although there are a few archaeological sites in Europe described as containing Upper Palaeolithic material culture before 48 ka BP, these really become an actual demonstrable demographic phenomenon after this date (Fig. 14.6). Again, cumulative increase through time is the primary relationship. A cubic positive relationship best explains mathematically the progressive increase in the numbers of Upper Palaeolithic sites in the period between 57 ka BP (when they are absent) and 24 ka. This is a highly significant relationship ( $F = 120.17894$ ,  $p < 0.0001$ ) that explains more than 88 per cent of the variance in the data ( $r^2 = 0.88164$ ).

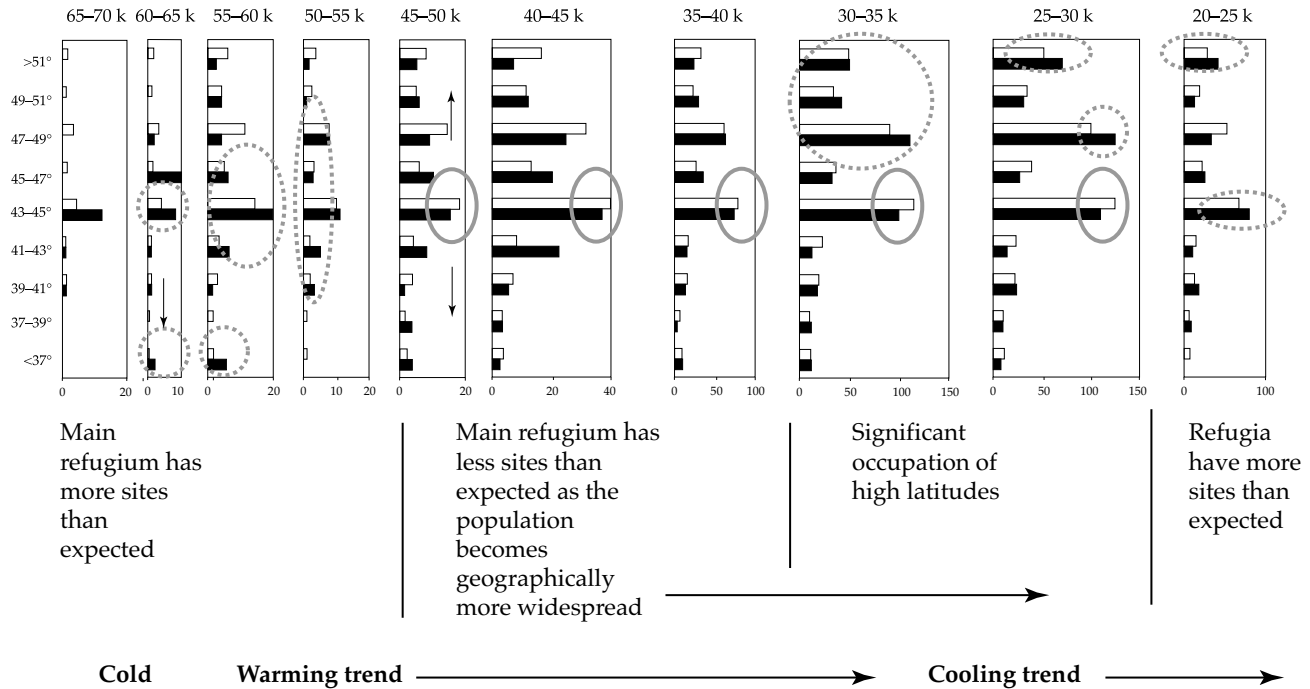
The analysis of the residual data fails to find any correlation with either the climatic variables ( $^{18}\text{O}$ :  $r^2 = 0.03$ ,  $p > 0.05$ ;  $\text{neg}^{18}\text{O}$ :  $r^2 = 0.053$ ,  $p > 0.05$ ;  $\text{pos}^{18}\text{O}$ :  $r^2 = 0.114$ ,  $p > 0.05$ ;  $\text{amp}^{18}\text{O}$ :  $r^2 = 10.193$ ,  $p > 0.05$ ), or with the total or partial residual data of number of Middle Palaeolithic sites through time (with Middle Palaeolithic residuals:  $r^2 = 0.104$ ,  $p > 0.05$ ; with Middle Palaeolithic residuals up to 37 ka BP:  $r^2 = 0.245$ ,  $p > 0.05$ ; with Middle Palaeolithic residuals from 37 ka BP:  $r^2 = 0.111$ ,  $p > 0.05$ ).

We also examined the data to see whether any climatic effects are lagged due to the time it takes a population to respond. Neither the actual number of



**Figure 14.6.** Number of Upper Palaeolithic sites over time, compared to the residual values of Middle Palaeolithic sites (top). Upper Palaeolithic sites increase over time after 57 following a cubic pattern (bottom).

sites, however, nor residual number of sites through time, correlate with lagged  $^{18}\text{O}$  values by 1000 years, or with the difference in  $^{18}\text{O}$  values from 1000-year period to the next. There is, however, a weak relationship between categories of difference between  $\delta^{18}\text{O}$  values (i.e. whether the difference in  $^{18}\text{O}$  values from one 1000-year period to the next was less than  $-0.5$ , between  $-0.5$  and  $+0.5$ , and greater than  $0.5$ ) and the total ( $F = 3.613$ ,  $p < 0.05$ ) and residual ( $F = 3.610$ ,  $p < 0.05$ ) number of Middle Palaeolithic sites.



**Figure 14.7.** Expected and observed numbers of archaeological sites for different phases of Stage 3. The vertical axes on the graphs show latitudinal bands, and the horizontal axes the percentage of archaeological sites at each of those bands. The graphs show successive chronological periods, from earlier to younger. The white bars on the histograms are expected numbers of sites based on the total archaeological distribution; the black bars are the observed number. According to the hypothesis (see text), observed sites should exceed expected in the preferred refugia during cold periods, and expected should exceed observed in the expansion zones during cold periods. In warmer periods this should be reversed. The data shown support this hypothesis.

In other words, a very high degree of climatic change did have some, albeit very small, effect on numbers of Middle Palaeolithic sites. As before, we observed that the number of Middle Palaeolithic sites in Europe was weakly affected by departures from climatic stability.

All analyses were repeated at 3000-year units (not shown), and a similar lack of association between archaeological demography and climatic change was observed.

## Discussion and conclusions

*The role of climate in modern human Eurasian dispersals*  
The analyses presented above, as well as those in other parts of this book (Chapter 4: van Andel *et al.* 2003b; Chapter 8: Davies & Gollop 2003) suggest that although it is clearly the case that Europe was colonized by modern humans during a period that was warmer than either the preceding Stage 4, or the succeeding Stage 2, and therefore broadly consistent with a model of Eurasian expansions associated with

warmer climates, nonetheless the data do not fit the general evolutionary model when applied at this high resolution level.

There are a number of methodological reasons why this may be the observed result. The obvious ones relate to the nature of the archaeological record and date-based data sets (Housley *et al.* 1997; Chapter 3: van Andel *et al.* 2003a). The archaeological record is far from perfect, with taphonomic distortions occurring at all levels. It may therefore be that the results described are a sampling artefact. Furthermore, the early periods of Stage 3 are notoriously difficult to date, and the later periods are subject to calibration problems that have yet to be resolved. Again, therefore, the results may be an artefact. In addition it could also be the case that the resolution of the archaeological data set simply does not meet that of the climatic record.

More subtly, it could be that there are strong geographical patterns in the data which have not been explored here, and these are masked by the total sample (see Chapter 8: Davies & Gollop 2003).

Finally, the analyses here use raw data, rather than smoothed time series, which may be a means of revealing hidden patterns.

While all these may be factors that explain the results, and are certainly worth further investigation, nonetheless if the observed patterns are not artefacts of the data and analyses, it is necessary to consider what their interpretation could be in terms of the early European dispersals of modern humans. Why might both the expansion of modern humans and the decline of the Neanderthals not be associated strongly with the fine-grained climatic changes of Stage 3?

The answer may lie in the interaction between the behaviour of the hominins and the geographical patterns. Let us suppose that in warmer periods hominin populations increase and so expand, resulting in dispersals into Europe, and further within Europe dispersals. When conditions become more difficult, those populations contract and either survive in a few refugia, or else become extinct. When conditions become better then, there will again be expansions out of any refugia. This, in effect is the evolutionary geography model described at the outset. However, the archaeological signature of this process will not be simple. These areas where there were refugia will show a relatively constant presence of humans, while only in those areas where humans could survive only in relatively warm conditions would there be a signal of flux and fragile, temporary populations. The overall signal of such flux would therefore be smothered by the 'noise' from the refugia.

We tested this hypothesis by considering the distribution of archaeological sites in latitudinal sections in Western Europe (Fig. 14.7). Using the archaeological data base (up to +10° longitude), the expected number of sites per latitudinal unit (2° units) for 5000-year periods between 70–20 ka BP was calculated. This was then compared to the observed number of sites. The data support the proposal that there is indeed a refugium where site numbers are greater than expected during colder phases, and lower than expected during warmer phases. Secondary refugia can also be identified. Conversely, areas that have few or no sites during colder periods have higher than expected numbers during the warmer periods. A  $X^2$  test showed that there is a significant difference between expected and observed sites at each latitude during 5000-year intervals ( $X^2 = 236.45$ ,  $p < 0.001$ ). This was the case whether all sites were treated together, or whether modern humans and Neanderthals were treated separately. The refugium

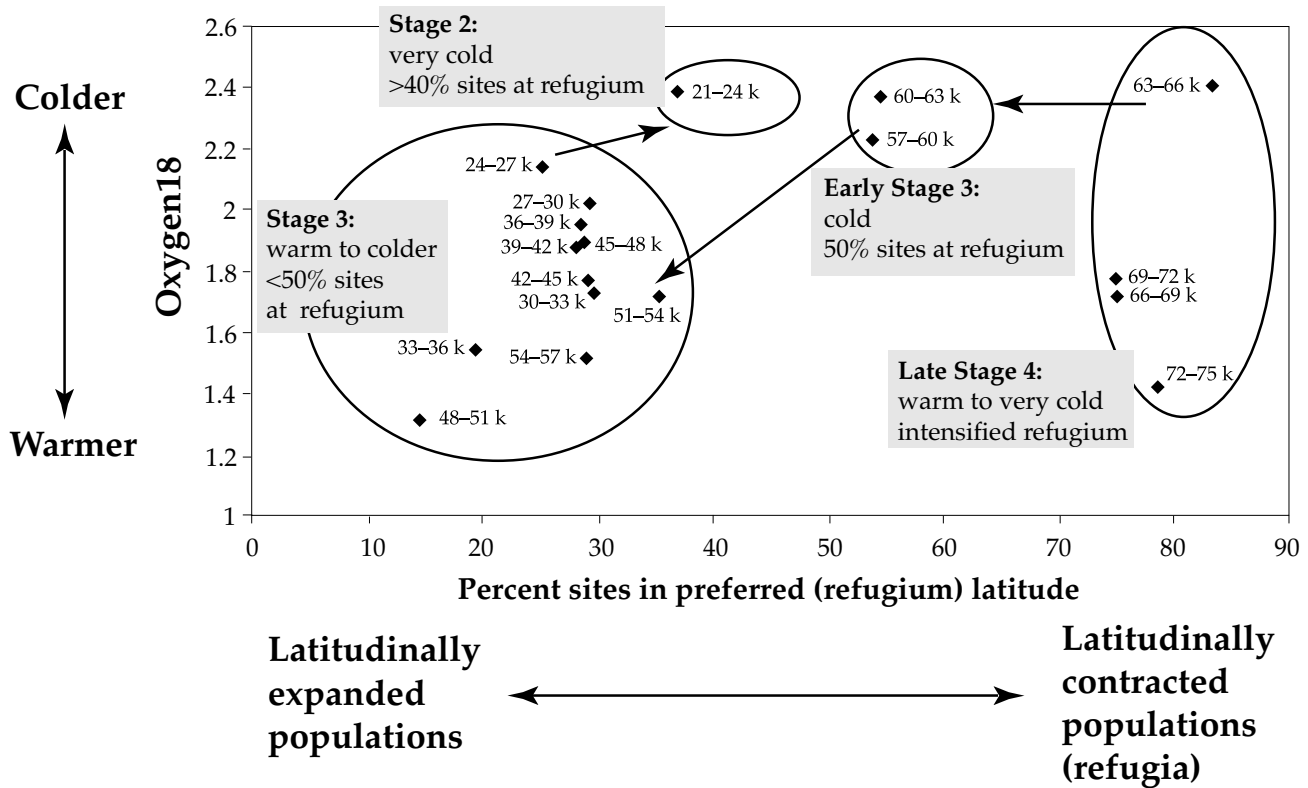
zone lies in the latitude 43–45°, which is consistent with the view that the southwest of France was an area where populations could be sustained during colder periods.

The link between human population history and the dynamism of the Stage 3 environment is thus complex, and is at least partially explicable in the context of a model of flux and fragility of hominin demography, and in the context of populations being confined to refugia in colder periods and expanding in warmer periods, thus giving rise to separate archaeological signatures. The various periods of Stage 3 can thus be categorized in terms of the percentage of archaeological sites confined to particular latitudes, and this can be related to time and temperature. Figure 14.8 shows that the end of Stage 4 has a high percentage of sites in the preferred latitudinal zones of the refugia; the bulk of Stage 3 shows a decline in that percentage, with a return towards a tighter latitudinal banding in Stage 2. The fact that it did not return to levels seen in Stage 4, however, may indicate the difference in adaptive tolerance of modern humans compared to Neanderthals.

To this more complex model, with its recognition of the difference between refugia and expansion zones, a further important idea can be added. When looked at in the broad context of human evolution in the Pleistocene, it appears more probable that hominins did not survive in many refugia during glacial periods, and therefore the signal of the Pleistocene dispersals is stronger. Two things, however, make the period of Stage 3 more complex. The first is that the climate itself seems to have been less extreme, probably allowing more refugia to retain populations. And second, the adaptations of both modern humans and Neanderthals may have been such as to allow them to be more buffered to these changes than was the case for earlier hominins such as *Homo heidelbergensis* and *Homo erectus/ergaster* (see Chapter 13: Stringer *et al.* 2003 for a discussion). Much has been made of differences between Neanderthals and modern humans, and indeed there must have been major adaptive differences, but these analyses show that there is also an overarching similarity in direction if not intensity of demographic response among all later Pleistocene hominins in Europe.

#### *Integrating genetic evidence*

Given the difficulties in applying quantitative techniques to the analysis of archaeological data, it might be thought that the evolutionary genetics evidence



**Figure 14.8.** Percentage of sites in latitude 43–45°, the refugial band. In late Stage 4 the Neanderthals are confined to this latitude to a very large extent; both warming during Stage 3 and the arrival of modern humans reduces this compression effect. Climatic cooling in at the end of Stage 3 reverses this trend, presumably associated with changes in modern human distribution and the extinction of the Neanderthals. Numbers (k) refer to thousand-year time intervals.

may provide a better approach. Certainly recent research in this field has provided key insights into patterns of human dispersals, and the chronological and geographical resolution of these is improving all the time. At this stage, however, it is unlikely that genetic data can resolve the fine-grained questions about human–climate relationships prompted by the results of the Stage 3 Project. While the resolution on chronometric estimates of archaeological and fossil data during Stage 3 might typically have confidence limits of approximately  $\pm 1500$  years, the confidence limits for coalescence estimates and for the age of demographic expansions might be in excess of 5000 years. In other words, while we might be comfortable in placing the earliest genetically-observable demographic expansion of humans in Europe at around 50,000 years ago (as a maximum estimate), in practice this is actually an estimate lying between 60,000 and 40,000 years ago. Phylogeographic methods can generate important hypotheses about possible correlations with the archaeological record (see for example Underhill *et al.* 2001), but they cannot be

used to test detailed chronological hypotheses.

#### Conclusions

In recent years both palaeoanthropologists and evolutionary geneticists have converged on a model of later human evolution in which dispersals, initially from Africa, but also more generally, are seen as a major mechanism for evolutionary change. As we have discussed here, this model is also consistent with the way in which evolutionary biologists have been thinking about processes of change. While genetics offers important insights into the history of human distribution and demography, at present it does not have the resolution to link events to the fine-grained environmental record available.

Multi-disciplinary approaches, such as the Stage 3 Project, offer a way forward. We have shown here that the relatively warmer environments of the Stage 3 phase of the last glacial fit a general model of hominin population expansions in relation to climatic change. Nonetheless it is currently not possible to show that such expansions were fine-tuned to

the climatic variability of the time. In general terms, it is possible to show that both modern humans and Neanderthals had the capacity to cope better with colder environments than their predecessors, and thus appear to be buffered in some ways. This supports the ideas developed elsewhere in this volume of the importance of refugia in maintaining population continuity through time and promoting intense competitive circumstances. Further work, however, is necessary to be able to discriminate statistically the demography of refuge areas and expansion zones.

Finally, we have attempted in this paper to exploit the high level of inter-disciplinarity and the development of quantified data bases that have been promoted by the Stage 3 Project. As palaeoanthropology matures, we can expect not just better and better resolution in the environmental, chronological and archaeological data, but also a response on the part of palaeoanthropologists to use quantitative techniques and formal models to analyze evolutionary issues.

### Acknowledgements

We thank Tjeerd van Andel for his invitation to be part of the Stage 3 Project, the wonderful dinners and discussions that it fostered, and the members of the project for stimulating our interest in this multi-disciplinary endeavour. We particularly thank William Davies for access to the archaeological data base, and for advice and help with its analysis. Clive Gamble read and commented on an earlier draft of this paper.

### References

- Barron, E. & D. Pollard, 2002. High-resolution climate simulations of Oxygen Isotope Stage 3 in Europe. *Quaternary Research* 58, 296–309.
- Barron, E., T.H. van Andel & D. Pollard, 2003. Glacial environments II: reconstructing the climate of Europe in the Last Glaciation, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 5, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 57–78.
- Davies, W. & P. Gollup, 2003. The human presence in Europe during the Last Glacial Period II: climate tolerance and climate preferences of mid- and late glacial hominids, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 8, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 131–46.
- Denys, C., 1985. Palaeoenvironmental and paleobiogeographical significance of the fossil rodent assemblages of Laetoli (Pliocene, Tanzania). *Palaeogeography Palaeoclimatology Palaeoecology* 52, 77–97.
- Foley, R.A., 1999. The evolutionary geography of Pliocene hominids, in *African Biogeography, Climatic Change, and Hominid Evolution*, eds. T. Bromage & F. Schrenk. Oxford: Oxford University Press, 328–48.
- Foley, R.A. & M.M. Lahr, 1997. Mode 3 technologies and the evolution of modern humans. *Cambridge Archaeological Journal* 7(1), 3–36.
- Foley, R.A. & M.M. Lahr, in press. Flux and fragility: demographic models and the relationships between Eurasian and African Late Pleistocene hominins, in *Biogeography and Neanderthal Evolution*, ed. C. Finlayson.
- Gamble, C., 1993. *Timewalkers*. London: Allen Lane.
- Housley, R.A., C. Gamble, M. Street & P. Pettitt, 1997. Radiocarbon evidence for the late glacial recolonisation of northern Europe. *Proceedings of the Prehistoric Society* 63, 25–54.
- Huntley, B. & J.R. Allen, 2003. Glacial environments III: palaeo-vegetation patterns in Late Glacial Europe, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 6, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 79–102.
- Ingman, M., H. Kaessmann, S. Paäbo & U. Gyllensten, 2000. Mitochondrial genome variation and the origin of modern humans. *Nature* 408, 708–13.
- Ke, Y.H., B. Su, X.F. Song, D.R. Lu, L.F. Chen, H.Y. Li, C.J. Qi, S. Marzuki, R. Deka, P. Underhill, C.J. Xiao, M. Shriver, J. Lell, D. Wallace, R.S. Wells, M. Seielstad, P. Oefner, D.L. Zhu, J.Z. Jin, W. Huang, R. Chakraborty, Z. Chen & L. Jin, 2001. African origin of modern humans in East Asia: A tale of 12,000 Y chromosomes. *Science* 292, 1151–3.
- Klein, R.G., 2000. Archeology and the evolution of human behavior. *Evolutionary Anthropology* 9, 17–36.
- Lahr, M.M. & R.A. Foley, 1994. Multiple dispersals and modern human origins. *Evolutionary Anthropology* 3, 48–60.
- Lahr, M.M. & R.A. Foley, 1998. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology* 41, 137–76.
- Loubere, P., 1988. Gradual Late Pliocene onset of glaciation: a deep-sea record from the northeast Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63, 327–34.
- Malatesta, A. & F. Zarlenga, 1988. Evidence of Middle Pleistocene marine transgressions along the Mediterranean coast. *Palaeogeography, Palaeoclimatology, Palaeoecology* 68, 311–15.
- Quintana-Murci, L., R. Veitia, S. Santachiara-Benerecetti, K. McElreavey, M. Fellous & T. Bourgeron, 1999. Mitochondrial DNA, Y chromosome and human population history. *M S-Medicine Sciences* 15, 974–82.

- Roberts, R.G., R. Jones, N.A. Spooner, M.J. Head, A.S. Murray & M.A. Smith, 1994. The human colonisation of Australia: optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. *Quaternary Science Reviews* 13, 575–86.
- Shackleton, N.J., 1987. Oxygen isotopes, ice volumes, and sea level. *Quaternary Science Review* 6, 183–90.
- Shackleton, N.J., 1996. New data on the evolution of Pliocene climatic variability, in *Palaeoclimate and Neogene Evolution*, ed. E. Vrba. New Haven (CT): Yale University Press, 282–90.
- Shackleton, N.J., M.A. Hall & E. Vincent, 2000. Phase relationships between millennial scale events 64,000 to 24,000 years ago. *Paleoceanography* 15, 565–9.
- Stringer, C., 2002. Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 357, 563–79.
- Stringer, C. & P. Andrews, 1988. Genetic and fossil evidence for the origin of modern humans. *Science* 239, 1263–8.
- Stringer, C. & C. Gamble, 1993. *In Search of the Neanderthals*. London: Thames and Hudson.
- Stringer, C., H. Päälike, T.H. van Andel, B. Huntley, P. Valdes & J.R.M. Allen, 2003. Climatic stress and the extinction of the Neanderthals, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 13, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 233–40.
- Tchernov, E., 1992a. Biochronology, paleoecology and dispersal events of hominids in the southern Levant, in *The Evolution and Dispersal of Modern Humans in Asia*, eds. T. Akazawa, K. Aoki & T. Kimura. Tokyo: Hokusen-sha Publ. Co., 149–88.
- Tchernov, E., 1992b. Eurasian-African biotic exchanges through the Levantine corridor during the Neogene and Quaternary. *Courier Forschungsinstitut Senckenberg* 153, 103–23.
- Torroni, A., M. Richards, V. Macaulay, P. Forster, R. Villems, S. Norby, M.L. Savontaus, K. Huoponen, R. Scozzari & H.-J. Bandelt, 2000. MtDNA haplogroups and frequency patterns in Europe. *American Journal of Human Genetics* 66, 1173–7.
- Underhill, P.A., G. Passarino, A.A. Lin, P. Shen, M.M. Lahr, R.A. Foley, P.J. Ofner & L.L. Cavalli-Sforza, 2001. The phylogeography of Y chromosome binary haplotypes and the origins of modern human populations. *Annals of Human Genetics* 65, 43–62.
- van Andel, T.H., 2002. The climate and landscape of the middle part of the Weichselian glaciation in Europe: The Stage 3 Project. *Quaternary Research* 57, 2–8.
- van Andel, T.H., 2003. Glacial environments I: the Weichselian climate in Europe between the end of the OIS-5 interglacial and the Last Glacial Maximum, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 2, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 9–20.
- van Andel, T.H., W. Davies, B. Weninger & O. Jöris, 2003a. Archaeological dates as proxies for the spatial and temporal human presence in Europe: a discourse on the method, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 3, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 21–30.
- van Andel, T.H., W. Davies & B. Weninger, 2003b. The human presence in Europe during the Last Glacial period I: human migrations and the changing climate, in *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, Chapter 4, eds. T.H. van Andel & W. Davies. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 31–56.
- van Valen, L., 1973. A new evolutionary law. *Evolutionary Theory* 1, 1–30.
- Vrba, E., 1993. Turnover-Pulses, the Red Queen, and related topics. *American Journal of Science* 293A, 418–52.
- Vrba, E., 1996. *Palaeoclimate and Neogene Evolution*. New Haven (CT): Yale University Press.
- Watson, E., P. Forster, M. Richards, & H.-J. Bandelt, 1997. Mitochondrial footprints of human expansions in Africa. *American Journal of Human Genetics* 61, 691–704.
- White, T.D., B. Asfaw, D. DeGusta, H. Gilbert, G.D. Richards, G. Suwa & F.C. Howell, 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423, 742–7.