



Population Kinetics in the Upper Palaeolithic in Western Europe

Jean-Pierre Bocquet-Appel

CNRS UPR 2147, 44 rue de l'Amiral Mouchez, 75014 Paris, France

Pierre-Yves Demars

Institut de Préhistoire et de Géologie du Quaternaire, Université Bordeaux, 1 Avenue des Facultés, 33405 Talence Cedex, France

(Received 12 December 1998, revised manuscript accepted 31 May 1999)

After 40 kyr BP, the distribution of archaeological sites shows that the occupation of the western-European peninsula, at the north of the Alpine arc, has the appearance of nodes of concentration, separated by vast zones which are either empty or with a negligible population density. The populational kinetics of the hunter-gatherers in this vast area is characterized by the permanence of a refuge zone located in northern Aquitaine. The leptokurtic aspect of the density distributions of sites observed from the Aurignacian to the Glacial Maximum but not at the Magdalenian suggest occasional long distance movement such as raids or opportunistic expeditions. During the Glacial Maximum, the response to the cold is marked by the complete abandonment of the northern peripheral zone, a contraction of the population mainly on the first peripheral zone surrounding the refuge zone, but without geographical change of position of the refuge zone. An optimistic estimate of the meta-population size of hunter-gatherers, which takes into account the change of area size due to the sea level variation, goes from the Aurignacian, 4000, to the Glacial Maximum 8000. During the Magdalenian a demographic explosion occurred with 40,000 individuals. © 2000 Academic Press

Keywords: UPPER PALAEOOLITHIC DEMOGRAPHY, PALAEODEMOGRAPHY, HUNTER-GATHERERS, WESTERN EUROPE.

Introduction

For a long time the demography of the populations of the Upper Palaeolithic in Europe has interested prehistorians (Nougier, 1959; Bordes, 1968; David, 1973; Bailey, 1983; Biraben, 1988; Rozoy, 1989). They have, thus, underlined very great inequalities of chronological and geographical distributions of archaeological sites. They have also detected a “demographic explosion” during the Magdalenian as well as a clear concentration of the sites in northern Aquitaine (Nougier, 1959; Bordes, 1968; Sonnevile-Bordes, 1973; Jochim, 1983; Rozoy, 1989). By environmental analogy with sub-actual societies of subarctic hunter-gatherers, these researchers estimated that the demographic density of the Palaeolithic hunter-gatherers may have been very low, in the order of two to ten inhabitants per 100 km² (Nougier, 1959; Bordes, 1968; Rozoy, 1989). In this article, we propose a demographic interpretation of the geographical and chronological distributions of several hundred archaeological sites, centred on the European western peninsula. The distribution of sites can be repre-

sented, demographically, in the form of distributions of densities and profiles of increased rates in different areas subdividing the western European peninsula. These distributions and profiles represent the traces of an Upper Palaeolithic meta-population of hunter-gatherers. The Palaeolithic settlements proceeded within a glacial-interglacial cyclic climatic framework, in the order of 125 kyr (Webb III & Bartlein, 1992). For the local populations that make up the meta-population, what are the consequences of this macro constraint and those of its relaxation on the spatial distribution of: (1) their densities, and (2) their increase rate? We will compare the distributions of density simulated under certain conditions of long distance migrations (Hewitt, 1996) with the populational traces left by hunter-gatherers of the Upper Palaeolithic in a homogeneous geographical area, on a continental scale. This area is represented by a corridor, which forms the large European northern plain north of the alpine arc. Which settlement scenario do these traces produce? Was this settlement uniformly distributed as suggested by the stepping stone model in population genetics? Or was it concentrated in refuge zones

(Jochim, 1983, 1987)? Subjected to a very strong ice advance and then its retreat, would the traces left by a meta-population of hunter-gatherers for nearly 30 kyr, allow the reconstruction of its populational kinetics, or would they produce a scrambled image? We will also discuss recurring problems in archaeological demography such as the quality of sampling (never sufficient) and the uniformitarian assumption (always bold). Are the number of caves that have produced archaeological remains a sample of density of a past population? Can one provide demographic estimates for Palaeolithic populations of hunter-gatherers by using ethnographic groups of reference?

Data

Geographical grid and chronological subdivisions

For reasons of geographical, ecological and archaeological homogeneity set out below, the data base is focused on the area formed by the Western-European peninsula, at the North of the alpine arc. The data were extracted from the maximum number of publications describing the Upper Palaeolithic sites. The location of the sites were generally given at the scale of the administrative unit, like the department, the province, the district, etc. (Demars, 1996, 1998). This scale determines a grid of the present Western Europe (approximately $1138.2 \times 100 \text{ km}^2$, excluding Ireland, Scotland and the Scandinavian countries) whose mesh is approximately 5000 to 10,000 km^2 . The currently immersed areas of the continental shelf are absent, which could have been occupied when the marine level was lower. It is difficult to evaluate the number of sites that have since disappeared. However, given the current distribution of the sites and the topography of the various littoral zones, it may be supposed that this number would be relatively low, except for the Tardiglaciaire where one perceives a distributional continuity between the sites localised in Great Britain and those of the continent (see Figure 1). In this article, a site represents the geographical location of a lithic industry, whatever its local quantity. The chronostratigraphy of lithic industries of the Upper Palaeolithic was used to make a chronological subdivision. The first industries of the Upper Palaeolithic were excluded (Chatelperronian, Szeletian) which are most probably the product of the Neanderthals having acculturated the mode of laminar cutting (Demars & Hublin, 1989). Four chronological periods were distinguished:

- (1) "Aurignacian", 40–29 kyr BP approx., with Protoaurignacians;
- (2) "Gravettian", 29–22 kyr BP approx.;
- (3) "Glacial Maximum" (or "lower Magdalenian"), 22–16.5 kyr BP approx., with the Solutrean on the Atlantic side;
- (4) "Magdalenian", 16.5–11.5 kyr BP approx., with the middle Magdalenian, upper and final, on the

Atlantic side; Magdalenian, Hambourgian and Creswellian (or the oldest part according to certain authors) in the northwest of Europe.

Relative to the temporal scale used this chronology rests on the assumption of rapid diffusions of the technical cultural traits for the hunter-gatherers (Leroi-Gourhan, 1943; Elkin, 1967; Mulvaney, 1976). When only one technical tradition covered all of Europe (Aurignacian, Gravettian), one would think that its speed of diffusion should not have been more than one century and was probably even much shorter. This is a very small duration compared to our time scale. When two technical traditions divided Europe (Glacial Maximum, Magdalenian), the absolute datings show shifts, for instance between the passage from Badegoulian to Magdalenian on the Atlantic side (roughly 16.5 kyr BP) and the passage from Lower to Upper Epigravettian (roughly 15.5 kyr BP). There can thus be differences of dating between the typological chronology and the real one. However, such differences do not seem to exceed 1 kyr, which is not negligible, but does not basically modify the geographical distributions.

Three sampling biases might exist: (1) an erroneous typological classification of prehistoric industries, (2) an imperfect geographical sampling for the site distributions, and (3) the influence of archaeological localism. We shall discuss these briefly.

Errors of classifications. Typological errors of classification can exist, in particular when the studied tool sample of a site is small or comes from an old excavation. When we were obliged to choose between the opinions of two or several authors, this was typically from the most recent publication.

Imperfect geographical sampling. Does the geographical distribution of the sites reflect the intensity of archaeological prospects in those areas? Prehistoric archaeology was born during the mid-nineteenth century in Europe. Since Lartet and Christy's work in 1860, the lower valley of Vézère remains the area having by far the greatest number of sites in Europe and the majority of the most important among them. In a century and a half no new discovery has fundamentally changed the distribution of sites of the Upper Palaeolithic of this continent. Recent discoveries have made it possible to better specify the settlement of an area but the basic patterns of distributions have not changed since early work (Mortillet, 1900).

Archaeological localism influence. The location of the geographical field of study of one of the authors (PYD) and/or that of his laboratory—both in Aquitaine—might be the cause of a sampling bias. The list of sites forming the data base used here does not differ significantly from others obtained by international teams (Oakley, 1971; Leroi-Gourhan, 1988; Orban, 1988, 1990, 1991; Gambier & Houet, 1993).

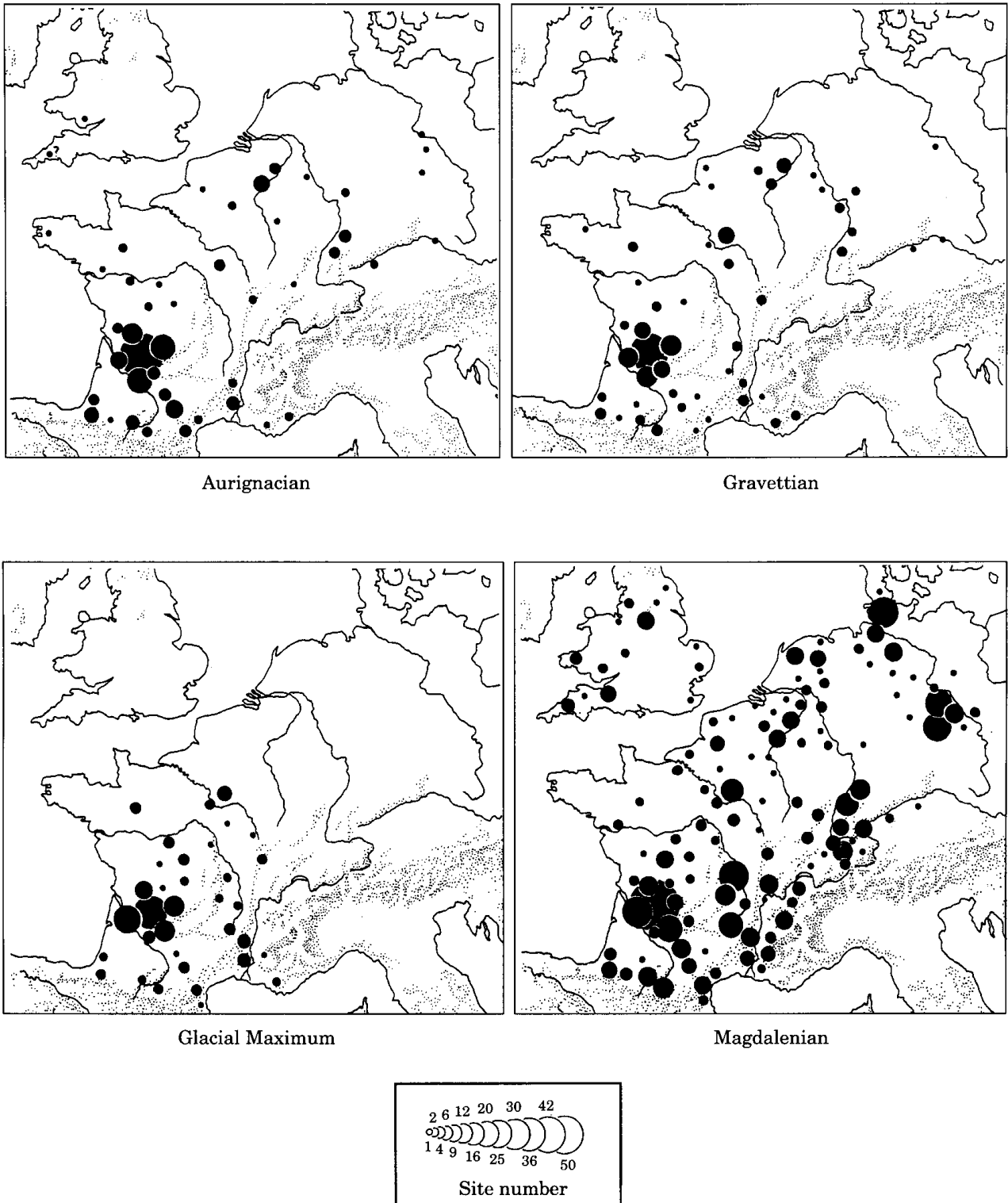


Figure 1. Geographical distribution of the sites in the western-European half-corridor, in the north of the alpine arc, during Aurignacian, Gravettian, Glacial Maximum and Magdalenian.

Distributions in the Western-European Peninsula

Figure 1 presents the geographical distributions in the western-European peninsula above the alpine arc for the four chronological periods. We will first describe them generally and then individually.

Adding the periods together, one can distinguish three areas of site concentration which lasted nearly 30 kyr. They are, in order of importance:

- (1) Northern Aquitaine and particularly the north-east;
- (2) Pyrenees (along with Cantabrie and Catalonia, which are just outside the border map used here);

(3) Belgium Wallone, especially along the Meuse valley.

Between these three concentration areas sites are spread more or less evenly, with weak regroupings (Bade-Wurtemberg, south of the Paris basi, South of France). The plains of northern Europe are empty. The northern latitudinal limit of occupation, at approximately 52°, is marked by the sites of Paviland (Wales of the south) and Hermannhöle (Saxony).

Aurignacian

The distribution of sites here is very uneven, with areas having high (North Aquitaine), average (Pyrenees, Belgium wallone), or small concentrations, and areas where sites are absent or very rare (northern plains).

Gravettian

The distribution pattern here is similar to that of the Aurignacian (see also Otte, 1981). Northern Aquitaine remains by far the densest area. Other areas present smaller concentrations (Belgium wallone, Pyrenees), while others remain empty (European plains beyond the latitude of 52° marked by Bilzingsleben; Montet White, 1996).

Glacial Maximum

Sites disappear from northern and central Europe in the north of the alpine arc. Only some rare sites remain, whose chronological position is dubious. However, in the northwest of the Mediterranean coast and on the Atlantic front there is a strong density of sites. Northern Aquitaine accounts for about half of these sites (136/219). As for the previous periods, the Pyrenean area may be distinguished (11/219). On the Mediterranean littoral one observes many regroupings.

Magdalenian

This period greatly extends the area of occupation as well as multiplying the number of sites. These are geographically distributed in a way that is much more regular than during the previous periods. Northern Aquitaine remains the area with the highest concentration, with 194/772 sites. Two concentration areas of the Aurignacian and Gravettian that has disappeared during the Glacial Maximum reappear but with a lower density [Belgium wallone (26/772)]. The Pyrenean axis, which was the equivalent in density of northern Aquitaine during the previous period, has 35/772 sites. New concentration areas, which did not exist before, appear. There are two very distinct phenomena: (1) sites that appear in areas of average mountains and foothills [the Pyrenees, in high altitude; the Central Massif (45/772); the Jura-Dauphinee (44/772)]; and (2) an extension of the occupation area towards the northern plains of Europe so far unoccupied [Paris basin; Great Britain (45/772); the North of

Germany and the Netherlands (Hambourgian: 91/772), Saxony-Thuringe (65/772)].

Glacial Constraints and Demodynamics of a Natural Meta-population

Before analysing the archaeological data, the consequences of glacial–interglacial cyclic mechanisms on demography of a natural meta-population should be remembered (for the genetic dynamics see Hewitt, 1994, 1996).

The habitat area of a meta-population is made up of local populations, those located at the centre and those on its periphery. Under the influence of macro-climatic fluctuations, such as glaciation (which we consider to come from the north) and deglaciation, the habitat area will move in directions which depend on the topography and vegetation. During glaciation, if the geographical space is unbounded, the habitat area will slip latitudinally towards the south. If the space is bounded by a geographical obstacle, the habitat area will contract on the topographically southern bound. During deglaciation, the habitat area will expand towards the northern latitudes, correlating with the glacial withdrawal. For the meta-population, the different movements of its habitat area will determine migrations on a front of contraction of (re)colonisation, beginning with the populations located at its periphery (Webb III & Bartlein, 1992). For the Palaeolithic hunter–gatherers, it may be surmised that the displacement velocity of these fronts of contraction or (re)colonisation depends on the displacement velocity of the front of the biomass of ungulates, which in turn is dependent on the displacement velocity of the front of the primary biomass. Its speed can be very fast, on the order of 50–500 m/year for vegetable species, observed around the Younger Dryas (Huntley & Birks, 1983; Huntley, 1990; Delpech, 1995). Recently, based on more than a hundred AMS radiocarbon datings, Housley *et al.* (1997) have given even higher estimates of the order of 500–2000 m/year, for the regional speeds of expansion of the hunter–gatherers during the recolonisation phase of Northern Europe at the end of the Glacial Maximum. In a front of contraction, the rate of increase is negative, determined mainly by the importance of the emigration (mortality+emigration > birth+immigration) along with, as shown below, by acute crises of mortality. On a front of (re)colonisation the rate of increase is positive, mainly determined by immigration. At the centre, the groups that have been established for a long time have their size correlated with the carrying capacity of the regional environment. Their rates of increase are thus practically null; they are those of replacement dynamics (Hewitt, 1996). As far as redistributions are concerned, Hewitt (1996) shows by simulations that the long distance migrations of a front of (re)colonisation generates leptokurtic distributions (unimodal, with only one more or less

lengthened tail, directed towards the zone of (re)colonisation). The distributions of densities of a front of bounded contraction were not simulated but, by comparison with the process described above, one can logically deduce that they go in the opposite direction: they are as little leptokurtic as the geographical contraction is important. This can be explained by the influence of the emigration. The trend of migratory movements, then, will no longer be turned towards the outside of the habitat area as during a recolonisation, but inward towards the zones already occupied (and crowded) by the populations that are more geographically central. Gamble (1993) has translated the process of contraction re-expansion into anthropological terms, by dividing it nicely into downturn, refuge and upturn phase. He puts forward the assumption that the sociological effects of the populational contraction on the refuge zone were those of social reorganisation, based on negotiations along different alliance networks (Gamble, 1993: 49). Housley *et al.* (1997) have refined the three-phase process by further dividing the upturn into a pioneer and a residential phase.

On a north-south geographical transect, the traces of a phenomenon of contraction-(re)colonisation of a meta-population can thus be perceived through the geographical distributions of two demographic variables expressing both the same underlying populational phenomenon: densities and rates of increase. What resembled these two distributions for populations of hunter-gatherers of the Upper Palaeolithic? That is now examined in the corridor formed by the large European northern plain in the North of the alpine arc.

An Area of Contraction-(Re)colonisation During the Upper Palaeolithic?

Geographical device: a half-corridor

Delpech (1998) has emphasised the role played by the large north-European plain: that of a migratory corridor for herds of ungulates. This corridor located north of the alpine arc is topographically opened in the East towards the north Caucasian steppes and is closed, in the West, by the Atlantic Ocean and the Pyrenean chain. During the cool interglacial this corridor constituted a very vast zone of habitat to the ungulate herds. During ice advancements the corridor was narrowed. Aquitaine, located within the southwestern lower limit of this corridor, was then transformed into a cul-de-sac region for the population movements of ungulates in Europe, making a more or less impermeable bound to their habitat areas (Delpech, 1989, 1995). Correlatively, for the groups of hunter-gatherers following these ungulates, during the severe climatic periods this bounded area might have been used as a refuge (Jochim, 1983, 1987; Soffer & Gamble, 1990; Hewitt, 1996), as shown by the geographical distributions (Figure 1). Conversely, during warm stages, it might

have also been used as a starting point for (re)colonisation movements (see also: Dolukhanov, 1979; Allain *et al.*, 1985; Desbrosses & Kozłowski, 1988; Gamble, 1993).

Thus, the scenario of a zone having been used as refuge then as a starting base may be tested by analysing the populational traces left by the groups of hunter-gatherers in this corridor during different periods of the Upper Palaeolithic. Since this vast corridor was geographically strangled in its northern part during the Glacial Maximum, probably even cut into two parts (Figure 1(c)), the area of analysis can be limited to its western half, i.e. to a half-corridor which corresponds today from east to west, to Germany and Great Britain, and France in the southwest. The axis of this half-corridor is in a northeastern/southwestern direction. From the statistical viewpoint, this vast area has been exploited archaeologically for more than a century and a half, producing probably relatively homogeneous sampling. In coherence with this scenario of contraction-expansion, the half-corridor described above was subdivided into three embodied areas, which successively determine a refuge zone, a primary zone, then a second peripheral zone, that we will, respectively, call A, B and C. Due to the existing administrative subdivisions, the three embodied areas, from the smallest (the refuge) to the largest, are successively the following ones: northern Aquitaine (zone A), current France (zones A and B), and the European northwestern peninsula, in the north of the alpine arc (Germany, Belgium, Denmark, France, England and Wales, Luxembourg, Netherlands; zones A, B and C). These three zones are represented in Figure 2. Scotland and Ireland were excluded because no Upper Palaeolithic site has ever been found with undisputed certainty.

During the Palaeolithic the zone sizes have changed, mainly in B and C. For demographic assessment reasons explained below, these zone sizes, for each time period, were estimated from palaeovegetation maps (Adams & Faure, 1997; Adams, 1997). For the Magdalenian and Glacial Maximum, the maps were taken at 14 and 18 kyr BP. They take into account sea level changes and the isostatic rebound of the Earth. For the two oldest periods, by analogy with the sea level (Webb III & Bartlein, 1992) in mid-periods of Gravettian (-80 m) and Aurignacian (-50 m), the maps were taken at 13 kyr and at 12-11 kyr BP, respectively. During the marine regressions, the northwest and southwest limits separating zones A and B were placed right on the corresponding latitudes. For all periods the northwest border between zones B and C was placed on the axis determined by the middle of the present day Channel. The maps used to estimate the zone sizes for the four chronological periods are shown in Figure 3.

The archaeological sites were generated in the area occupied by the biosphere, which we shall call viable areas, i.e. excluding that occupied by ice and polar

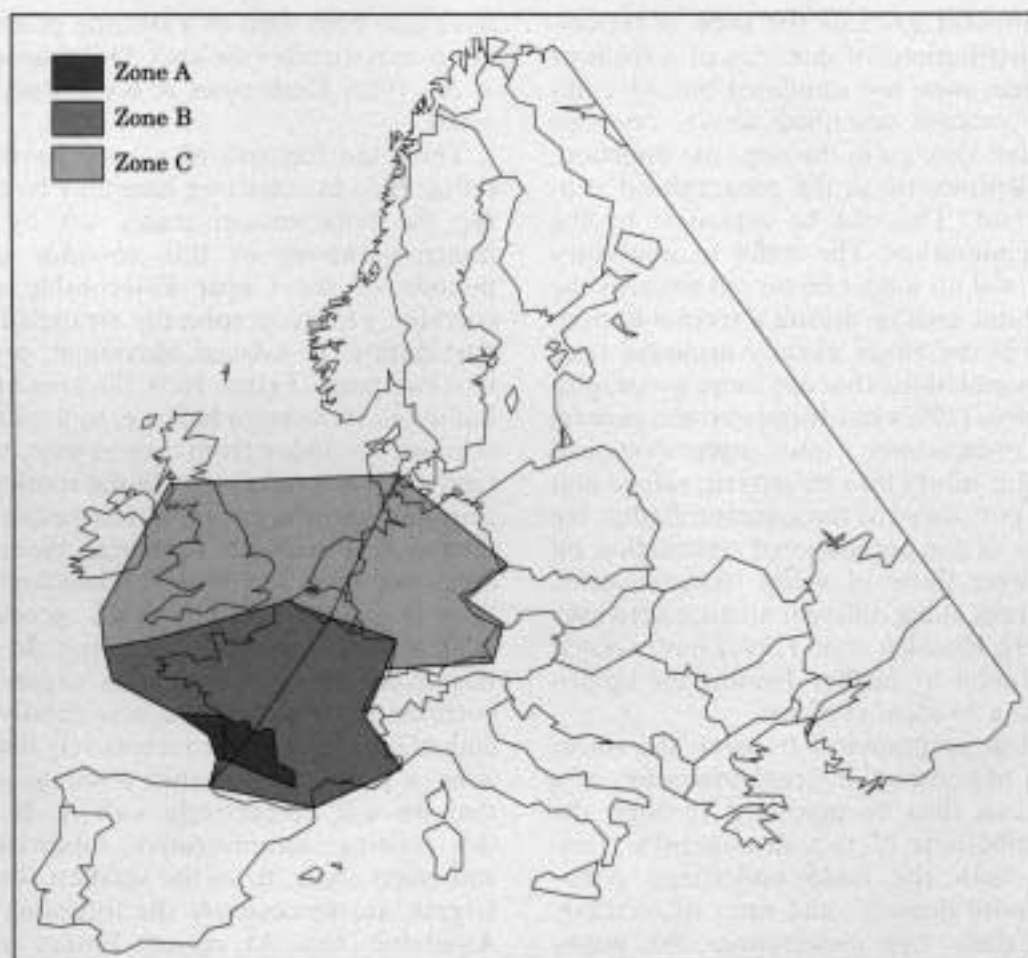


Figure 2. Three geographical zones (A, B, C) corresponding to the western-European half-corridor, in the north of the alpine arc. Note: a transect indicates the approximate centre of the different zones.

desert. During the Palaeolithic the size of the viable area changed. For estimates of density, it is necessary to distinguish the size of the viable area such as it was during a past period, and the surface size coinciding today with the past viable area, which we will call coinciding surface. For example, at the Glacial Maximum, the size of the viable area of zone C, taking into account the marine regression but excluding the surface occupied by the ice and the polar desert, covered roughly $2960 \times 100 \text{ km}^2$. However the coinciding surface (the original viable area minus the surface now occupied by the sea) is only $2450 \times 100 \text{ km}^2$. It is represented by a coastal strip in the south of England and by an area in continental Europe starting roughly from latitude 51° (broadly the limit of the past inhospitable area) to the French border, which delineates zone B. It is the size of the coinciding surface in each zone that may be considered as a sample of the past viable area, which is necessary to take into consideration for the calculation of the densities of the archaeological sites, and not the current zone size. However, this remains largely theoretical, since only zone C, at the Glacial Maximum, has a current zone size which is not equal to the size of the coinciding surface. But, as we shall see below, zone C has no archaeological sites during this period making its site density null. For the

three other periods, the size of the coinciding surface corresponds to the current zone sizes. Table 1 provides, by zone, the estimated sizes of the viable areas and their corresponding coinciding surfaces at the mid-periods of the four chronological subdivisions.

Demographic variables: density and rate of increase per zone for the archaeological sites

Two groups of data represent the geographical distribution of the sites. The first archaeologically distinguishes the caves and rock-shelters from open air sites (Demars, 1996), but it is restricted to the sites distributed in the area currently represented by France (zones A and B). It includes 1098 sites. This group will be called "two zone data". The second group does not make an archaeological distinction but includes all the sites in the half-corridor (zones A, B and C), which numbers 1451 sites. This second group will be called "three zone data". Tables 2 and 3 provide the geographical and chronological distributions, respectively, for the "two zone data" and "three zone data".

For the i -th zone ($i=A, B, C$) during the t -th chronological period, the density of the sites, D_{it} , is equal to the sites number n_{it} divided by the duration of the chronological period, d_t , and by the size of the

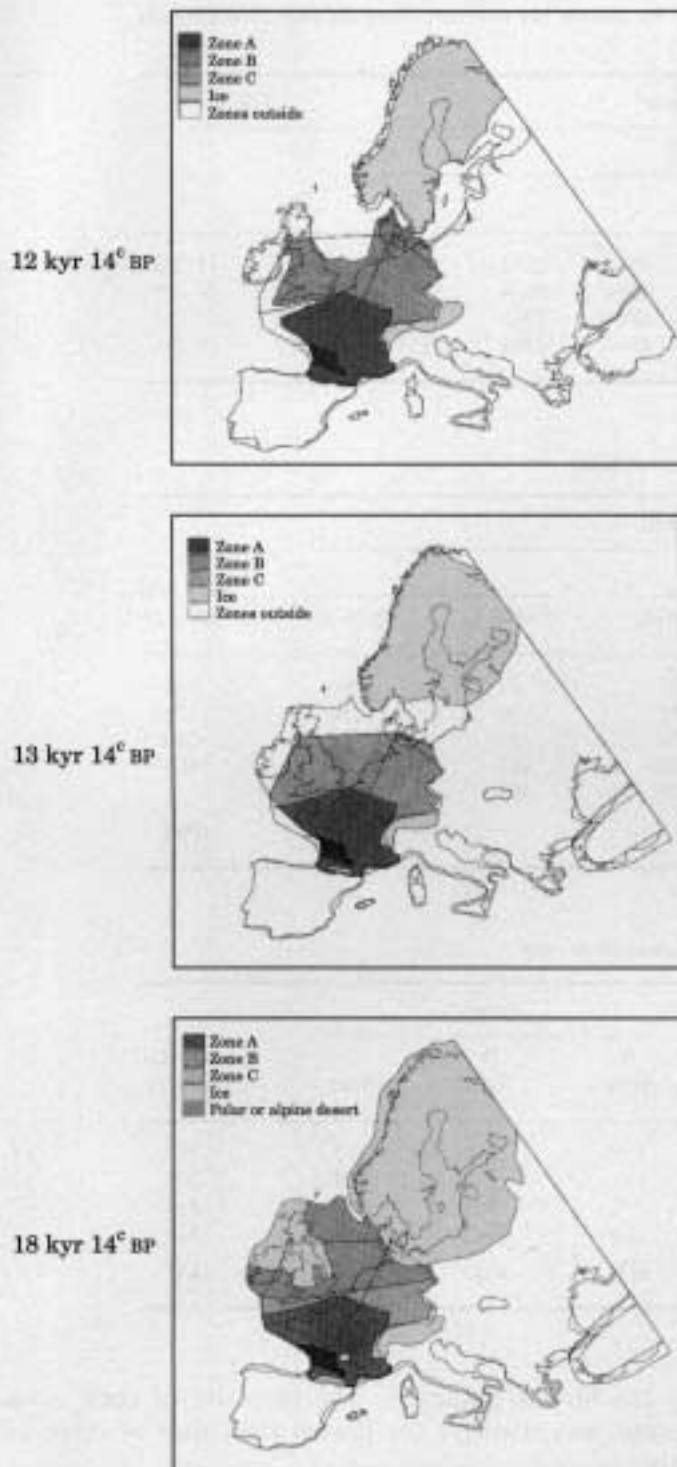


Figure 3. Maps used to estimate the zone sizes at four chronological periods in the Upper Palaeolithic, representing the viable areas of the geographical zones at 12 kyr, 13 kyr and 18 kyr ^{14}C BP (Adams, 1997; Adams & Faure, 1997).

coinciding surface in the zone, s_{it} ; thus $D_{it} = n_{it}/(d_i s_{it})$. D_{it} represents the archaeological density, in absolute value, per unit of coinciding surface in a zone. In addition to the absolute value, the relative value of this density will be examined, i.e. in the relative frequency of its distribution during the same period. In the same period, the frequency of the sites in a zone (the percentage) relative to the total number of sites in the semi-corridor has a density of the relative frequency,

n_{it}/N_t , divided by the corresponding coinciding surface: $f_{it} = n_{it}/(N_t s_{it})$, where N_t is the total number, with $\sum f_{it} s_{it} = 1$. f_{it} represents the archaeological density, in relative value, per unit of coinciding surface in a zone. Within a period, the relative density, f_{it} , has the same meaning as the absolute density D_{it} , in which the total number of sites of the former, N_t , is replaced by the duration in the latter, d_t . Between periods, the histogram representation of the distributions of the relative densities allows a comparison to be made, independently of the absolute value of their site number, for the sum of each of these relative density distributions is equal to 1, while it is equal to N_t for the distribution of the absolute densities.

The increase rate of the absolute densities within zone r_{it} , during the average time between two successive periods, $\frac{1}{2}(d_t + d_{t+1})$, is obtained by raising the observed proportion of increase, D_{it+1}/D_{it} , by the inverse of the average time between the periods minus 1. Thus: $r_{it} = (D_{it+1}/D_{it})^{2/(d_t + d_{t+1})} - 1$. Notice that since the time duration, d_t , is given in kyr in Tables 2 and 3 it should be multiplied by 1000 when using the formula. One frequently associates a more concrete value with the increase rate: the doubling time of the population. It is the shape variation of the histogram of relative density distribution and of these rate profiles represented on a geographical axis, both viewed as indicators of change for the peopling of the zones between the periods, given the climatic variations, which we will analyse further.

Sampling of the Archaeological Sites and Population Traces

Until now, we have assumed that the space-time distributions of the archaeological sites were random samplings of the sites occupied by the hunter-gatherers and that these distributions produced a direct demographic interpretation. There are, at least, two objections because some sites are topographically pre-determined. Compared to the sites in the open air, whose locations, or at least discoveries, are a priori fortuitous, the caves and rock-shelters are not. What are the possible consequences of this topographic pre-determination of the cavities (caves and rock-shelters) on the estimate of density?

The first consequence is that cavity locations are always known by humans (archaeologists and hunter-gatherers as well). Thus, they could have been excavated and/or occupied preferentially. Concerning the possible influence on the regional distributions of the sites, of a preferential excavation of the cavities, one might think that the activity of archaeologists on the cavities was not exerted in favour of one area than another. The archaeological pressure was thus probably uniform from all areas. The influence of such pressure, favouring the cavities systematically, can thus be regarded as negligible on the geographical distribution of the sites.

Table 1. Estimated sizes ($\times 1000 \text{ km}^2$) of the viable areas (v) by zone at the mid-periods of the four chronological subdivisions and the corresponding coinciding surfaces (s)

Industry	Mid-dates (kyr)	Zone						Total	
		A		B		C		v	s
		v	s	v	s	v	s		
Aurignacian	34.5	657	578	5458	4864	8312	5853	14,427	11,295
Gravettian	25.5	659	578	5616	4864	9504	5853	15,779	11,295
Glacial Maximum	18	753	578	5794	4864	2961	2450	9508	7892
Magdalenian	14	659	578	5616	4864	9504	5853	15,779	11,295

Table 2. Distribution of the two zone data for four chronological periods

Industry	Duration (kyr)	Zone				Sub-total Industry
		A		B		
		Cavities	Open-air	Cavities	Open-air	
Aurignacian	11	124	35	37	20	216
Gravettian	7	100	19	30	29	178
Glacial Maximum	5.5	102	34	51	32	219
Magdalenian	5	175	19	185	106	485
Sub-total zone		501	107	303	187	
Total zone			608		490	1098

Table 3. Distribution of the three zone data for the four chronological periods

Industry	Date (kyr)	Duration	Zones			Sub-total Industry
			A	B	C	
			Sites	Sites	Sites	
Aurignacian	40–29	11	159	60	32	251
Gravettian	29–22	7	119	61	29	209
Glacial Maximum	22–16.5	5.5	136	83	0	219
Magdalenian	16.5–11.5	5	194	294	284	772
Sub-total zone			608	498	344	1451

The cause of the topographic predetermination is the geological substrate. The geographical distribution of the cavities can thus be influenced by the substrate rather than by the past activity of the hunter-gatherers. Archaeologists have discovered more caves and rock-shelters in certain areas, simply because there are geologically more of them. The caves and the rock-shelters can thus not be a random sample of all the archaeological sites (cavities and open air sites). This induces a possible bias of geographical distribution of the densities, of which it is necessary to try to evaluate the importance. The risk of bias thus appears circumscribed with the following two situations. The topographically predetermined sites are: (1) distributed, geographically, mainly like the geological substrate of the cavities rather than like the past population density; and (2) were occupied differentially

by the hunter-gatherers. The intensity of their occupation was stronger (or lower) than that of open air sites.

In the next part, we shall first test the risk due to the geological substrate and then try to measure the influence of a differential representativeness of the sites via six scenarios, separately weighting the cavities and the open air sites. The issue is therefore: do these scenarios generate significantly different populational patterns for the half-corridor?

Geological substrate: density of the natural versus archaeological cavities

Proposal (1), described above, can be tested by measuring the distribution deviation to the null hypothesis, H_0 , namely that, geographically, the archaeological

Table 4. Goodness of fit chi-square test for the null hypothesis that the archaeologically-excavated caves and rock-shelters are geographically distributed in proportion to natural cavities by zone. For all cases the null hypothesis is rejected

Industries	χ^2	ϕ	P
Aurignacian	223.34	1.178	<0.0001
Gravettian	179.67	1.176	<0.0001
Glacial Maximum	135.35	0.940	<0.0001
Magdalenian	99.89	0.527	<0.0001

cavities are distributed in proportion to the natural ones. The two zone data (A, B) make it possible to test H_0 . The statistical test is the usual goodness-of-fit chi-square ($\chi^2 = \sum_{i=A}^B (O_i - E_i)^2 / E_i$) with 1 *df*, where O_i and E_i represent, for the i -th zone ($i=A, B$), the observed and the expected sample size under H_0 (archaeological cavities are distributed like the natural ones) of the archaeological cavities, respectively. The expected sample size E_i is given by the a priori probability π_i of the natural cavities in zone i , applied to the total number N of archaeological cavities (caves and rock-shelters) of the chronological period $E_i = N\pi_i$. The a priori probabilities were calculated from Chabert (1981), by selecting the natural cavities whose development is horizontal and whose entry is <500 m of altitude. Those located higher were in their quasi total-ity unoccupied during the Upper Palaeolithic, due to the altitudinal limit of the biosphere. The a priori probability for the natural cavities in a zone is: $\pi_A = 166/647 = 0.256$ and $\pi_B = 481/647 = 0.743$, for zones A and B, respectively. The chi-square statistics can easily be calculated from the archaeological cavity distribution of the two zone data and their sub-total, given in Table 2. Besides this, instead of a chi-square, one can use the ϕ coefficient, which is (the square-root of) a chi-square standardised by its sample size. It allows the comparison of chi-squares between groups when their sizes differ. Table 4 gives the ϕ values for the four periods. Clearly, the null hypothesis is rejected for all the periods. The archaeological cavities are not distributed geographically like geology. An analysis of the deviations (not shown here to economise space) indicates that the number present in zone A is much higher than the theoretically expected number. Relative to zone B, there was an over-occupation of the caves in zone A. The ϕ coefficient (Table 4) shows that the over-occupation is very strong during the Aurignacian and Gravettian, then decreases until the Magdalenian, without being influenced by the ice advance during the Glacial Maximum. During the Upper Palaeolithic, there is a trend of reduction in the over-occupation of zone A, but it remains effective until the end. The natural explanation is that of a preferential habitat area, at all times during the Upper Palaeolithic, determined by ecological (climate and fauna) and topographic (cul-de-sac) causes (Jochim, 1983).

Six scenarios

We will now consider six scenarios of site distribution from the two situations described above in (1) and (2) and their combinations. They will be applied to the two zone data. These scenarios are formalised by different weights given to the archaeological cavities and to the open air sites in the observed data. Let g_{it} and p_{it} be the observed number of archaeological cavities and open air sites, respectively, and w_g and w_p some weightings, depending on the nature of the archaeological sites, where the subscripts g and p designate the cavities and the open air sites. A new weighted value for the total number of the sites (archaeological cavities and open air) in the i -th zone and time t , given those weights, is: $n_{it}^* = g_{it} w_g + p_{it} w_p$. If $w_g = w_p = 1$, then the new weighted value and the total number are the same: $n_{it}^* = n_{it}$. We shall use those weights to compare different scenarios of sampling sites and their consequences on the estimates of the demographic parameters. The goal of these weightings is not so much to reflect exactly what could have occurred, but to compare the scenarios in order to measure their demographic consequences in the zones. Are hunter-gatherer occupancy rates, which differ according to the sites and/or the influence of geology on the geographical distribution of the cavities, likely to produce different demographical patterns? Or does one obtain a single pattern, robust to the consequences of a relatively broad range of generating populational scenarios for the data? In this article one hypothesises that the distributions of the densities of the sites which are produced by the scenarios represent, up to an unknown factor, the distributions of the populations. The six scenarios follow.

Scenario 1. The observed distribution of the sites (archaeological cavities and open air) is a direct sample of the past population: $w_g = w_p = 1$.

Scenario 2. The occupancy rate of the cavities by the hunter-gatherers is higher than that of the open air sites: $w_g = 10$, $w_p = 1$.

Scenario 3. The observed number of open air sites represents a small fraction of the true number of sites: $w_g = 1$, $w_p = 10$.

Scenario 4. The observed distribution of the archaeological cavities is influenced by geology which is expressed by the distribution of the a priori probabilities of natural cavities in zones A and B. If there was no geographical influence of geology, what would the distribution of the archaeological cavities be like? The influence of geology is eliminated by weighting the observed sample size of the archaeological cavities of the i -th zone by the inverse of the a priori probability for the natural cavities π_i : $w_{ig} = \pi_i^{-1}$. The distribution of the open air sites remains unchanged, relative to the cavities, by restandardising it by the sum of the new distribution obtained for the cavities in the

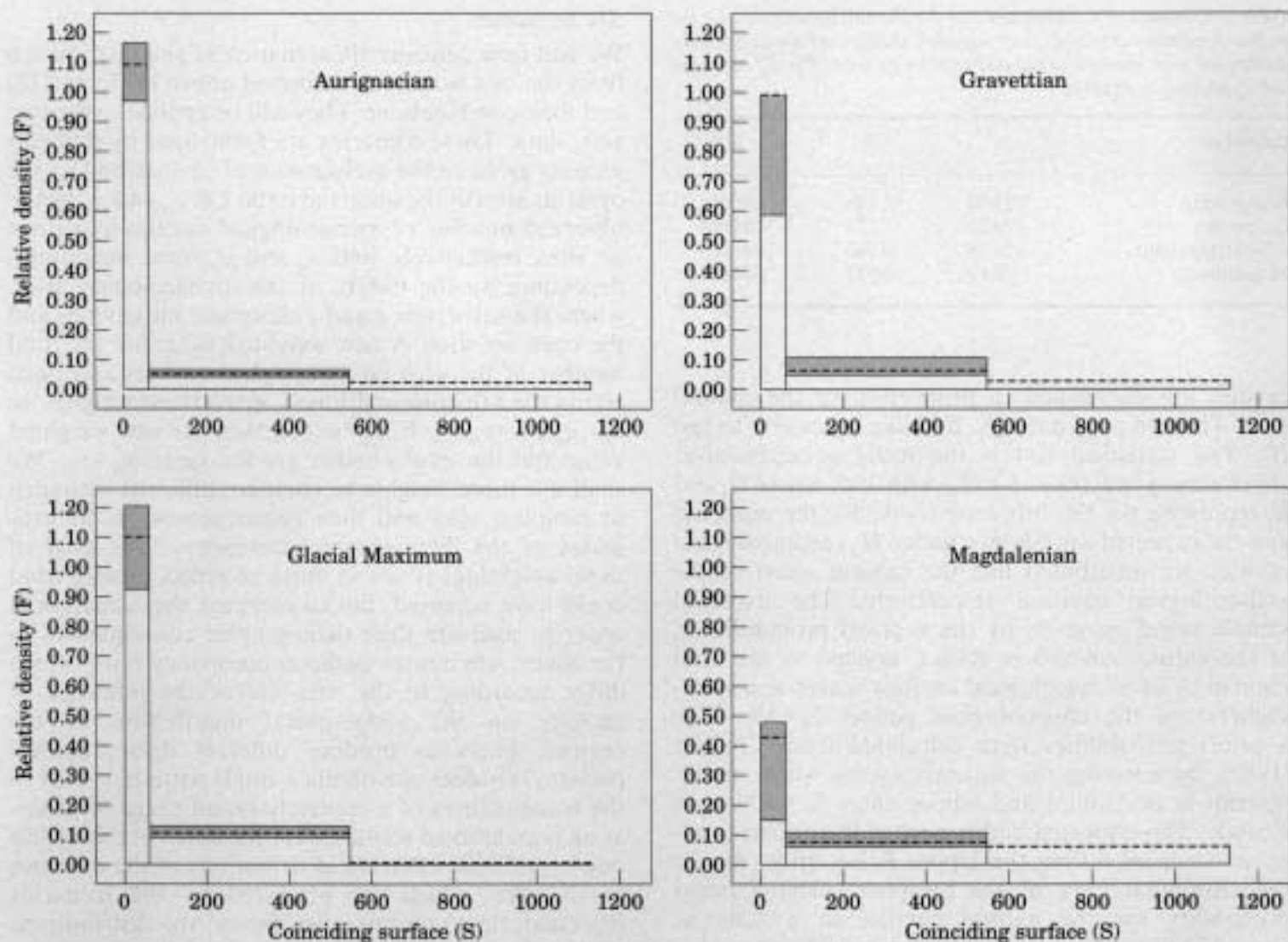


Figure 4. Histograms representing the distribution of the relative densities of the archaeological sites for the extreme values generated by six populational scenarios, at four chronological periods in the Upper Palaeolithic. Note: the horizontal axis represents the size of the coinciding surfaces. The distribution of the original data (scenario 1) is indicated by a dotted line.

chronological subdivision, which corresponds to $w_p = w_g$.

Scenario 5. The putative influence of the geology on the distribution of archaeological cavities is eliminated (scenario 4), and the observed number of open air sites is only a small fraction of the number of real sites: $w_{ig} = \pi_i^{-1}$, $w_p = 10 w_g$.

Scenario 6. The observed distribution of open air sites represents that of the past population: $w_g = 0$, $w_p = 1$. By eliminating the cavities completely there is no longer any archaeological and/or ethnological differential influences on the estimates of density.

These scenarios may be applied only to the two zone data and thus generate two zone distributions of relative site density. Only scenario 1 has two and three zones data. We thus used the relative density distributions and the rates of increase in the three zone data of scenario 1 to give an order of magnitude to the demographic parameters in zone C, where otherwise they would be missing. Finally, the comparison was

limited to the results generated by the scenarios which provided for the two zone data the most extreme values of the relative frequency and the rates of increase.

Interpretation of Results

Figures 4 and 5 represent the relative density distributions and the profiles of the increase rates in the half-corridor, by periods, for the most extreme values (zones A and B) along with the values of scenario 1 (the only ones we have for zone C). In the histograms (Figure 4), the two zone distributions of relative frequency were adjusted so that they have the same scale as the three zone distribution (scenario 1). It should be noticed that the three zone data from scenario 1 are within the extreme limits of the other scenarios. We will then compare in parallel the shape variation of the distributions and the profiles with the variation in intensity of the cold for each period. This intensity is estimated by the total volume of the ice during each period, respectively, to the volume of today (in %)

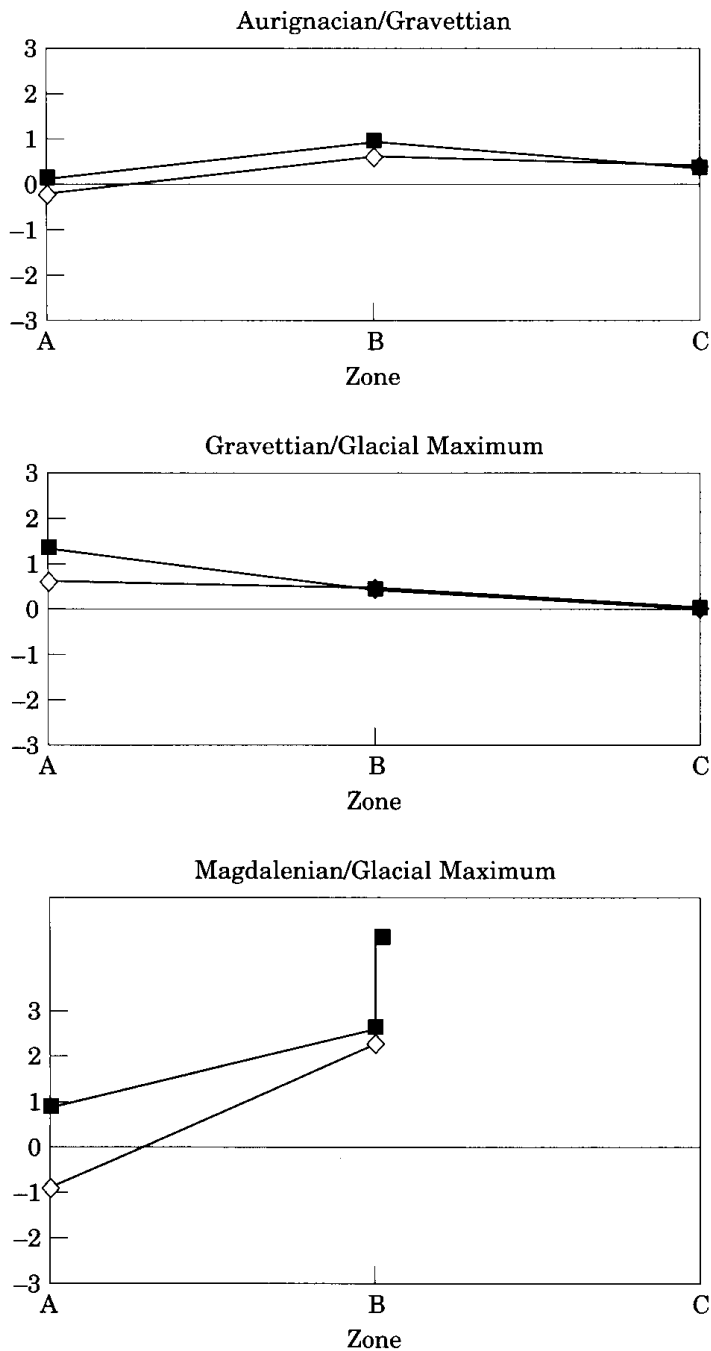


Figure 5. Profiles of the increase rates within zone between periods for the two extreme values generated by the populational scenarios, at three inter-periods in the Upper Palaeolithic. ◇ = minimum level, ■ = maximum level. Note: the single value of zone C is drawn from the three zone data (scenario 1).

which takes the values, in the Aurignacian, Gravettian, Glacial Maximum and Magdalenian, of 143, 162, 186 and 128, respectively (Webb III & Bartlein, 1992, deduced from the graph of their Figure 3: p. 154). Put otherwise, that means that the total volume of the ice was $(100+\%)/100=2.43$ times higher than present during the Aurignacian, 2.62 at the Gravettian, etc.

Distribution of relative densities (Figure 4)

Aurignacian and Gravettian. The two distributions are very similar. They appear very contracted in zone A, whereas zones A, B and C account, respectively, for

5%, 43% and 52% of the total coinciding surface of the half-corridor during these periods, regrouped, respectively, in Aurignacian 67–56%, 31–20% and 13%, and in Gravettian 57–34%, 52–29% and 14% of the distribution. The density is very high in zone A relative to the size of the area. The important fact to note is that, although the volume of the ice increases appreciably between the two periods, the ice advance does not influence the spatial distribution of the meta-population which remains unchanged. The Gravettian peopling is maintained where one would have rather expected its contraction, and even its density, relative to the Aurignacian, seems to increase a little in zone B towards the north, i.e. in the direction of the glacial front which progressed slowly during this period.

Glacial Maximum. The distribution is roughly identical to the two preceding in the left part (zone A), where more than 68–52% of the density is concentrated, and 48–32% in zone B. However, there is nothing in zone C, which had become a polar desert, inhospitable for humans.

Magdalenian. The distribution clearly spreads towards the right of the graph, in a northeast direction. Zones B and C contain 91–72% of the density distribution versus 48–32% previously. This can be interpreted as a (re)colonisation movement. Although it has decreased, zone A still contains the greatest (absolute or relative) density per unit of coinciding surface.

Profiles of the increase rates within-zones between-periods (Figure 5)

These rates are very small, so they were multiplied by 10,000. Given their smallness and the inaccuracy which results from this, rather than being interested in the absolute values of these rates it is better to be interested in their relative values between zones, i.e. with the geographical profiles which they form when they are juxtaposed.

Aurignacian–Gravettian. Zone A frames the stationarity (0.18– – 0.18). Zone B increases (0.52–0.91) and zone C only marginally does (0.35).

Gravettian–Glacial Maximum. Zones A and B both increase (0.58–1.32; 0.35–0.88). At the Glacial Maximum, the absolute density of zone C is null, and so is its increase rate.

Glacial Maximum–Magdalenian. Zone A frames the stationarity with, perhaps, a decreasing tendency (0.86– – 0.93). Zone B increases appreciably relative to all of the rates obtained in the Upper Palaeolithic (2.21–2.59). Zone C increases asymptotically ($+\infty$) due to the null absolute density of the previous period.

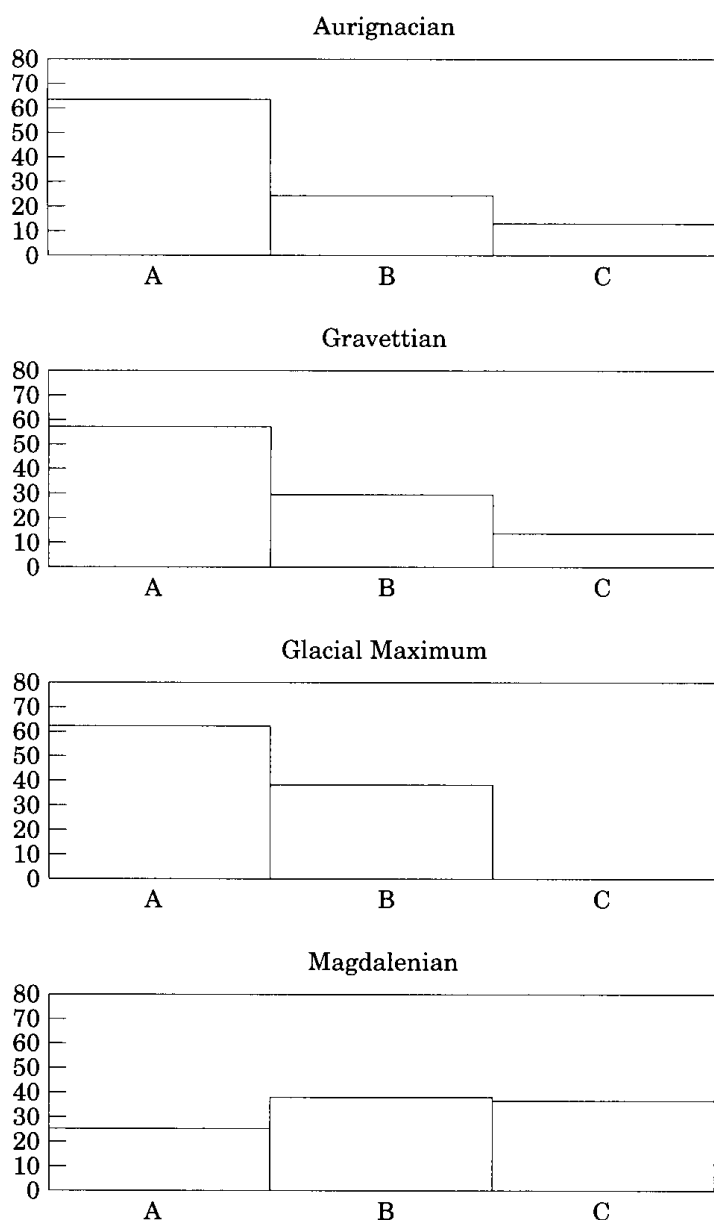


Figure 6. Bar charts representing the percentage of the sites per zone at four chronological periods in the Upper Palaeolithic. Note: it may be observed that there is a slight increase in distribution, from the Aurignacian to Gravettian, towards the second peripheral zone C; in Glacial Maximum there is a contraction mainly of zone C towards the first peripheral zone B; and in Magdalenian there is a complete redistribution towards the two peripheral zones B and C.

A view of the whole

Changes of distributions of relative densities. As shown above, the histograms of scenario 1 representing the distribution of relative density for the three zones reach the extreme values generated by the scenarios. These histograms can thus be regarded as a sample of the same pattern with the same tendency strongly marking the data. One can thus take the changes of distributions of scenario 1 as a qualitative indicator of the pattern for the changes of relative densities between zones. These changes of distributions are better demonstrated by bar charts (which do not take into account the coinciding surface sizes). This is represented in Figure 6. In Aurignacian and Gravettian, the distributions have roughly the same three-stair profile.

The steps are very sharp in Aurignacian and less sharp in Gravettian. At the Glacial Maximum, zone A's distribution remains basically unchanged. There is especially a stacking of zone C in zone B. In Magdalenian, the pattern of distribution leaning on zone A is replaced by a roughly uniform distribution, indicating a considerable increase in distribution in zones B and C.

During the first three chronological periods, the distribution of the (absolute and relative) site density can be expressed by an exponential decreasing on a geographical axis: $D = a e^{-b \cdot d}$, where D is the site density, a and b are the fitting parameters and d the value of the geographical variable. The geographical variable can represent the sum of successive embodied coinciding surfaces, from zone A to C, or the geographical distance, measured on a transect, moving away from zone A while going towards zone C. This transect can be selected so that it represents the approximate geographical position of the centre of the different zones. It goes in a northeastern/southwestern direction, on the Biarritz–Copenhagen line, on which the positions of the centre of zones A, B and C are those corresponding to the latitudes of Bordeaux, Orleans and Wessel (see Figure 2). Both geographical variables provide similar results. They express the fact that the density of the sites, from the refuge zone A, has a leptokurtic distribution which decreases asymptotically in the northeastern direction. Figure 7 shows the fits of the absolute and relative density distributions of the sites against the sum of the embodied surfaces, in the half-corridor for the three first periods (three zone data: scenario 1). The exponential was fitted by using the Gauss–Newton algorithm to obtain the derivatives. However, in Magdalenian the exponential curve deviates considerably from the data (not shown here to save space). The fit of a beta function could have been tried, but without much theoretical justification.

The leptokurtic distribution predicted on a recolonisation front (Hewitt, 1996) is observed for the first three periods but not for the Magdalenian, which is precisely a period of major recolonisation of the area during the Upper Palaeolithic. In fact, even if the recolonisation could have produced this distribution in its initial phase, the pioneer phase of Housley *et al.* (1997), one can think that this initial distribution was erased by the stacking of the successive layers of other possibly leptokurtic distributions during the whole recolonisation process, slipping more and more towards the limits north of the continent, bounded by the Baltic Sea, until the stabilisation of the process—the residential phase of Housley *et al.* (1997). A leptokurtic distribution simply represents the traces of an occupancy rate which decreases asymptotically with geography. It is thus not the signature of a single population process such as recolonisation. It simply suggests long distance moves in these zones, such as raids or opportunistic expeditions.

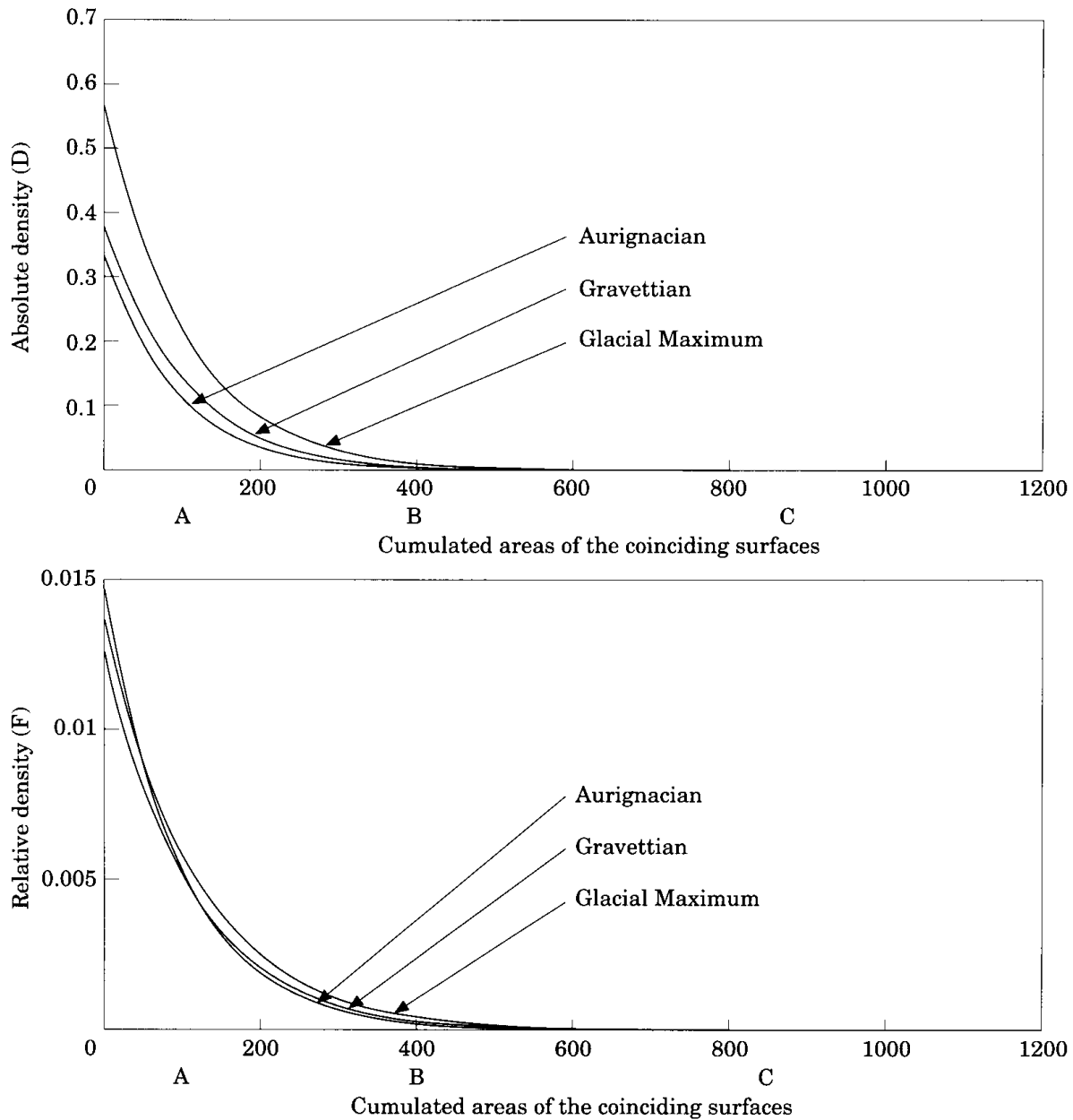


Figure 7. Fitting of the exponential function to the distributions of the absolute (top) and the relative (bottom) densities of the archaeological sites in the western-European half-corridor, from Aurignacian to Glacial Maximum (three zone data, scenario 1). All the distributions are leptokurtic, indicating a decrease in the site density in the north-eastern direction.

Throughout the Upper Palaeolithic, the site density is considerably higher in zone A than in any other zone. This has been measured, in particular, by the very high over-frequentation of the cavities in zone A relative to their natural proportion on a regional scale. We have shown above that the reasons for this over-frequentation were not geological but, most probably, ecological determined by the favourable geographic location of zone A. The trend for this geographic over-frequentation was declining during the Upper Palaeolithic, but always remained very important.

To schematise the pattern of rate of increase within zones between periods, the minimum and maximum values generated by the scenarios were replaced by “0”, “+” or “-” when they framed a null (stationary), positive or negative rate, respectively (see Table 5). During the Aurignacian–Gravettian, the population is stationary in the refuge zone A, while a positive

increase is observed in the two peripheral zones B and C. During Gravettian–Glacial Maximum, there is a retraction of the positive rates in the southern direction of zones B and A. During Glacial

Table 5. Space–time pattern of the rate of increase ($r \times 10,000$) for the absolute densities of the sites during the Upper Paleolithic in the half corridor. This pattern is obtained by replacing the extreme values generated by the populational scenarios, which frame a rate of null, or a positive or negative increase, with the symbols “0”, “+” and “-”, respectively

	A	Zones B	C
Aurignacian–Gravettian	0	+	+
Gravettian–Glacial Maximum	+	+	0
Glacial Maximum–Magdalenian	0	+	+

Table 6. Total number (N_t), increase in absolute densities (D_t/D_{t-1}), increase rate ($r_t \times 10,000$) of sites, estimates of population densities (ω_t ; to 100 km²), and the size for the meta-population (P_t) in the half corridor. Note: estimates for the size of the viable area were taken from Table 1

Industries	Duration (kyr)	N_t	D_t/D_{t-1}	r_t	ω_t	P_t			Total
						A	B	C	
Aurignacian	11	251	1.308	0.30	0.376	3421	1303	706	5430
Gravettian	7	208	1.908	1.03	0.492	4429	2254	1088	7771
Glacial Maximum	5.5	219	2.709	1.90	0.940	5541	3396	0	8937
Magdalenian	5	772			2.547	10,046	15,271	14,860	40,186

Maximum–Magdalenian, there is an expansion of the positive rates in zones B and C, once again following the original Aurignacian–Gravettian pattern. That can be interpreted as a succession of geographical expansion–retraction–expansion for the meta-population, starting from the refuge zone, initially in a stationary state, marked during the expansion phase by positive rates of increase in the two peripheral zones (B and C), then during the contraction phase positive in the refuge and the first peripheral zone (A and B). If we compare the average rates of increase within-zones ($r \times 10,000$) for the two extreme values, they are for zones A, B and C, 0.30, 1.24 and ∞ , respectively. This can be interpreted as three population zones which are, on average: the first at the equilibrium state with the carrying capacity (doubling time: 23.1 kyr), the second moderately increasing (doubling time 5.6 kyr), and the third asymptotically increasing, corresponding to a tension zone. If one compares the increase rates between periods, on a global scale for the meta-population in the half-corridor (scenario 1, Table 6), these rates increase continuously, even during the passage of the Gravettian–Glacial Maximum. This indicates a continuous improvement of the meta-population's adaptation and, in particular, of the hunting productivity. It should be remembered that these rates are average rates over millennia, representing very long term trends. Thus, they cover very important negative and positive fluctuations.

From the Aurignacian to the Gravettian, while the climatic conditions slowly worsened, a populational extension towards the north is nevertheless perceived. From the Gravettian to the Glacial Maximum one witnesses a contraction, mostly in zone B, with a complete abandonment of zone C, but without reduction in the average rate of natural increase on the global scale. Finally, during the Magdalenian, a turn of tendency is noticeable showing an increase in density north of zone A along with a complete change in the geographical pattern of peopling. The pluri-millennium pattern of peopling, which was characterised by a concentration zone (a refuge zone) in an almost empty space, is replaced by a site distribution much more uniform and homogeneous on the map.

During the Upper Palaeolithic, where a cold or polar climate prevailed in the European western peninsula, the archaeological data seem to indicate that apart from zone A, which was the usual zone of peopling of the hunter–gatherers, settlement took place sporadically, perhaps as the result of favourable or unfavourable seasonal variations (see also Dennell, 1983; Jochim, 1983, 1987).

Palaeolithic archaeology and demographic inferences

To estimate the meta-population size the following procedure was used. From an ethnographic reference sample of hunter–gatherers, the demographic densities of the groups which fell within the climatic bounds estimated from the Glacial Maximum have been averaged, roughly within the north and south latitudinal limits of the occupation of the half-corridor (Figure 1). The average population density of the ethnographic groups of reference can be considered as an optimistic estimate during prehistory, mainly due to technical reasons of equipment of these groups which we will discuss later. This average population density, fixed for the Glacial Maximum, was multiplied by the increased proportions between periods, as deduced from all of the archaeological sites given by the three zone data in the coinciding surfaces of the half-corridor (scenario 1; Table 6), before (Glacial Maximum–Gravettian, Gravettian–Aurignacian) and after the Glacial Maximum (Glacial Maximum–Magdalenian). By visual inspection and in qualitative terms, we have considered that the three zone data were a sample of a population pattern which strongly shapes the data, a pattern robust to a strong variation in the generating scenarios. New population densities then were obtained, per period, and were multiplied by the estimated size of the corresponding viable area (see Table 6). Thus, the meta-population size at the period $t-1$, at the global scale of the semi-corridor, P_{t-1} , is equal to the population density estimated at the periods t , ω_t , multiplied by the inverse of the increased proportion of the absolute archaeological density between-periods $(D_t/D_{t-1})^{-1}$, and by the estimated size of the corresponding viable area, v_{t-1} , i.e. $P_{t-1} = (\omega_t D_{t-1} v_{t-1}) / D_t$.

Table 7. Selected ethnographic groups corresponding to the estimated boundaries of ET (effective temperature) at the glacial maximum in the European western half-corridor and the causes of possible exclusion from the demographic reference sample

Groups	ET	Cause of exclusion	References
Chipewyan	10.3	Fishing: 40%	Mooney, 1928: 4; Smith, 1981: 274; Kelly, 1995: 67
Hare	10.5	None	See Table 8
Kaska	10.4	Fishing: 50%	Kroeber, 1939: 141; Kelly, 1995: 67
Kutchin	10.5	Fishing: 50%	Kelly, 1995: 67
Montagnais	11.6	None	See Table 8
Naskapi	10.0	None	See Table 8
Selk nam	9.0	Dependent on dogs	Gusinde, 1931; Kelly, 1995: 67
Tanaina	10.4	Fishing: 50%	Kelly, 1995: 67
Tanana	10.9		Kelly, 1995: 67

This approach supposes that the site density–population density relationship remained roughly constant during the Upper Palaeolithic. In particular, it supposes that the climatic changes did not cause a variation in the site number mainly because of sociological changes (communal hunting versus more individual hunting) rather than demographic changes. In the case of an increase in individual huntings, one should expect a shift from nucleated settlement to dispersed patterns, which should correspond to an increase in the number of “small” sites in the distributions (e.g. containing <1000 tools) compared to the “large” sites (≥ 1000). A random sampling in our database (two zone data) shows that the proportions of “large” sites do not differ significantly between the four periods, representing about 10–11%, with the values of 15/138=10.9%, 13/104=12.5%, 13/112=11.6% and 20/180=11.1%, respectively, except within one period. In the final Magdalenian one observes a sharp reduction (by 10) of the number of “large” sites in each of the two zones. But this change can be considered as marginal, for it is located at the limit of our chronological window.

The main ethnographic reference sample comes from Murdock (1967, 1981). In order to obtain a sample of precontact European hunter–gatherers, who had escaped from the smallpox epidemics and the incipient colonial economy, it was filtered by Keeley (1988). In fact the groups included in the Keeley sample were retained, and elimination was carried out on those whose level of fish alimentation was higher than 20% (Kelly, 1995). There is evidence of fishing (in rivers and coastal seas) only in the final Magdalenian (Le Gall, 1992, 1995). Although two seal bones were in the past recorded in Perigord (Hardy, 1891; Peyrony, 1935), raising the issue of possible coastal hunting for sea mammals, whose archaeological remains could have disappeared due to the rise in sea level, it should be noted that, to the best of our knowledge, no trace was found in the coastal Cantabric sites whose proximity with the sea was not affected by climatic variations. The climate is represented by the ET variable (effective temperature), which provides a simultaneous measure-

ment of the average insolation and its annual distribution (Bailey, 1960; Binford, 1980; Kelly, 1995). The values of ET were taken from Kelly (1995) or were calculated if they were missing.

To 18 ¹⁴C kyr BP (in fact, 25 to 15 “real” kyr BP) the half-corridor is occupied by dry tundra, represented as scattered patches of grassland undergrowth, which does not have an equivalent today (Adams & Faure, 1997). By comparison, at 13 ¹⁴C kyr BP (14.7 “real” kyr BP) the half-corridor is occupied primarily by an open moor and a vegetation of tundra, accompanied by small occasional patches of undergrowth and wood in favourable localities. This vegetable formation is localised today in Iceland (Huntley, 1990, Cluster 27). To 18 ¹⁴C kyr BP, estimates of the minima and maxima of the seasonal average temperatures, with the latitudes of Munich and Bordeaux (Adams, 1997: 10), provide ET values of 10.2 and 10.4, respectively.

Table 7 provides the list of groups extracted from the ethnographic database in the climatic bounds, ET=10–11 (10 coinciding roughly with the limit of the permanent permafrost), before selection on the importance of fish in the food of the groups described above. In this list, it must be noted that the Naskapi eskimos (ET=10.0) are not dissociated from the contiguous group of the sub-arctic Montagnais Indians (ET=11.6) and they were thus kept together. Table 8 provides the densities to 100 km² for the only two groups remaining after a careful re-evaluation of their demographic data. This one was in the direction of a density increase. The density calculated on the whole population size and the corresponding areas is of 0.94 inhabitants/100 km². Table 6 provides estimated meta-population sizes for the four mid-periods. They range from 5400 individuals in the Aurignacian to 40,000 in Magdalenian.

Ethnographic References, Cultural Attributes and Palaeolithic Estimates

The approach used in this article consisted of using a sample of ethnographic reference. This has been frequently employed in archaeology (see, for example, in

Table 8. Selected ethnographic groups remaining

Groups	Density (100 km ²)	ET	Note
Naskapi-Montagnais	0.93	10.0 11.6	With the European contact 4–5000 inhabitants/483,871 km ² (Smith, 1981: 275; Roger & Leacock, 1981: 169–189; Gordon, 1990: 290). Elimination of: (Kroeber, 1939: 141) 0.44 inhabitants/100 km ² , for Kroeber gathers also the Têtes de Boule (synonymous: Attikamek) mainly fishermen (McNalty & Gilbert, 1981: 208–216). Use of canoe (Roger & Leacock, 1981: 169–189).
Hare	1.03	10.5	With the European contact 7800 inhabitants/72,580 km ² (Mooney, 1928: 26; Osgood, 1936; Savishinsky & Hara, 1981: 317).

a demographic context: Bocquet & Masset, 1977). This approach has been criticised in that it is nothing more than a simple projection of the present in the past, leading only to the vitrification of the past (for a discussion, see Bailey, 1983). Indeed, the ethnographic sample contains relationships between ecological, cultural and demographic variables, sometimes formalised by correlations (Keeley, 1988), which certainly do not correspond to natural laws, comparable to those of Bergmann-Allen in biometrics or Rapoport in biodiversity. At the 1000-year-old demographic scale of populations without writing, these relationships of demography–ecology–culture are historically dated, even if their speeds of change were slow. Accordingly, it is interesting to discuss two important features of the technical equipment of hunter–gatherers and to raise the issue of their impacts in demographic estimates of the Palaeolithic: means of transportation and hunting techniques.

Means of transportation

The mobility of a group of hunter–gatherers, given its demography (size, age-pyramid), is the expression of its adjustment speed to the variability of volume of the available resources. The possibility of an apparition of a local gap between the demography of a group and the volume of the resources, the importance of such a deviation, its speed of realisation, generates a potential danger to the demographic integrity of the group. In an environment with strong seasonality like that of a roughly “subarctic” region, the displacement speed of a group, the distance which it can travel, the possible number of the migratory movements that it can make during the year, in short its mobility, will make it possible to decrease this danger. These three variables, determining the speed of adjustment, depend on the nature of the means of transportation used, from walking to artificial means. All the ethnographic groups of the subarctic North-American area make use of artificial means of transportation (toboggan, draught dog, sled drawn by dogs, canoe). Hayden (1981: 382–383) thinks that of vast areas of North-American boreal regions could have been uninhabit-

able by the hunter–gatherers as long as an aide in means of transportation did not exist.

Hunting technique

Its effect is to increase the hunting productivity, i.e. to raise the level of the carrying capacity of the environment to an optimum. In the ethnographic subarctic conditions the most productive hunts are related to herds of ungulates. They take place on their migratory routes which cross rivers, in spring and in autumn (Gordon, 1990: 282). These hunts are not individual, but are collective organisations intended to channel, concentrate, and confine the animals of the herds in a small geographic area, by using topography and/or of light constructions (corral). The killing technique is relatively unimportant compared to that of concentration (Driver, 1990). All the ethnographic groups of reference practiced collective hunting of this kind (for example Naskapi; Gordon, 1990: 290), without the perceptible effect of the dog, except for Selk man (Gusinde, 1931).

A simple model of population density given an environmental framework “subarctic” fixed by ET, would be thus: density|ET = average density + effect of the means of transportation + effect of the hunting technique + uncontrolled residual. What happens if we try to fix the two technical variables at the minimum, i.e. displacement occurs only by walking and hunting is carried out without any technical devices for herd concentration? No ethnographic data exists, to our knowledge, comprising these two variables set at the minimum (to zero) in subarctic conditions. It is thus necessary to try to imagine them.

The effect of the absence of a means of transportation, the reason for walking, will be to fix at a minimum level the adaptability of a group to environmental variability, and thus to the biomass. One can think that to a minimum level of adaptability corresponds also a minimal exposure to environmental variability. Within a concrete natural framework, many solutions are possible to carry out this situation, such as:

- (1) a decrease in environmental variability, without leaving the habitat area of the herd(s). This is

carried out when the latitude and/or the longitude of an occupation area decreases, producing an increase in the ET-value. Within the geographical framework of the half-corridor this could occur while moving to refuge zone A (see also Gamble, 1983);

- (2) an adherence to the mobility of the resources, i.e. to the herds of ungulates. Environmental variability will then be that determined by the seasonal mobility of the herds, i.e. by their speed and their distance of migration. The choice may be fixed on the ecological zone providing a minimum seasonal mobility. This could also be carried out while moving to refuge zone A.

With regard to the hunting techniques, in the ethnographic data they are dependent on the local density of the prey. Hunting becomes collective when the density is high (Driver, 1990) and its technical organisation is primarily intended for the concentration. Perhaps it is then necessary to start by distinguishing hunts of animals living in herds and those living in small droves. The first lend themselves more easily to productive techniques of concentration than the second ones. From the very beginning of Middle Palaeolithic, in western central Europe, among the hunted animals of the cold periods, and observed in more than 300 archaeological sites or layers (with, invariably: the horse, the reindeer, the mammoth and the woolly rhinoceros; Bosinski, 1967), only one lives in herds (the reindeer) and two live in small droves (the horse and the mammoth; Jones, 1990). The hunting of herds in the geographical zone is thus very old. But as of this period, the concentration of the small droves (of horses) is also well attested to (Levine, 1983). The archaeological data produce demographic profiles of killing identical to those of droves of living animals, as if they had been channelled. In this case, techniques of concentration would have been used with a (very) low level of demographic density of the prey, a level without equivalence in the ethnographic data of reference.

The demographic model of density sketched above does not take into account the social network. In the Arctic groups the social networks, i.e. the secular contacts between close groups, is intended to minimise the environmental risk (Gamble, 1986; Whallon, 1989) which means, in our context, to reduce the frequency of the stochastic fluctuations of mortality. Demographically, a meta-population living mainly off herds is density-dependent. Facing environmental stochastic fluctuations in the short term, this ensures its persistence, as well as a robust internal regulation (Barbault, 1992; Royama, 1992); and from the point of view of the meta-population, a visibility of provisioning. Nevertheless, density-dependence does not provide protection from demographic fluctuations in prey, of large amplitudes, caused, for example, by regional epizooties (not necessarily local) or climatic fluctu-

ations modifying migratory roads. The demographic impact of fluctuations in prey on the groups of hunter-gatherers can be high. Ethnographic data show that the frequency of food shortages and famines increases considerably with latitude (Keeley, 1988: 400; Krupnik, 1993: 138–139, 221, 229), in other words with seasonality. One may thus think that the probability of extinction in the northeastern direction of the transect of Figure 2, which indicates a linear diminishing of ET, increased asymptotically, and thus correlatively, the need for a social network.

Finally, what we called coinciding surfaces are a kind of sampling of surfaces on which archaeological sites are distributed. These surfaces are not random sampling, in the statistical sense, even if the site distributions on these surfaces are roughly random when the size of the areas increases. The coinciding surface represent roughly: $11,295/14,427=78\%$, $11,295/15,779=71\%$, $7892/9508=83\%$, and $11,295/15,779=71\%$ of the viable half-corridor during each of our chronological subdivisions of the Upper Palaeolithic (from Table 1). But their locations on the map are not due to chance. During severe climatic fluctuations, the altitudinal limits of the biosphere went down, correlatively with the lowering of the sea level, perhaps to a level of 350 m today, then went up during the favourable fluctuations. The coinciding surfaces result from a systematic altitudinal selection which, perhaps, skewed the archaeological sampling. For instance, it is known that there is a demographic continentality of the modern hunter-gatherers in the west-east direction of the North American continent, determined mainly by pluviometry (Keeley, 1988). This continentality is detectable on the data of the half-corridor via the interpretation of an indicator of mobility, represented by average distance sites (archaeological)-procurement (of raw material), which form a gradient, going from 35 km to 85 km in the west-east direction (calculated from Feblot-Augustins, 1995). How much time is required so that such a continentality is established in an initial phase of colonisation, as was the case for Aurignacian? Which economical forms did it take in the area occupied today in the western part by the continental shelf? A simple prolongation of the continuum of the hunters (hunting mainly ungulates), sampled archaeologically on what are currently the coinciding surfaces located to the east of this shelf, or a continentality (now undetectable) determined by ecological zones, for example, able to sustain the hunting of sea mammals in certain zones along previous sea shore lines? Selected pieces of the picture are still missing and one remains prisoner of the surrounding pieces to reconstitute it.

Conclusion

Before 40 kyr BP, the statistical data are rare and very dubious. Among the rare data, two skeletal series of

pre- and Neanderthals, Atapuerca (HS; >300 kyr BP) and Krapina (130 kyr BP) have numbers of individuals that are abnormally high and age distributions that evoke those of a living population, suggesting the impacts of catastrophe mortality (Bocquet-Appel & Arsuaga, 1999).

After 40 kyr BP, the data show that the occupation of Europe occurred through the aspect of concentration poles, regrouping the majority of the sites, separated by vast zones which were empty or having a negligible density. The north of Aquitaine plays a dominating role by regrouping the 2/5th of the sites' total for most of the Upper Palaeolithic. The data, distributed among three embodied areas, have allowed a realistic reconstruction of the population kinetics of the hunter-gatherers in the European western half-corridor. Perhaps would it be better to speak about immobility rather than of kinetics, because what characterises it is the permanence of a refuge zone located in northern Aquitaine, during 30 kyr, with successive zones of peopling to very low density when one goes up in the northeastern direction. In a premonitory way, in 1933, this zone was christened by Peyrony (1933: 557) the "garden of Eden". From Aurignacian to Glacial Maximum, the leptokurtic aspect of the distribution of site densities would suggest moves at long distances in these zones, such as raids or opportunistic expeditions. During the Glacial Maximum, the response to the cold is marked only by the complete abandonment of the second peripheral zone along with a contraction of the local populations mainly in the first peripheral zone, but without geographical change of position of the refuge zone, nor a reduction in the size of the meta-population. The average rate of increase, although very small, is always positive and rises continuously, even during the Glacial Maximum. This indicates a constant improvement of the hunting productivity as well as a formidable trend of adaptation to severe ecological constraints of which some have become to us unthinkable. These average increase rates mask erratic fluctuations, which were undoubtedly considerable (see also Krupnik, 1993: 257), but which are archaeologically indiscernible. An optimistic estimate of the meta-population size of hunter-gatherers in the half-corridor area goes from the Aurignacian to the Glacial Maximum, from 5400 to 8900 people. At the end of the Glacial Maximum, a demographic explosion occurred with about 40,000 individuals.

In the future, something to be examined in the archaeological data is from which period the two variables of the very simple model of population density sketched above ceased being at zero. But then new issues are raised. How to recognize, in the archaeological data, the parameters such as: "adhering to the mobility of the small drove/the herd", "individual/collective hunting", "means of transportation", "abandoned migratory camps/area of local extinction"? It would also be necessary to look further into this first analysis of the geographical distribution

of the sites, by taking into account their sizes (and their altitude), and by more finely distinguishing the large sites from the small ones, as outlined above. A change in proportion of these two entities is perhaps an indicator of a more collective or more individual relationship to hunting, as suggested by Gamble (pers. comm.). It is while endeavouring to show archaeological markers of these situations, and even to try to quantify them (frequencies of the herds/the drove funnelling, and their seasonalities) that one may end up with "the tyranny of the ethnography" (Wobst, 1978) and to give up the uniformitarian approach. This is the price in order to reconstruct a demography for the Middle and Upper Palaeolithic.

Acknowledgements

We thank F. Delpech, J. Féblot-Augustins, and C. Masset for their stimulating participation in the seminar "Archaeology and demographical inferences" of the Collège de France (Y. Coppens, Chair of Paleo-anthropology and Prehistory) and J. M. Adams and particularly C. Gamble for valuable comments of an early draft. The manuscript was prepared by M. F. Leroy and M. Tersis and the artwork was done by D. Fouchier.

References

- Adams, J. M. (1997). *Global Land Environments Since the Last Interglacial*. www.esd.ornl.gov/ern/qen/nerc.html.
- Adams, J. M. & Faure, H. (1997). Preliminary vegetation maps of the world since the last Glacial Maximum: an aid to archaeological understanding. *Journal of Archaeological Science* **24**, 623–647.
- Allain, J., Desbrosses, R., Kozłowski, J. K. & Rigaud, A. (1985). Le Magdalénien à Navettes. *Gallia Préhistoire* **28**, 37–124.
- Bailey, G. (1983). Hunter-gatherer behavior in prehistory: problems and perspectives. In (G. Bailey, Ed.) *Hunter-Gatherer Economy in Prehistory*. Cambridge: Cambridge University Press, pp. 1–6.
- Bailey, H. (1960). A method of determining warmth and temperateness of climate. *Geografiska Annaler* **43**, 1–16.
- Barbault, R. (1992). *Ecologie des Peuplements*. Paris: Masson.
- Binford, L. A. (1980). Willow smoke and dogs tails: hunter-gatherer settlement systems and archaeological site formation. *Am. Ant.* **45**, 4–20.
- Biraben, J. N. (1988). La Préhistoire. In *Histoire de la Population Française*, Vol. 1. *Des origines à la Renaissance*. Paris: Puf, pp. 19–61.
- Bocquet-Appel, J. P. & Arsuaga, J. L. (1999). Age distributions of Hominid samples at Atapuerca (SH) and Krapina may indicate accumulation by catastrophe. *Journal of Archaeological Science* **26**, 327–338.
- Bocquet, J. P. & Masset, Cl. (1977). Estimateurs en paléodémographie. *L'Homme* **XVIII**, 65–90.
- Bordes, F. (1968). *La Paléolithique dans le monde*. Paris: Hachette.
- Bosinski, G. (1967). *Die Mittelpaläolithischen Funde im Westlichen Mitteleuropa*. Köln: Böhlau verlag.
- Chabert, Cl. (1981). *Les Grandes Cavités Françaises*. Paris: Fédération Française de Spéléologie.
- David, N. (1973). On upper palaeolithic society, ecology and technological change: the Noaillan case. In (C. Renfrew, Ed.) *The Explanation of Culture Change: Models in Prehistory*. London: Duckworth, pp. 277–303.
- Delpech, F. (1989). L'environnement animal des Magdaléniens. Le Magdalénien en Europe. *Eraul* **38**, 5–29.

- Delpéch, F. (1995). *Biomasse diongulés au paléolithique et inférences démographiques*. Seminar: Archéologie Paléolithique et Inférences démographiques, Collège de France, March 1995.
- Demars, P.-Y. (1996). Démographie et occupation de l'espace au Paléolithique supérieur et au Mésolithique en France. *Préhistoire Européenne* 8, 3–26.
- Demars, P.-Y. (1998). Le peuplement de l'Europe occidentale au paléolithique supérieur. Unpublished manuscript.
- Demars, P.-Y. & Hublin, J.-J. (1989). La transition Néandertaliens/Hommes de type moderne en Europe occidentale: aspects paléontologiques et culturels. In *L'homme de Néandertal, Vol. 7. L'extinction, ERAUL 34*. Liège, pp. 23–37.
- Dennell, R. W. (1983). *European Economic Prehistory: A New Approach*. London: Academic Press.
- Desbrosse, R. & Kozłowski, J. K. (1988). Le Paléolithique final entre Atlantique et Vistule: comparaisons entre les civilisations de la plaine et celles des plateaux. In (M. Otte, Ed.) *De la Loire à l'Oder. Les Civilisations du Paléolithique final dans le nord-ouest européen*. Oxford: British Archaeological Report, pp. 655–681.
- Dolukhanov, M. (1979). Evolution des systèmes éco-sociaux en Europe durant le Pléistocène récent et le début de l'holocène. In (D. de Sonneville-Bordes, Ed.) *La Fin des Temps Glaciaires en Europe: Chronostratigraphie et Écologie des Cultures du Paléolithique Final*. Paris: Colloques internationaux CNRS 271, pp. 869–876.
- Driver, J. C. (1990). Meat in due season: the timing of communal hunts. In (L. B. Davis & B. O. K. Reeves, Eds) *Hunters of the Recent Past*. London: Unwin Hyman, pp. 11–33.
- Elkin, A. P. (1967). *Les Aborigènes Australiens*. NRF, Ed. Gallimard.
- Feblot-Augustins, J. (1995). *La Mobilité des Groupes Paléolithiques*. Seminar: Archéologie Paléolithique et Inférences démographiques, Collège de France, March 1995.
- Gambier, D. & Houet, F. (1993). Hominid remains. An up-date. France, Upper Paleolithic Supp. In (R. Orban, Ed.) *Anthropologie et Préhistoire* 6.
- Gamble, C. (1983). Culture and society in the Upper Palaeolithic of Europe. In (G. Bailey, Ed.) *Hunter-gatherer Economy in Prehistory*. Cambridge: Cambridge University Press, pp. 201–208.
- Gamble, C. (1986). *The Palaeolithic Settlement of Europe*. Cambridge: Cambridge University Press.
- Gamble, C. (1993). People on the move: interpretations of regional variation in Palaeolithic Europe. In (J. C. Chapman & P. Dolukhanov, Eds) *Cultural Transformations and Interactions in Eastern Europe*. Aldershot: Aveburg.
- Gordon, B. C. (1990). World Rangifer communal hunting. In (L. B. Davis & B. O. K. Reeves, Eds) *Hunters of the Recent Past*. London: Unwin Hyman, pp. 277–303.
- Gusinde, M. (1931). *Die Feuerland Indianer*. Mödling bei Wien: Verlag der internationalen Zeitschrift "Anthropos".
- Hardy, M. (1891). La datation quaternaire de Raymondens à Chancelade (Dordogne) et la sépulture d'un chasseur de rennes. *Bulletin de la Société Hist. Et. Archéol. du Périgord XVIII*, 195–212.
- Hayden, B. (1981). Subsistence and ecological adaptation of modern hunter/gatherers. In (R. S. O. Harding & G. Teleki, Eds) *Omnivorous Primates*. New York: Columbia University Press, pp. 344–421.
- Hewitt, G. M. (1994). The genetic consequences of long distance dispersal during colonization. *Heredity* 72, 312–317.
- Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58, 247–276.
- Housley, R. A., Gamble, C. S., Street, M. & Pettitt, P. (1997). Radiocarbon evidence for the Late glacial human recolonisation of Northern Europe. *Proceedings of the Prehistoric Society* 63, 25–54.
- Huntley, B. (1990). European vegetation history: palaeovegetation maps from pollen data—13,000 years BP to present. *Journal of Quaternary Science* 5, 103–122.
- Huntley, B. & Birks, H. J. B. (1983). *An Atlas of Past and Present Pollen Maps for Europe: 0–13,000 Years Ago*. Cambridge: Cambridge University Press.
- Jochim, M. A. (1983). Palaeolithic cave art in ecological perspective. In (G. Bailey, Ed.) *Hunter-gatherer Economy in Prehistory*. Cambridge: Cambridge University Press, pp. 212–219.
- Jochim, M. A. (1987). Late pleistocene refugia in Europe. In (O. Soffer, Ed.) *The Pleistocene Old World. Regional Perspectives*. New York: Plenum, pp. 317–331.
- Jones, B. A. (1990). Paleoindians and proboscideans: ecological determinants of selectivity in the southwestern United States. In (L. B. Davis & B. O. K. Reeves, Eds) *Hunters of the Recent Past*. London: Unwin Hyman, pp. 68–86.
- Keeley, L. H. (1988). Hunter-gatherer economic complexity and "population pressure": a cross-cultural analysis. *Journal of Anthropological Archaeology* 7, 373–411.
- Kelly, R. L. (1995). *The Foraging Spectrum. Diversity in Hunter-gatherer Life Ways*. Washington, DC: Smithsonian Institution Press.
- Krupnik, I. (1993). *Arctic Adaptations*. Hanover: University Press of New England.
- Le Gall, O. (1992). Poissons et pêches au Paléolithique (Quelques données de l'Europe occidentale). *L'Anthropologie* 96, 121–134.
- Le Gall, O. (1995). Aperçu des pêches maritimes préhistoriques en Europe occidentale. *L'Homme Préhistorique et la Mer*, 120^e congrès CTHS, Aix en Provence, 377–385.
- Leroi-Gourhan, A. (1943). *Evolution et Technique. L'Homme et la Matière*. Paris: A. Michel.
- Leroi-Gourhan, A. (1988). *Dictionnaire de la Préhistoire*. Paris: Presses Universitaires de France.
- Levine, M. A. (1983). Mortality models and the interpretation of horse population structure. In (G. Bailey, Ed.) *Hunter-gatherer Economy in Prehistory*. Cambridge: Cambridge University Press, pp. 23–46.
- Montet White, A. (1966). *Le Paléolithique en ancienne Yougoslavie*. Grenoble: Jérôme Million.
- Mortillet, G. de. (1990). *La Préhistoire*. Paris: Reiwald.
- Mulvaney, D. J. (1976). "The chain of connection": the material evidence. In (N. Peterson, Ed.) *Tribes and Boundaries in Australia*. Canberra: Publisher?.
- Murdock, G. P. (1967). Ethnographic atlas: a summary. *Ethnology* 6, 109–236.
- Murdock, G. P. (1981). *Atlas of World Cultures*. Pittsburgh: University of Pittsburgh Press.
- Nougier, L. R. (1959). *Géographie Humaine Préhistoire*. Paris: Gallimard.
- Oakley, K. P. (1971). *Catalog of Fossil Hominids*. Part II, Europe, British Museum (Natural History). London.
- Orban, R. (1988). Hominid remains. An up-date. Italy. Suppl. In (R. Orban, Ed.) *Anthropologie et Préhistoire*.
- Orban, R. (1990). Hominid remains. An up-date. British Isles and Eastern Germany. Suppl. In (R. Orban, Ed.) *Anthropologie et Préhistoire* 3.
- Orban, R. (1991). Hominid remains. An up-date. Spain. In (R. Orban, Ed.) *Anthropologie et Préhistoire* 4.
- Otte, M. (1981). Le Gravettien en Europe. In *Dissertationes Archaeologicae Gandenses XX*. Bruges: de Tempel.
- Peyrony, D. (1933). Les industries aurignaciennes dans le bassin de la Vézère. Aurignacien et Périgordien. *Bull. Soc. Préhist. Française* 30, 543–559.
- Peyrony, D. (1935). Le gisement Castanet, vallon de Castanet, commune de Sergeac (Dordogne). Aurignacien I et II. *Bull. Soc. Préhist. Française* 32, 418–443.
- Royama, T. (1992). Analytical population dynamics. *Population and Community Biology*, 10. London: Chapman and Hall.
- Rozoy, J.-G. (1989). Roc-la-Tour et la démographie du Magdalénien. In *Le Magdalénien en Europe. Actes du Colloque de Mayence—1987*, Dir. J.-Ph. Rigaud. *ERAUL* 38, Liège, pp. 81–97.
- Soffer, O. & Gamble, C. S. (Eds) (1990). *The World at 18,000 BP. Vol. 1, High Latitudes*. London: Unwin Hyman.
- Sonneville-Bordes, D. de. (1973). The upper palaeolithic. In (D. G. E. Piggott & C. B. M. McBurney, Eds) *France before the Romans*. Park Ridge, NJ: Noyes Press, pp. 30–60.

570 J.-P. Bocquet-Appel and P.-Y. Demars

- Webb III, T. & Bartlein, P. J. (1992). Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics* **23**, 141–173.
- Whallon, R. (1989). Elements of cultural change in the later Palaeolithic. In (P. Mellars & C. Stringer, Eds) *The Human Revolution*.

- Behavioral and Biological Perspectives in the Origins of Modern Humans*. Edinburgh: Edinburgh University Press, pp. 433–454.
- Wobst, M. (1978). The archaeo-ethnology of hunter gatherers on the tyranny of the ethnographic record in archaeology. *Am. Ant.* **43**, 303–309.