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The demography of the Upper Palaeolithic hunter–gatherers of Southwestern France: A multi-proxy approach using archaeological data

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A B S T R A C T

Demographic change is increasingly cited as an explanation for many of the patterns seen in the Palaeolithic archaeological record, following the assumption of a relationship between population size and material culture espoused by dual inheritance theory. However, the empirical testing of this relationship relies on the ability to extract information about past population patterns from the archaeological record. Using the extensive and well-studied record of the Upper Palaeolithic (~39,500–11,500 cal BP) hunter–gatherers of Southwestern France as a case-study, this paper compares the evidence for changes in relative population size as seen in three popular archaeological proxies for demographic change (site counts, site sizes, and occupation intensity estimates). These proxies present conflicting results across the sequence; a finding which is explored through the impact of taphonomic biases and past research agendas. Numbers of sheltered sites and quantities of retouched stone tools are suggested to be the most reliable demographic proxies. The problem of equifinality of interpretation in archaeological proxies for demography is examined for the Aurignacian and Gravettian periods in the region, with changes in lithic raw material, faunal acquisition strategies, and hunter–gatherer mobility all potentially contributing to the patterns documented.

1. Introduction

Archaeological theories about the role of demography in social and cultural change have developed a new lease of life recently through their investigation within human behavioural ecological and evolutionary frameworks. Drawing on *life history theory*, several scholars have advocated studying the long-term population trends documented in the archaeological record from the perspective of the decisions of individuals, designed to maximise their reproductive success (Boone, 2002; Hammel and Howell, 1987; Hill, 1993; Read and LeBlanc, 2003; Shennan, 2002, 2009). Concomitant with this interest in the role of the individual in demographic change is the study of material culture within a framework of *dual inheritance theory* (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981), which maintains that in addition to a biological inheritance system, humans also possess a cultural inheritance system which is subject to similar evolutionary processes. Within this framework population dynamics (particularly fluctuations in population size) are viewed as the most important factor in understanding cultural change (Shennan, 2000: 821) as "we cannot explain regional culture historical patterns without first understanding regional demography" (Shennan and Edinborough, 2007: 1344).

This link between population size and cultural change has been used to explain several features of the Palaeolithic archaeological record, most prominently the spatially and temporally piece-meal appearance of 'modern human behaviour' (Culotta, 2010; Powell et al., 2009, 2010; Richerson et al., 2009; Shennan, 2001) and the seeming lack of cultural diversity and innovation across much of the global archaeological record of the Lower and Middle Palaeolithic (Bocquet-Appel and Tuffreau, 2009; Hopkinson et al., 2013; Hosfield, 2005; Nowell and White, 2010; Premo, 2012; Premo and Kuhn, 2010). These studies draw on models and experiments which demonstrate the prominent influence of population size on social learning and the frequency of random selection processes (Richerson et al., 2009: 211), affecting both rates of innovation and the maintenance of cultural traits ('cumulative culture') (Derex et al., 2013; Ghirlanda and Enquist, 2007; Ghirlanda et al., 2010; Henrich, 2004, 2006; Kempe and Mesoudi, 2014; Kline and Boyd, 2010; Neiman, 1995; Riede and Bentley, 2008; Shennan, 2001; cf. Fitzhugh and Trusler, 2009; Read, 2006, 2012).

It has been proposed that the link between material culture and demography espoused by dual inheritance theory is likely to be more pronounced in the Palaeolithic, as the acquisition of the

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techniques of artefact production would have focused heavily on vertical transmission between parent and offspring (Shennan and Steele, 1999). Variations in material culture would thus be strongly related to the ebb and flow of the populations in question. However, Collard et al. (2013a) have recently recommended caution in the use of population size as an explanation for patterns in the Palaeolithic archaeological record, pointing out ambiguities in previous studies of hunter–gatherer groups and the limited testing of models against empirical archaeological data (see also Collard et al., 2005, 2011, 2013b; Read, 2012). Palaeolithic archaeologists have clearly benefitted from the demographic data generated from the modelling studies discussed above, as well as the ever-increasing corpus of palaeo-genetic studies which estimate past population sizes and trends (e.g. Atkinson et al., 2008; Beaumont, 2004; Chikhi et al., 2010; Cox et al., 2009; Excoffier, 2002; Excoffier and Schneider, 1999; Fabre et al., 2009; Garrigan et al., 2007; Harpending et al., 1998; Harris and Hey, 1999; Scheinfeldt et al., 2010; Stajich and Hahn, 2005). Nonetheless, the testing of the relationship between demography and cultural change in the Palaeolithic is dependent on the availability of data on population patterns from the *archaeological* record (Steele and Shennan, 2009: 114).

To this end, this paper builds on earlier studies which examine Palaeolithic demography using archaeological data (e.g. Ashton and Hosfield, 2010; Ashton and Lewis, 2002; Bocquet-Appel and Demars, 2000a, 2000b; Conard et al., 2012; Demars, 1996, 1998; French and Collins, 2015; Gamble et al., 2004, 2005; Grayson and Delpech, 2003; Grove, 2010; Hosfield, 1999, 2005; Meignen et al., 2006; Mellars and French, 2011, 2013 (cf. Dogandžić and McPherron, 2013); Morin, 2008; Petraglia et al., 2009; Schmidt et al., 2012; Stiner, 2001, 2009; Stiner and Munro, 2002; Stiner et al., 1999, 2000, 2008; Straus, 2011; Straus et al., 2000; see French, 2015 for a review), focusing on the case-study of the hunter–gatherers of the Upper Palaeolithic (~39,500–11,500 cal BP) of Southwestern France. A multi-proxy approach initially applied by Mellars and French (2011) is used, in an attempt to overcome the biases inherent with different types of data, and to; (1) explore how the demographic patterns generated through each proxy compare or converge, and; (2) assess which types of proxy data can be obtained most reliably from the Palaeolithic archaeological record.

2. Palaeodemography: how do we study demography from the archaeological record?

Palaeodemography is the demography of past populations for which no written source material is available. Three demographic variables are the immediate causes of all population change; (1) fertility (the process by which a population bears children); (2) mortality (the process by which the members of a population are reduced by death), and; (3) migration (both immigration and emigration) (Hinde, 2002: 18). Changes in a population's size, density, or growth rate are the result of variation in at least one of these variables (Daugherty and Kammeyer, 1995: 11). Unfortunately, data on these variables are unavailable for the palaeodemographer. Palaeodemography is thus largely restricted to the study of *relative* chronological and geographical changes in population density, distribution and size, rather than the specific demographic variations that caused these changes (although some estimates of changes in fertility and mortality rates have been inferred from osteological remains; e.g. Buikstra and Konigsberg, 1985; Buikstra et al., 1986; Greene et al., 1986; Konigsberg and Frankenberg, 2005; cf. Bocquet-Appel and Masset, 1982; Corruccini et al., 1989; Petersen, 1975, and these parameters can be modelled; Bocquet-Appel and Degioanni, 2013; Sørensen, 2011; Surovell, 2000; Zubrow, 1989).

Three of the most common approaches to the study of demographic archaeology are summarised in Table 1 and form the basis of this study. These are; (1) site counts; (2) settlement/site size analysis, and; (3) accumulations research (see Varian and Ortman, 2005). Within a palaeodemographic framework, the magnitude of chronological variation in these proxies is indicative of the magnitude of variation in population size or density (Attenbrow, 2006: 13). The use of radiocarbon date summed probability distributions ('dates as data' (Rick, 1987)) is also a popular palaeodemographic approach (e.g. Anderson et al., 2011; Armit et al., 2013; Bocquet-Appel et al., 2005, 2009; Hinz et al., 2012; Kelly et al., 2013; Martínez et al., 2013; Meeks and Anderson, 2012; Munoz et al., 2010; Shennan, 2009, 2013; Shennan and Edinborough, 2007; Tallavaara and Seppä, 2011; Tallavaara et al., 2010; Wicks and Mithen, 2014; Williams, 2012, 2013; Williams et al., 2010) which has already been applied to the dataset under discussion here (French and Collins, 2015).

Two main difficulties are common to these approaches (French, 2015). Firstly, they rely on proxy data; the archaeological material itself contains no direct demographic information (Chapman, 1999). The methods listed in Table 1 provide the required means to convert the archaeological proxy data into statements about demographic change. However, all of these approaches suffer from the problem of equifinality; multiple different explanations could be evoked validly to explain the patterns seen in the data. For example, different rates of artefact accumulation between sites could indicate changes in the number of individuals inhabiting them, but could also be related to differing occupation lengths or alternative living arrangements (e.g. Heizer, 1960: 93; Hiscock, 1986; Ross, 1985: 82–83). For hunter–gatherers, such as those discussed here, the most frequently cited alternative explanation for patterns in the data is that of a change in mobility or land-use strategy (e.g. Attenbrow, 2006; Schmidt et al., 2012).

The other difficulty is what is termed the "contemporaneity problem" (Schacht, 1984). This refers to the practice of classifying remains of the same period as contemporary when it is unlikely

Table 1
Summary of the three palaeodemographic methods employed in the study, and key examples of their application to the Palaeolithic archaeological record.

Methodology	Theoretical assumption	Key Palaeolithic examples
Site counts	Number and distribution of sites reflects the relative size and distribution of past populations	Bocquet-Appel and Demars (2000b), Bocquet-Appel et al. (2005), Demars (1996, 1998), Lahr and Foley (2003), Mellars and French (2011, 2013), Schmidt et al. (2012), Straus (2011), Straus et al. (2000), van Andel et al. (2003)
Site size	Positive correlation between site area and number of inhabitants	Burke (2006), Grove (2010), Hayden (2012), Mellars (1973), Mellars and French (2011, 2013), White (1985)
Accumulations research	Positive correlation between the amount of cultural material deposited at a site and the number of inhabitants	Ashton and Hosfield (2010), Ashton and Lewis (2002), Conard et al. (2012), Grayson and Delpech (2003), Hosfield (1999, 2005), Meignen et al. (2006), Mellars and French (2011, 2013)

that they are *strictly* contemporary. For example, a sample of sites in the landscape may date to the same period, but poor chronological resolution and data palimpsests make it difficult to assess whether they were occupied simultaneously or sequentially. This distorts population estimates by combining centuries or millennia into a single phase (Freter, 1997), ignoring change within periods, and forcing a reliance on the equation of 'populations' with certain classes of material culture (for attempts to overcome the contemporaneity problem see Ammerman et al., 1976; Grove, 2012; Hill, 1970; Schacht, 1981).

While archaeologists are increasingly citing demographic change as an explanation for patterns in the Palaeolithic archaeological record, the dual problems of chronological control and equifinality of interpretations are more pertinent than for later prehistoric periods. The range of cultural material available as proxy data is more limited, and difficulties of data resolution and palimpsests of occupation are more pronounced (Conard, 2001), particularly as the applicability of ^{14}C dating is restricted to only the later stage (post ~40 kya) of the period. Doubts have also been raised about the suitability of palaeodemographic methods to the study of archaeological records generated by archaic hominins (e.g. Hassan, 1981: 84), although the focus of this study on Upper Palaeolithic *Homo sapiens* populations bypasses this problem in the current instance. Despite these reservations, results from earlier studies (see Table 1) suggest that examining relative demographic trends in the Palaeolithic (particular the Upper Palaeolithic), is within the limits of archaeological data, especially when a multi-proxy approach is taken and the results are situated within the wider framework of the demography of ethnographically documented hunter–gatherers.

3. Background: The Upper Palaeolithic geography and history of Southwestern France

The Upper Palaeolithic of Southwestern France is an ideal case study for exploring and testing a range of demographic approaches to the Palaeolithic archaeological record. The archaeological record of the region is exceptional, coupling continuous Pleistocene occupation with a long history of research extending back to the mid-19th century (see Sackett, 1981), the broadly uniform intensity of which, both in chronological and geographical terms, goes some way to eliminate the problems of sampling and taphonomic bias which often hamper demographic studies. Despite this, previous palaeodemographic efforts are limited, and for the most part superficial or based on only one type of archaeological data (e.g. de Sonneville-Bordes, 1960, 1973; David, 1973; Mellars, 1985; Smith, 1966 cf. Grayson and Delpech, 2003; Langlais et al., 2012; Mellars and French, 2011).

The specific area of Southwestern France chosen for this study centres on the modern administrative *département* of Dordogne and incorporates the six surrounding *départements* of Charente-Maritime, Charente, Corrèze, Lot, Lot-et-Garonne and Gironde (Fig. 1). The area spans approximately 1.5 degrees in latitude, from 44°3″N in Lot-et-Garonne, to 45°7″N in Charente-Maritime, and covers ~50,000 km^2, although the area available for occupation was undoubtedly larger in the late Pleistocene and has since been reduced due to rises in global sea-levels and altering coastlines (Lambeck et al., 2002).

The study area consists of a roughly triangular-shaped sedimentary basin, lying between the Massif Central to the East, the Pyrénees to the South and the Atlantic Ocean to the West. A wide

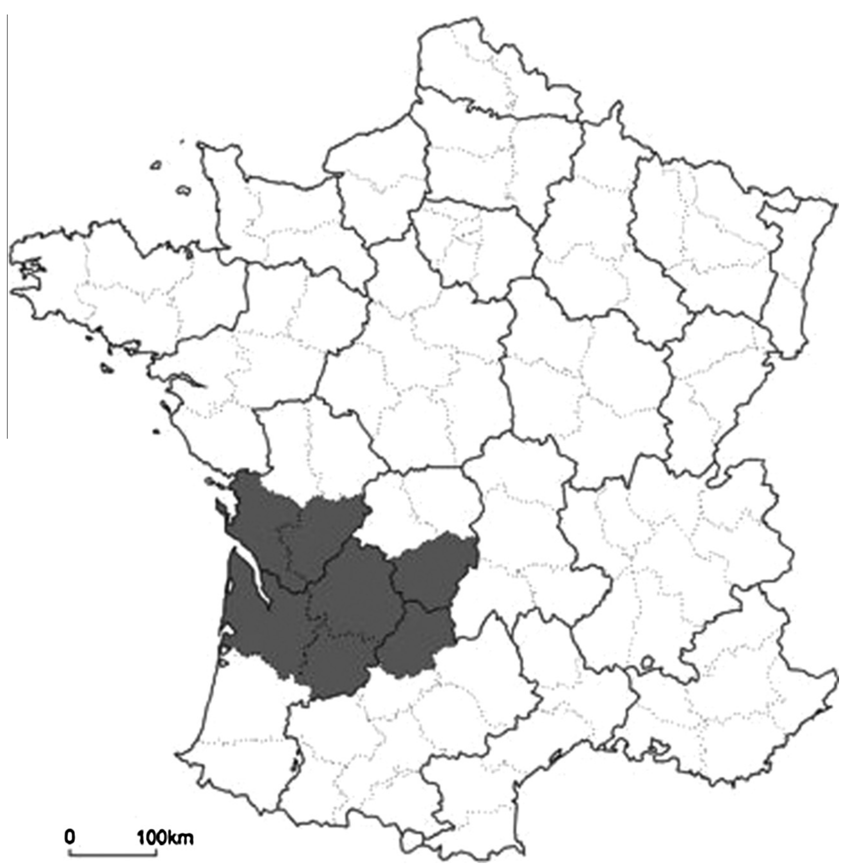


Fig. 1. Map of France showing the location of the study region.

range of landscapes, with associated underlying geology, are present, including the Aquitaine plains, the plateaux of the Massif Central, terraced alluvial valleys and the coastal region of the Poitou in the North. Two great rivers flow through the region, both of which have numerous tributaries; (1) The Garonne, which runs through Charente-Maritime, Gironde and Lot-et-Garonne as it flows North from the Pyrénees before heading North-West, and; (2) The Dordogne, which runs through Corrèze, Lot, Dordogne, and Gironde before joining the Gironde estuary.

The dominant geological features of the region are caves (*grottes*) and rock-shelters (*abris*) from which the majority of Upper Palaeolithic finds have been recovered. These occur throughout the study region but are most common in the Cretaceous limestone dominated landscapes of the Dordogne, specifically the Dordogne and Vézère valleys in the southeast (Laville et al., 1980: 4; Tixier, 2009: 12), creating a landscape of sheltered river valleys and contrasting limestone plateaux, the topography of which is suggested to have changed little since the late Pleistocene (White, 1985: 51). The abundance of naturally occurring shelters is considered to be one of the main factors that favoured human occupation of the region throughout the span of the Upper Palaeolithic (Mellars, 1985, 1996: 50).

The Upper Palaeolithic occupation of the region by hunter–gatherer populations occurred in the late Pleistocene from ~39,500 to 11,500 cal BP. Terrestrial and marine climatic proxy records from the region including speleothem sequences (Genty et al., 2003, 2010; Wainer et al., 2009), sediment profiles (Bertran, 2005; Bertran et al., 2008, 2013), lacustrine pollen sequences (Ampel et al., 2008, 2010; Wohlfarth et al., 2008), and marine cores from the European Atlantic ocean margin of both France and nearby Northern Iberia (Daniau et al., 2009; Genty et al., 2010; Naughton et al., 2007, 2009; Sánchez-Goñi et al., 2008) indicate that late Pleistocene global climatic changes (Dansgaard–Oeschger cycles; Dansgaard et al., 1993; Grootes et al., 1993; Svensson et al., 2008, and Heinrich events; Andrews, 1998; Hemming, 2004) had local climatic and environmental effects in Southwestern France, although these may have been subject to time-lags (Blaauw et al., 2010).

Archaeologically, the Upper Palaeolithic of Southwestern France is divided into five broad successive periods; Aurignacian (~39,500–34,000 cal BP), Gravettian (~34,000–26,100 cal BP), Solutrean (~26,100–24,600 cal BP), Magdalenian (~24,600–15,500 cal BP) and Azilian (~15,500–11,500 cal BP). These five periods show a clear chronological and stratigraphic succession, originally identified through the presence of diagnostic lithic 'type-fossils' (*fossils directeurs*), and later by radiometric dates. These phases are divided further into sub-phases, although ambiguities are present throughout the chronological sequence as a result of conflicts between absolute dates and stratigraphy, and questions surrounding the chronologically diagnostic nature of some type-fossils (e.g. Bon, 2002; Ducasse, 2012). In view of these ambiguities simplified sub-divisions of each of the five periods were adopted for this study. This simplified archaeological sequence is presented in Table 2 (see Supplementary Material for detailed discussion on both the absolute dating of these phases and their sub-divisions).

Table 2
The Upper Palaeolithic succession in Southwestern France, showing start dates and length of each phase for the simplified archaeological sequence used in this analysis. See Supplementary Material for detailed discussion of how these phases were determined.

Period	Start date (kya cal BP, IntCal 13)	Length of phase (kyr)
Aurignacian		5.5
Early Aurignacian	39.5	3.5
Late Aurignacian	36.0	2.0
Gravettian		7.9
Early Gravettian	34.0	2.5
Middle Gravettian	31.5	2.0
Late Gravettian	29.5	3.4
Solutrean		1.5
Early/Middle Solutrean	26.1	0.6
Late Solutrean	25.5	0.9
Magdalenian		9.1
Badegoulian	24.6	2.8
Middle Magdalenian	21.8	3.6
Upper Magdalenian	18.2	1.2
Final Magdalenian	17.0	1.5
Azilian	15.5	4.0

4. Methods

The data for the study were collected through a comprehensive literature review, compiled into a database which includes all the recorded sites in the study region which can be dated either absolutely or relatively (typologically) to any of the five main periods of the Upper Palaeolithic of Southwestern France. A total of 542 sites (865 occupations as many of the sites were occupied in multiple periods) were included in the database (Table S3, Supplementary Material). Specifically, data on the three different parameters listed in Table 1 were collected and analysed as described below. These proxies were studied with the aim of examining chronological variations between and, where possible, within periods, although the lack of data restricted the comparative analysis of these sub-stages to the analysis of numbers of archaeological sites. Due to the varying sample sizes, and the resultant wide range of values, medians were preferred over means as a measure of average values. The availability of the required data for all three of the proxies was heavily variable and dependent on such factors as location within the study region, type of site (whether sheltered or open-air), period(s) of occupation within the Upper Palaeolithic sequence, and date of site excavation. As such, not all of the methods described below were applied to all of the sites included in the database. Nonetheless, the study adheres to the idea of 'safety in numbers' within palaeodemographic analysis; that interpretations be based on the results of multiple proxies, and that for each of these proxies the study of multiple sites will average out or minimise much inter-site variation (whether behavioural, taphonomic or introduced by differing excavation/analytical techniques) to provide an reasonable assessment of the wider trend.

(1) Numbers of archaeological sites

Data on the number of archaeological sites belonging to each stage of the Upper Palaeolithic were collected following the assumption that variations in the number of sites reflect fluctuations in the relative size and distribution of past populations. A 'site' was defined as any location where at least one lithic artefact chronologically diagnostic of any of the 5 periods of the Upper Palaeolithic was present. Each period was divided further into the sub-stages presented in Table 2. Sites from the study area which have been radiometrically dated to the Upper Palaeolithic but contain no artefactual evidence for human occupation were not included. Painted/decorated caves were only included where chronologically diagnostic artefactual material was also present. The definition of a 'site' used explicitly does not assume that all of those included in the database were permanent or long-term habitation sites, nor that all of the sites documented for each period were occupied simultaneously.

To account for the different lengths of each period and sub-stage, site counts were standardised by converting these into estimates of the number of sites/1000 years, assuming the approximate lengths given in Table 2 and rounded to the nearest whole number. The figures generated represent *averages* over the time-scale of the period in question, and do not imply that the numbers of archaeological sites remained constant within periods. To compensate for taphonomic bias relative to time-depth, and to prevent their artificial over-representation (relative to the number that existed in the past) later in the Upper Palaeolithic sequence, the taphonomic correction curve of Surovell et al. (2009) was applied to the open-air site counts, taking the chronological mid-point of each period as the correction factor. While sheltered sites are also likely subject to some taphonomic loss relative to time-depth, no similar curve currently exists to accommodate for this, and these deposits are generally better protected than those at open-air sites (see discussion in Surovell et al., 2009).

(2) Site size

Data on the size (m^2) of Upper Palaeolithic sites were collected from the literature, following the assumption of a positive (although not necessarily linear) correlation between site area and the number of inhabitants. One difficulty is identifying how many occupation episodes are represented by the archaeological remains at a site, and the extent to which successive visits caused the zones of occupation to shift laterally; large sites could be the result of the single occupation of a large group, or successive (re)occupations by smaller groups over an extended time period, although small sites could only feasibly have been occupied by small groups. While there is some ambiguity in correlating group size and site size as far as larger sites are concerned, it is reasonable to assume that small sites reflect occupation by a small group, especially in instances where the site size is either spatially constrained or remains small despite the potential for expansion.

Data on site sizes were gathered from 3 main sources; (1) White's (1985) study of the Upper Palaeolithic sites of the Périgord region; (2) written descriptions in site reports, and; (3) excavation plans and sections. Very few authors offered a clear definition of 'site size' in their reports which reduces the comparability of the data. 'Site size' in this study refers to the overall extent as delineated by cultural occupation remains. For cave and rock-shelter sites this equates to the sheltered area, plus the associated terrace (*sensu* White, 1985). Due to the lack of spatial constraints, the absence of clear sections from which to estimate site size, and the difficulty of assessing whether outlying occupation remains are associated with the site proper, or represent an additional find-spot on the landscape, the estimates are invariably much cruder for open-air sites.

Site size data were used to calculate the number of small ($<500\ m^2$) and large ($\geqslant 500\ m^2$) sites present for each period. One fundamental (but largely insurmountable) caveat of this is the multi-period use of the majority of these sites, and the inability to assess from the literature when the size quoted was attained. However, this concern is limited to sites which lack clear spatial restrictions and the use of only two broad size categories minimises the impact of this problem on the overall patterns generated.

Where the data permit, specific areas of documented occupation for a period at a site were also collected in order to study specific chronological fluctuations in the area occupied (Table S4, Supplementary Material). For multi-period sites, the area over which material diagnostic of each period was documented through excavation was taken. For single-period sites, the total area of the site was taken, following the assumption that all cultural material belongs to the same period. Many of the sites in Southwestern France have not been excavated or surveyed in their entirety and these estimates remain therefore minimum estimates of both the overall site area and the extent of occupation in each period as known site size is clearly affected by the extent of excavation (see, for example Roebroeks' et al. (2011) recent work at the site of Laugerie-Haute Est (Dordogne)). Sites where only small sondage/trial excavations have occurred (defined here as $<10\ m^2$) were excluded from the analysis.

(3) Occupation intensity (accumulations research)

Occupation intensity was calculated following the assumption of a positive correlation between the amount of cultural material at a site and the number of inhabitants. Four further assumptions underpin the use of this proxy; (1) that the density of occupation residue calculated is representative of that over the whole site; (2) that differential selection and excavation strategies have not distorted the estimates; (3) that the different potential functions of the sites analysed (e.g. within part of a seasonal/annual round of settlement) have only a minimal impact on the values produced, once averages are taken across periods, and; (4) that occupation intensity values are expressed in strictly relative terms and explicitly do not assume continuous human occupation of any of the sites over the time-ranges in question.

Two different forms of occupation residue were analysed: (1) quantities of retouched stone tools, and; (2) estimates of ungulate meat weights (kg) (Tables S5 and S6, Supplementary Material).

(a) Retouched tool counts

Quantities of lithic artefacts were chosen as they are the most common type of material culture found in the Upper Palaeolithic archaeological record. The total quantity of lithic material was rejected as a viable proxy as the collection and curation of non-diagnostic flakes and perceived lithic 'waste' products was limited throughout a large part of the 20th century, during which a significant number of the sites in the study region were excavated (Clark and Lindly, 1991: 578; Rigaud and Simek, 1987: 49; Sackett, 1981). To enhance comparability across sites and assemblages, the analysis was restricted to counts of retouched tools classified by the de Sonneville-Bordes and Perrot (1953) 'type-list' of 97 formal Upper Palaeolithic retouched tool types.

(b) Ungulate meat weight

Ungulate meat weight was chosen as a viable palaeodemographic proxy, following the assumption that faunal assemblages represent the food debris of the main source of dietary protein for hunter–gatherers in the European Upper Palaeolithic (Drucker and Henry-Gambier, 2005; Richards, 2009) and can provide an indication of the potential quantity of food, and therefore number of consumers, at a site.

Counts of the Minimum Number of Individuals (MNI) represented by an assemblage were collected from the literature for the 10 most prevalent ungulate taxa in the region (Table S6, Supplementary Material). Only ungulate assemblages which were deemed to have been accumulated by human groups were included in the analysis (see Cruz-Uribe, 1991; Kuhn et al., 2010; Pickering, 2002). The remains of carnivores and small vertebrates were excluded, as they are likely to have accumulated largely through non-human activity and to have made only a minimal contribution to the diet of Upper Palaeolithic groups.

To calculate the total meat weight represented by an assemblage the MNI (per taxon) was multiplied by the amount of meat one individual of the taxon would provide (see White, 1953), using the estimates given in Table S7 (Supplementary Material). Estimates of available meat (defined as all parts of the animal exclusive of bone and hide (Lyman, 1979: 536)) were used over estimates of consumable meat as the latter is likely to be culturally defined (Reitz and Wing, 2008: 233).

Where data on age and sex accompany the published MNI count the appropriate adjusted estimates given in Table S7 were used. Where these data were unavailable or difficult to correlate with the published MNI counts, the mean adult weight was used. Given the rarity of this information in the literature, the estimates given in this study should be considered the maximum potential meat weight (food).

In order to maximise the available database, where published MNI counts were unavailable, estimates were used, extrapolated from published NISP (Number of Identified Specimens Present) counts, following the method outlined in Mellars and French (2011). Briefly, this involved a systematic comparison between the reported NISP and MNI values for the 10 taxa studied from 12 sites included in the analysis for which quantitative data on both values were given in the published faunal reports (Table S8, Supplementary Material). A NISP:MNI ratio was calculated for each (achieved by dividing the NISP value by the MNI value) and the median value (rounded to the nearest whole number) of the calculated ratios was taken to provide an appropriate 'conversion' factor for each species. Meat weight estimates based on these extrapolated MNI counts followed the procedure given above.

All sites in the study region were included for which explicit numerical counts of each/either of the two forms of occupation residues were available, along with a clear estimate of the area (m^2) from which these residues derived and reasonable confidence in the integrity of the assemblage. Where possible, the results of the most recent analysis of the site/assemblage were used, following the assumption that these would adhere to stricter excavation and analytical criteria. Clear cases of reworked sequences and mixed assemblages were discarded from the analysis, although stratigraphic integrity has only been studied for a handful of (mostly Aurignacian) sites in the region (e.g. Le Piage, Roc-de-Combe (Bordes, 2002, 2003), Le Flageolet, La Ferrassie (Michel, 2010)). As with the site counts, to compensate for the differences in the duration of each period, densities were standardised for each site in terms of the quantity of occupation residue recorded per square metre of the excavated occupation levels, per 1000 years of the documented occupation sequence. Calculations based on areas of occupation were preferred to those based on volume of sediments, due to the influence of such factors as localised rock falls and other geological and climatic factors on overall sedimentation rates during occupation sequences. For each site, the overall duration of occupation in each period was based on the assumption that the sites were potentially open and available for occupation during the whole of the known time-span (see Dogandžić and McPherron, 2013: 312 for a critique) and the occupation density/m^2 estimates were divided by the figures given in Table 2. Where there is clear evidence that only a certain sub-stage of a period is present at a site, occupation density was only calculated for that stage. Where more than one occupation level belonging to a sub-stage is present at a site, the mean area of the levels in question was used in the calculation.

5. Results

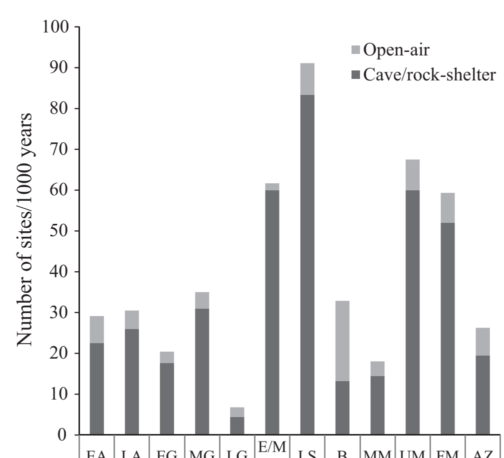
5.1. Site counts

Numbers of archaeological sites vary greatly across the techno-complexes of the Upper Palaeolithic. Extreme peaks in numbers of archaeological sites/1000 years are seen in the Solutrean and Upper/Final Magdalenian, with smaller spikes in the Middle Gravettian and Badegoulian. The gross numbers of sites for these periods are not exceptionally higher than those for other periods, suggesting that the short duration of the phases in question are driving this spike in the demographic signature (with the exception of the longer Middle Gravettian and Badegoulian). Dips in the number of archaeological sites are seen in the Early Gravettian, the Middle Magdalenian and Azilian, with the lowest number seen in the Final Gravettian (Fig. 2).

The impact of taphonomic loss with time-depth was assessed for open-air sites by applying the correction curve of Surovell et al. (2009). For each period the total number of sheltered sites, the total number of open-air sites, and the corrected value for open-air sites were scaled between 0 and 1 by dividing each value by the maximum observed value in that category. The relative temporal frequencies are displayed in Fig. 3. While similarities are seen in places (most noticeably the decreases seen in both site types ~33,000 cal BP), the distributions of open-air and sheltered sites differ throughout the Upper Palaeolithic, even when open-air sites are corrected for taphonomic bias. Mostly noticeably, a peak in the frequency of open-air sites ~23,000 cal BP (Badegoulian) contrasts with a clear dip in the frequency of sheltered sites, and in the latter part of the sequence (20,000–16,000 cal BP), the frequency of open-air sites decreases, while that of sheltered sites increases. These differences pose problems for the interpretation of relative demographic trends from these data. One possible explanation for this difference is that the study region is outside of the geographical region of applicability of Surovell et al.'s (2009) correction curve. Alternatively, periods of clear divergence between the frequency distributions of the sheltered and open-air sites may reflect the deliberate and/or preferential selection by the hunter–gatherers of Upper Palaeolithic Southwestern France of either type of site.

5.2. Site size

The quantity of large (⩾500 m^2) and small (<500 m^2) sites show remarkable consistency in their relative frequency throughout the span of the Upper Palaeolithic. Small sites constitute between 68.2% (Azilian) and 77.1% (Gravettian) of the known sample for any given period, and large sites between 22.9% (Gravettian) and 31.8% (Azilian) (Table 3).



	EA	LA	EG	MG	LG	E/M S	LS	B	MM	UM	FM	AZ
Open-air	7	5	3	4	2	2	8	20	4	8	7	7
Cave/rock-shelter	23	26	18	31	4	60	83	13	14	60	52	20

Fig. 2. Fluctuations in the number of sites/1000 years across the main periods of the Upper Palaeolithic in Southwestern France. EA = Early Aurignacian; LA = Late Aurignacian; EG = Early Gravettian; MG = Middle Gravettian; LG = Late Gravettian; E/M S = Early/Middle Solutrean; LS = Late Solutrean; B = Badegoulian; MM = Middle Magdalenian; UM = Upper Magdalenian; FM = Final Magdalenian; AZ = Azilian. Reproduced from French and Collins (2015).

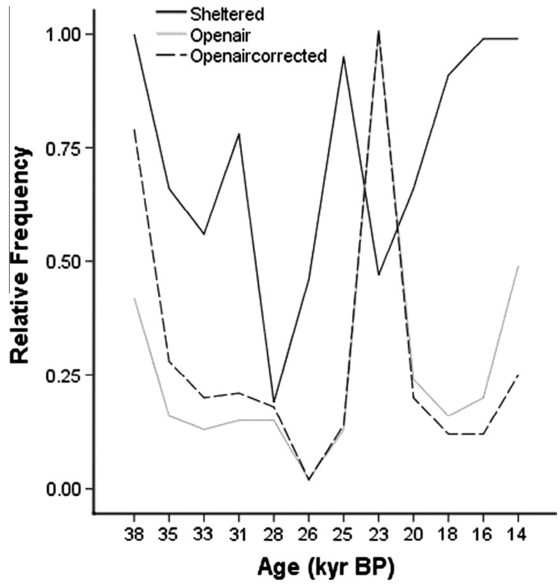


Fig. 3. Temporal frequency distribution of numbers of archaeological sites across the Upper Palaeolithic of Southwestern France, showing the different distributions of; (a) sheltered (cave/rock-shelter) sites; (b) open-air sites, and; (c) open-air sites once corrected for taphonomic bias using the curve of Surovell et al. (2009). All values have been standardised between zero and one, and show strictly relative difference in the frequency of sites. Reproduced from French and Collins (2015).

Table 3
Site size data for the Upper Palaeolithic sequence in Southwestern France, documenting number and frequencies of large (⩾500 m^2) and small (<500 m^2) sites, and the median documented areas of occupation for cave and rock-shelter sites. See Table S4, Supplementary Material for data on areas of occupation.

	Period	*n*	Small sites	Large sites
Number and frequency of large and small sites	Aurignacian	100	76 (76%)	24 (24%)
	Gravettian	83	64 (77.1%)	19 (22.9%)
	Solutrean	74	54 (73%)	20 (27%)
	Magdalenian	135	98 (72.6%)	37 (27.4%)
	Azilian	44	30 (68.2%)	14 (31.8%)
			Median documented area of occupation (m^2)	
Documented areas of occupation	Aurignacian	26	87.0	
	Gravettian	19	64.0	
	Solutrean	12	71.3	
	Magdalenian	38	112.0	
	Azilian	9	35.0	

Data on documented areas of occupation were available for 139 occupations. Magdalenian sites show the largest documented area of occupation ($n = 57$, $Md = 120.0$ m^2) and Azilian the smallest ($n = 12$, $Md = 35.5$ m^2), although a Kruskal–Wallis test showed no statistically significant differences between documented areas of occupation based on techno-complex ($n = 139$, $\chi^2(4) = 5.186$, $p = 0.269$). Analysis of only the cave and rock-shelter sites (for which the estimates are likely a truer reflection of past areas of occupation due to their spatially restrictive nature) showed a similar pattern with the largest documented areas of occupation seen in the Magdalenian ($n = 38$, $Md = 112.0$ m^2) and the smallest the Azilian ($n = 9$, $Md = 35.0$ m^2). While the differences between the documented area of occupation was shown to be statistically significantly across the techno-complexes (Kruskal–Wallis test $n = 104$, $\chi^2(4) = 11.386$, $p = 0.023$), pairwise comparisons (corrected using the Bonferroni correction) revealed that this significance was restricted to the differences between the Magdalenian and Azilian ($p = 0.014$) (Table 3).

5.3. Occupation intensity

5.3.1. Retouched tools

Data on quantities of retouched tools and the area (m^2) from which the tools derived were available for 60 cave/rock-shelter and 14 open-air occupations, the majority of which were excavated and/or analysed post-1970. An analysis of data from both open-air and sheltered sites shows the greatest density of retouched tools during the Solutrean ($n = 5$, $Md = 40.0$ tools/m^2/1000 years) and the lowest in the Magdalenian ($n = 16$, $Md = 4.9$ tools/m^2/1000 years). However, the small relative sample size of the Solutrean may be biasing the results, as well as the lack of data from open-air sites for both the Solutrean and Azilian periods. A Kruskal–Wallis test showed no statistically significant differences in quantities of retouched tools between chronological periods ($n = 74$, $\chi^2(4) = 3.928$, $p = 0.416$).

When only the more reliable data from the cave/rock-shelter sites are considered, a similar pattern is found, with the greatest densities of retouched tools still found in the Solutrean ($n = 5$, $Md = 40.0$ tools/m^2/1000 years) and the lowest in the Azilian ($n = 10$, $Md = 5.8$ tools/m^2/1000 years). Again, there were no statistically significant differences in quantities of retouched tools between chronological periods (Kruskal–Wallis test; $n = 60$, $\chi^2(4) = 3.997$, $p = 0.406$) (Fig. 4).

5.3.2. Faunal meat weights

Data on faunal assemblage meat weights and the area (m^2) from which the assemblages derived were available for 24 sites (39 occupations) all of which were caves and rock-shelters, and the majority of which were excavated and/or analysed post-1970. Of these, 13 sites had published MNI counts and the rest were converted from NISP counts using the conversion factors shown in Table S8. Due to the small number of sites for which data were available, sites with published MNI values and sites with converted MNI values were combined in the analysis. The greatest faunal meat weight densities was found in the Azilian ($n = 5$, $Md = 185.3$ kg/m^2/1000 years) and the smallest in the Gravettian ($n = 9$, $Md = 48.0$ kg/m^2/1000 years) (Fig. 4). A Kruskal–Wallis test showed no statistically significant differences in faunal meat weights between chronological periods ($n = 39$, $\chi^2(4) = 1.326$, $p = 0.857$).

6. Discussion

There are clear fluctuations in all the proxies suggesting that relative population sizes were not uniform across the Upper Palaeolithic in Southwestern France. This is not unexpected, as ethnographic data demonstrate that regional hunter–gatherer populations are subject to frequent fluctuations in relative population growth and decline, often liked with environmental factors and their associated impact on resource availability (Binford, 2001; Pennington, 2001). This is likely to have been the case in the Upper Palaeolithic, despite assumptions of relatively stable, slow-growing, global Pleistocene populations (see Hassan, 1981). Where these patterns have been tested for statistical significance, in the majority of cases the results were deemed to not be statistically significant. Nonetheless, the samples are often small, and it is incorrect to assume that because a relationship is not statistically significant, it is not archaeologically significant (and vice versa). The following discussion assumes that the patterns documented in the data are archaeologically significant and interprets them as such.

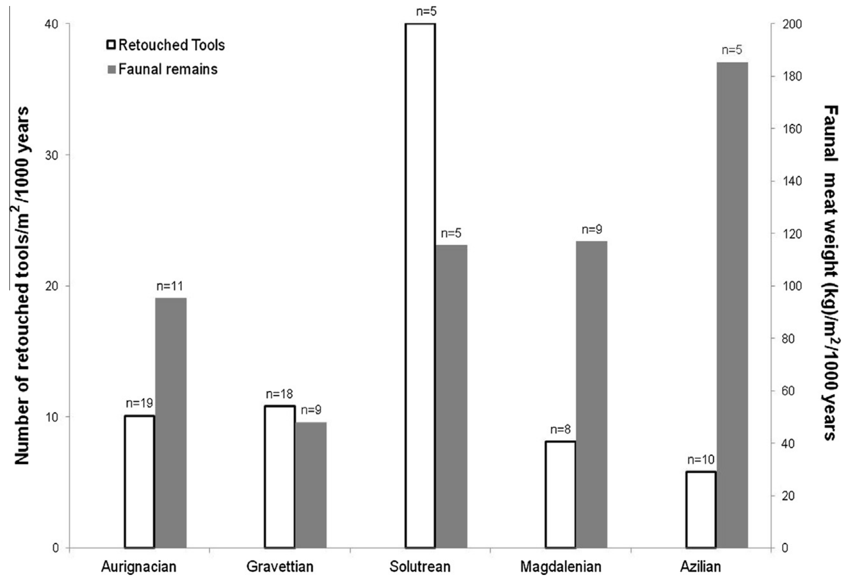


Fig. 4. Documented median occupation intensity values measured through retouched tool counts and faunal meat weight at archaeological sites across the Upper Palaeolithic in Southwestern France. See Tables S5 and S6, Supplementary Material for full data.

Site counts indicate a peak in population in the Solutrean, and a clear dip in the Gravettian. In particular, the Late Gravettian is identified by this proxy to be a period of low regional population density. The peak in the Late Solutrean supports the long-held hypothesis of Southwestern France as a population refugium during the Last Glacial Maximum (Jochim, 1987). The results presented here also support the hypothesis of the Final Magdalenian as a period of high population density in the region although this is actually a decrease from the preceding Upper Magdalenian, rather than the increase proposed by de Sonneville-Bordes (1960: 93) and Mellars (1973: 271). A similar pattern of demographic fluctuations across the Upper Palaeolithic sequence of Southwestern France was demonstrated by French and Collins (2015) using summed probability distributions of radiocarbon dates.

In terms of site size, the ratio of small:large sites is very consistent across the Upper Palaeolithic, although due to the relationship between site size and type of site discussed earlier, this fluctuates slightly depending on the ratio of sheltered: open-air sites. This pattern suggests similar group sizes amongst hunter–gatherers in each period, and a similar regional population density as rates of group population and dispersal, and the relative frequency of time spent in groups at either end of this continuum, could reasonably be interpreted as consistent across the Upper Palaeolithic sequence. Nonetheless, chronological differences are apparent in the more accurate proxy of documented area of occupation of sheltered sites, especially the contrast between the largest Magdalenian sites and smallest Azilian sites, suggesting possible differences in group size between techno-complexes.

In contrast, occupation intensity as measured through retouched tools at sheltered sites suggests differing group sizes between periods, with the highest values (and largest groups) seen in the Solutrean and the lowest values (and smallest groups) in the Azilian. Occupation intensity as measured through faunal meat weights showed a different pattern, being highest in the Azilian and lowest in the Gravettian.

As discussed earlier, a range of proxies have been used in this study in an attempt to overcome the biases inherent in each, and to provide a more holistic view of past demographic change through the consideration of multiple strands of archaeological evidence. However, the conflicting patterns presented in the data for each period call into question the assumption that all the proxies are measuring demographic change. These differences highlight the range of possible patterns of relative demographic change that can be inferred from the archaeological record depending on the proxy used. It is worth considering the extent to which taphonomic factors and data availability have affected both the different proxies and/or introduced biases at specific chronological points of the Upper Palaeolithic sequence.

6.1. The utility of old collections for demographic analysis

The aforementioned long and intensive history of Palaeolithic research in Southwestern France, while providing a large corpus of data, has introduced its own set of biases and limitations which have impacted the results of this study. As a high proportion of the Upper Palaeolithic sites in the region were excavated and published in the early 20th century, the collection and presentation of the data reflect the contemporary research priorities (see Sackett, 1981, 1991). Specifically, these refer to research strategies which had the primary aim of data collection for building regional chronologies. This predominant interest in chronology involved greater attention to the vertical, as opposed to horizontal, exposure of the site, and a tendency to concentrate on the richest archaeological sites (usually caves/rock-shelters) where the largest number of chronologically diagnostic lithic type fossils could be found, often conflating several stratigraphic levels (Sackett, 1968: 68).

These research priorities and excavation strategies have affected the availability of the data required for this analysis. Many sites mentioned in the literature were unpublished, the majority of which were excavated in the early 20th century prior to the professionalization of archaeological research in the region (White, 2002: 73). As the majority of the required data from these sites were missing, these function as little more than 'dots on a distribution map' of the Upper Palaeolithic settlement of Southwestern France. Data on the spatial extent of occupations was most clearly lacking; data on site size were only available for 238 sites (44% of the total sample), and several of the larger multi-level sites in the region, which would have permitted the study of temporal inter-site occupation intensity fluctuations had to be excluded due to a lack of data on the areas of the deposits excavated (e.g. La Madeleine, Laugerie-Haute Est/Ouest (Dordogne)). However, while the exact impact of these different research priorities and excavation strategies on the demographic patterns presented here is difficult to quantify there is no *a priori* reason to assume that they did not impact all of the sub-periods of the Upper Palaeolithic equally.

6.2. Taphonomy

The application of the taphonomic correction curve of Surovell et al. (2009) to the open-air sites including in the site count dataset has, theoretically, prevented the over-representation of younger sites in the demographic signature generated through this proxy, although the open-air sites form only 1/3 of the total site sample. The aforementioned similarities in the patterns generated through the use of site counts and the alternative demographic proxy of radiocarbon date summed probability distributions (French and Collins, 2015) does, however, suggest that time-transgressive taphonomic bias is not substantially impacting the pattern seen in the site count analysis and enhances the reliability of the trends documented (as the different materials being studied – organic materials for radiocarbon dating and stone tools as a proxy of site presence – are subject to very different taphonomic processes). With regard to the other proxies, the notion of a simple linear relationship between the archaeological data and age (i.e. that older materials are less frequent due to increased taphonomic loss with time-depth) is refuted by the patterns presented above, which show no clear chronological directionality.

Despite the application of the correction curve to numbers of open-air sites, it is still suggested that the number of sheltered sites documented in the site counts analysis is a better representation of the number of such sites occupied in the past, due to the twin factors of enhanced visibility (resulting in a bias towards the discovery of these sites; Laville et al., 1980; Wobst, 1974: 149) and greater protection of associated archaeological deposits. However, recent rescue excavations in the region conducted by INRAP have demonstrated the presence of previously unknown Palaeolithic open-air sites (Bourguignon et al., 2004). The question thus remains for the other proxies as to whether data from sheltered sites can be accepted as representative of all past activity, or whether their use was seasonal, linked to wider climatic/environmental conditions or reflected some other behavioural preference. Some relationships are, however, demonstrated between the type of site and the proxy data studied. Estimates of site size from sheltered sites are suggested to be more reliable, as open-air sites are more susceptible to problems of shifting lateral occupations, horizontal displacement of materials due to periglacial solifluction (Lenoble et al., 2008), and limited excavation relative to the estimated overall extent of the site. No data on faunal meat weight estimates were available from open-air sites due to poor preservation of organic remains. Data on retouched tool densities were, however, available from both types of site. Despite the robusticity of lithics, estimates based on data from sheltered sites were deemed more reliable due to factors similar to those listed above for the site size analysis, although it should be noted that rock-shelters in the valley floors are susceptible to possible flooding and scouring of occupation deposits (Straus, 1990: 259), and those on slopes can suffer intermittent episodes of slopewash processes and both scouring of deposits and accelerated infill (Attenbrow, 2006: 106; see Roebroeks et al., 2011 for the study region). However, detailed taphonomic studies of many of the sheltered sites included in this analysis are lacking, preventing a more detailed consideration of the impact of differential destruction and preservation both within and between proxies and site types, and across the chronological span of the Upper Palaeolithic.

7. Behavioural explanations for patterns in the proxy data: focus on the Aurignacian and Gravettian

In addition to uncertainties introduced through the incompleteness of the archaeological record, and the use of 'old' data, the aforementioned difficulty of equifinality of interpretation requires consideration. Differences in the behaviour of hunter–gatherers across the chronological span of the Upper Palaeolithic could feasibly account for the variations seen both within and across the proxy data. The Aurignacian–Gravettian (excluding the Late Gravettian) sequence is the only phase of the Upper Palaeolithic in the region with enough data (defined as $\geqslant 5$ assemblages) to examine changes in the proxies across sub-periods. The three most important behavioural variables are discussed below with reference to this well-documented sequence.

7.1. Mobility

A change in mobility strategy is frequently cited as a possible explanation for variations in the types of proxy data used in this study, particularly numbers of archaeological sites (Attenbrow, 2006). Variations in numbers of sites could reflect differences in the ways that people used the landscape and moved around the region, with people possibly; (a) moving between sites more or less frequently; (b) organising their movement differently, or; (c) spending different amounts of time in various stages of group fission/fusion (aggregation and dispersal) as is characteristic of ethnographic hunter–gatherers (Pedersen and Woehle, 1991; Turnbull, 1968, 1972; Woodburn, 1968, 1972). In particular, differences in mobility strategy adopted by hunter–gatherers along Binford's (1980) forager/collector continuum affect both the number of potential archaeological sites generated and their subsequent visibility, likelihood of survival, and eventual incorporation into archaeological datasets. However, the two explanations are not mutually exclusive and the exact relationship between demography and mobility is unclear, the two variables being both inter-dependent (see Grove, 2009; Kelly, 2003) and affected by external factors, including environmental setting (Kelly, 1983, 2013; Whallon, 2006). At a minimum there is a correlation between group size and population density and mobility *strategy*, with larger group sizes and higher population densities found amongst groups practising logistical (collector) mobility (Binford, 2001).

As shown in Fig. 2, numbers of archaeological sites/1000 years are highest in this period in the Middle Gravettian, and lowest in the Early Gravettian and Late Gravettian with a considerable decrease in the numbers of sites between the Middle Gravettian and the Late Gravettian. The question remains as to what extent changes in mobility across the Aurignacian and Gravettian, rather than demographic changes, are affecting the patterns seen in the

Table 4
Numbers of new sites created and the relative frequency (%) of cave/rock-shelter sites for the Aurignacian and Gravettian in the study region.

Period	Number of new sites/1000 years and % of total site sample	% of cave/rock-shelter sites
Early Aurignacian	12 (41%)	77.5
Late Aurignacian	4.5 (15%)	85.2
Early Gravettian	6 (29%)	86.3
Middle Gravettian	7 (20%)	88.6
Late Gravettian	2.6 (39%)	65.2

number of archaeological sites. One way to address this is to consider some secondary site characteristics (Table 4). For example, the similar relative frequency of sheltered: open-air sites throughout the Aurignacian and Gravettian sequence in the region (ranging from 65.2% of the known sample in the Late Gravettian to 88.6% of sites in the Middle Gravettian) suggests that differences in the settlement pattern in terms of relative use (and subsequent preservation and archaeological discovery of) of open-air sites to sheltered sites, cannot account for the large scale differences in the documented number of archaeological sites. While data on the number of sites established in each period (i.e. at which the first traces of human occupation dated to the period under consideration) support the notion of the Late Gravettian as a period of low population density (with only 2.6 new sites established/1000 years), these accounted for one of the highest proportions of the total number of sites seen across the sequence (39% of all sites). In contrast, in the Middle Gravettian only 20% of the documented sites were first occupied by humans during this period. Differences in the relative visibility and importance to mobile hunter–gatherer groups of sites that were either newly established or well-known and had been occupied previously may affect the correlation between regional population density and numbers of archaeological sites. In particular, the creation of relatively more new sites in the Late Gravettian period, compared with both the Early and Middle Gravettian could be related to higher residential mobility as small hunter–gatherer groups moved repeatedly around the landscape to collect food resources, although this is somewhat at odds with the overall low number of sites documented for this period. The aforementioned lack of data on occupation intensity in the Late Gravettian makes this hypothesis difficult to test. However, data from the Middle Gravettian show high numbers of sites, fewer new sites created, and high densities of retouched tools (see below), possibly suggesting increased regional population density, accompanied by an increase in logistical mobility in which more sites acted as intensively occupied 'home-bases' where large groups camped, and fewer low-density new sites were created.

7.2. Lithic technology

As shown in Fig. 4, occupation intensity as measured through retouched tool counts at sheltered sites was slightly higher in the Gravettian than the Aurignacian, although this difference is not statistically significant. Divided into sub-periods, the lowest rate of occupation intensity was found in the Early Aurignacian ($n = 15$, $Md = 6.8$ retouched tools/m^2/1000 years) and the highest in the Middle Gravettian ($n = 13$, $Md = 17.7$ retouched tools/m^2/1000 years) (Fig. 5). Again, there were no statistically significant differences in quantities of retouched tools between the sub-periods (Kruskal–Wallis test: $n = 51$, $\chi^2(3) = 2.906$, $p = 0.406$).

There are several behavioural variables which could affect the quantities of retouched tools independent of number of people, including; (a) changes in the importance of retouched tools compared to un-retouched flakes and blades; (b) changes in the importance of lithic tools in the cultural repertoire compared to organic (bone, antler) tools; (c) changes in location of artefact discard; (d) variations in lithic manufacturing technology, including differences in the rate of tool reduction/re-sharpening, and; (e) the effects of variable raw material supplies on rates of tool manufacture, use, and discard. Of these variables, the best available comparative data relates to raw material selection across the Aurignacian and Gravettian and data on technological strategies from the key site of Abri Pataud (Dordogne).

Variations in raw material and distances of procurement can affect the lithic assemblage, through the organisational strategy that shows an inverse relationship between the amount of material transported, which usually decreases with distance from sources, and the extent to which the material is utilised, which increases with distance (Blades, 1999a: 712). Due to the extra effort involved in procuring the material, any artefacts made from non-local sources are likely to be considered less expedient than those for which the material is locally abundant, and as a result should be subjected to a greater degree of re-working/re-sharpening. Demars (1999) has demonstrated a link in the study region between raw material type and tool types, with high-quality,

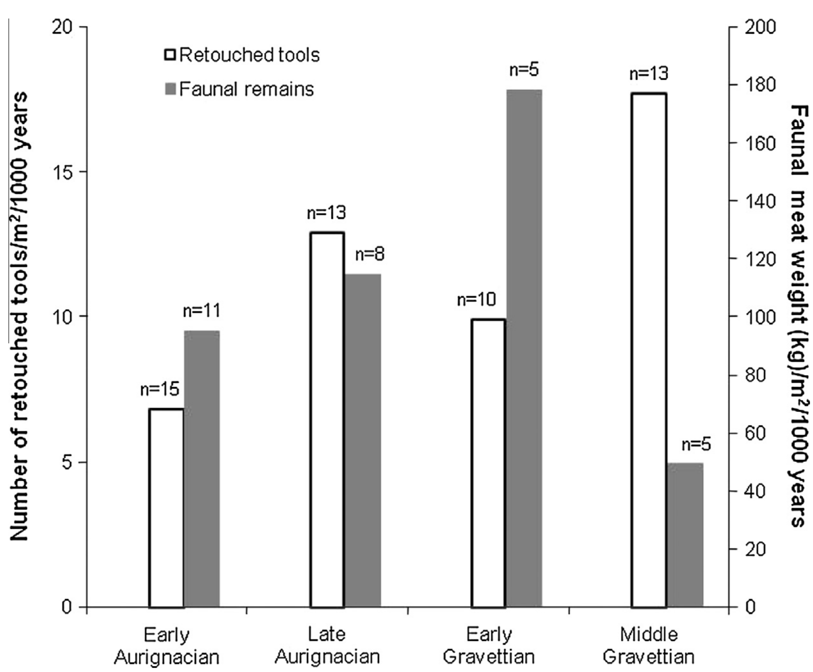


Fig. 5. Documented median occupation intensity values measured through retouched tool counts and faunal meat weight at archaeological sites across the sub-periods of the Aurignacian and Gravettian in Southwestern France. Data on the Late Gravettian was excluded due to an inadequate sample size (<5 assemblages). See Tables S5 and S6, Supplementary Material for full data.

non-local flint being used preferentially for the making of 'prestigious' tool forms, and 'essential' tools, which form the bulk of the tool–kit (primarily scrapers and burins) made from locally abundant and easy to access sources. How could these factors have impacted the quantities of retouched tools across the Aurignacian and Gravettian sequence?

Studies of the raw material from numerous sites in the study region demonstrate a positive correlation between the frequency of high-quality, non-local Bergerac flint and Upper Palaeolithic industries dominated by blade production (Chiotti, 2005; Demars, 1984, 1999; Nespoulet, 2000). As such, the relative abundance of this flint type is higher in Early Aurignacian and Gravettian assemblages than Late Aurignacian assemblages. Demars (1999: 7) also notes a high proportion of Gravette and Font-Robert points manufactured in Bergerac flint. These assemblages largely adhere to the aforementioned link between mode of raw material transport and distance from site, with non-local flint introduced at a site in an already worked form, and more stages of the production sequence evident at the site for local flint (Demars, 1999: 8), although this does vary across the study region (Morala, 1984; Morala and Turq, 1990). While the correlation between an emphasis on blade production and raw material would affect the total amount of lithic material brought to sites, this would primarily affect differences in the quantity of all lithic debitage, rather than retouched tool counts. The use of non-local flint for Gravettian 'Gravette' and 'Font-Robert' points might partially account for the decreased retouched tool count for the Early Gravettian (following the assumption that these would have been preferentially re-worked rather than discarded), although these only form a small component of the total retouched tool repertoire. The presence of increased retouched intensity in Early Aurignacian assemblages (heavy 'Aurignacian retouch'), indicative of increased tool re-sharpening and re-use, in combination with the relative abundance of flint from non-local sources, and the Late Aurignacian technological strategy which produced more blanks per core (Blades, 1999a, 1999b, 2001), could potentially accommodate the increase in numbers of retouched tools seen between the Early and Late Aurignacian.

As one of the few sites in the region which covers the full Aurignacian and Gravettian sequence (with the exception of the Proto-Aurignacian) and for which seemingly reliable data on total quantities of lithic material (including debitage and nuclei) are present, the site of Abri Pataud (Dordogne) provides a rare opportunity to assess chronological differences in the relative frequency of retouched tools relative to the total lithic assemblage. The mean values of retouched tools percentages are similar across the Early and Late Aurignacian (16.1% and 17.6% respectively), although the values for each level fluctuate greatly (Table 5). The data from Abri Pataud also permit the comparison of occupation intensity values based on number of lithic pieces with those seen through retouched tool counts (Fig. 6). The documented trends are similar in both proxies, with the exception of an increase in lithic pieces not seen in the retouched tool counts in the Early Gravettian. This increase in lithic pieces is the opposite of what would be expected for this period, as the increased quantity of high-quality Bergerac flint found in this level (Nespoulet, 2008: 143) should, as discussed above, be associated with a decrease in on-site tool production and associated debris. While this pattern from the Abri Pataud cannot be extended to all of the sites studied (particularly as the sequence from the Abri Pataud differs from the overall

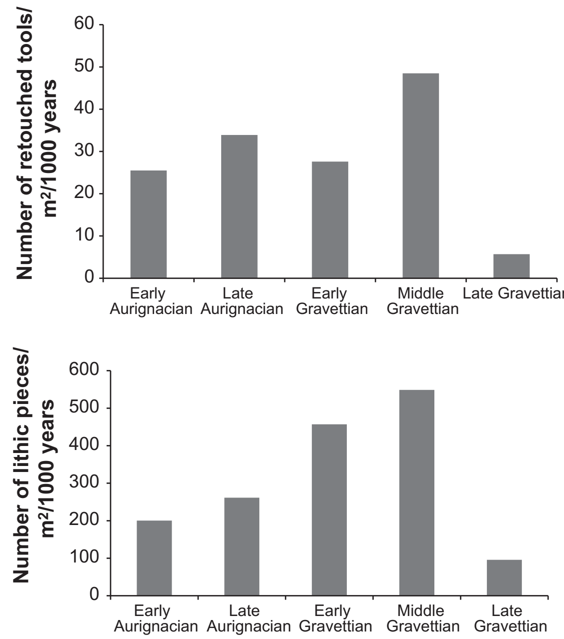


Fig. 6. Comparison of occupation intensity values for the site of Abri Pataud (Dordogne) through the proxies of retouched tool counts (above) and total number of lithic pieces (below). See Table S5, Supplementary Material for data.

Table 5
Total lithic counts, % of retouched tools in the assemblage and occupation intensity values based on the two proxies of retouched tool counts and total lithic counts for the site of Abri Pataud (Dordogne). Data for the Aurignacian from Chiotti (2005) and Nespoulet (2008) for the Gravettian. Areas used in calculations are the mean of all levels dated to that sub-period. See Table S5, Supplementary Material for full data on numbers of retouched tools and areas used.

Level	Total quantity of lithic pieces	% of retouched tools	Occupation intensity (number of retouched tools/m^2/1000 years)	Occupation intensity (number of lithic pieces/m^2/1000 years)	Cultural attribution
14	1466	15.8	25.5	200.4	Early Aurignacian
13	1302	6.1			
12	2819	18.1			
11	6759	17.8			
10/11	279	22.6			
10	772	9.6	33.9	261.3	Late Aurignacian
9	319	9.4			
8	5676	11.8			
7 upper	5308	15.8			
7 lower	556	22.1			
6/7	289	28.0			
6	3802	26.3			
5	5800	6.0	27.6	457.1	Early Gravettian
4	8833	8.8	48.5	548.8	Middle Gravettian
3	1656	4.9	5.7	95.7	Late Gravettian
2	1845	7.3			

trend of an increase in occupation intensity values between the Early and Late Aurignacian), the near correlation of the retouched tool and lithic piece values lends credence to the suggestion that fluctuations in retouched tool intensity values may reflect a demographic signature and are not being obscured by behavioural and technological variation.

7.3. Faunal acquisition and processing strategies

As seen in Fig. 4, occupation intensity measured through faunal meat weights was much greater in the Aurignacian than the Gravettian. Divided into sub-periods, the lowest rate of occupation intensity was found in the Middle Gravettian ($n = 5$, $Md = 49.4$ kg/m^2/1000 years) and the highest in the Early Gravettian ($n = 5$, $Md = 178.5$ kg/m^2/1000 years) (Fig. 5). Again none of the differences seen between periods were statistically significant (Kruskal–Wallis test: $n = 29$, $\chi^2(3) = 2.604$, $p = 0.457$). Interestingly, the peaks and troughs in the data are the opposite of those found with the retouched tools, although it should be noted, that in contrast to the retouched tool analysis, the available sample for the Gravettian sub-periods was up to ~50% smaller than those for the Aurignacian.

As with the retouched tools, there are several behavioural variables that could impact the quantity of faunal remains at archaeological sites independent of the number of consumers. These include; (a) variations in hunting strategies and the effects of different age/sex profiles of the animals killed on the quantity of meat provided; (b) variations in the storage of animal remains; (c) potential destruction of the faunal remains through the actions of various cultural practices (e.g. burning bones as a source of fuel); (d) variable spatial patterns of discard of the faunal remains within the sites, or changes in the location of discard; (e) variation in the intensity and exploitation of the animal carcass for consumption, and; (f) variation in transportation of animal carcasses due to factors such as distance from kill site. Data on these variables are mostly related to faunal procurement and processing, although the lack of comparative studies across the Aurignacian and Gravettian sequences forces a reliance on 'snap-shots' of behaviour, and the impact of any differences on the patterns documented in the occupation intensity analysis are difficult to assess.

One of the defining differences between the Early and Late Aurignacian in the study region is the decrease in the relative frequency of reindeer in faunal assemblages between the two periods (Boyle, 1990: 185; Grayson and Delpech, 2003, 2005; Grayson et al., 2001; Mellars, 2004). Several studies of Early Aurignacian processing strategies of both reindeer and other ungulates in the study region suggest intensive on-site carcass exploitation, reporting cut-marks concurrent with on-site skinning of carcasses and disarticulation of prime meat-yielding elements (Sollier and Mallye, 2012), and evidence of long-bone fracturing for marrow extraction (Morin, 2004), with reindeer remains indicating that most of the consumption took place on site (Binford's (1978) 'inverse bulk curve') (Chiotti et al., 2003 cf. Blades, 1999b: 107). Unfortunately (for present purposes), these data are most often compared to that from the earlier Mousterian and Châtelperronian periods, rather than the Late Aurignacian.

Boyle's (1990: 240) study of the butchery and carcass management strategies used throughout the Gravettian at the site of Abri Pataud (Dordogne) show some chronological differences across the period. There is evidence of more intensive processing in the Late Gravettian, corresponding with a 'bulk curve' and a 'gourmet curve' focusing on high-utility parts in the Early and Middle Gravettian. Data on faunal meat weights from the site show a concomitant decrease in the Late Gravettian (from 481.5 kg/m^2/1000 years in the Middle Gravettian to 110.7 kg/m^2/1000 years in the Late Gravettian (Table S6, Supplementary Material), although the reliance on converted MNI estimates for the meat weight analysis makes taking this correlation further tenuous. However, a similar processing strategy has been documented for the reindeer assemblage for the Middle Gravettian at the site of Le Flageolet I (Dordogne) (Enloe, 1993).

Differences in processing strategies of different species further complicates the assessment of the impact of this behavioural variable on the occupation intensity estimates generated, with differences seen between reindeer and horse assemblages in both Aurignacian (Chiotti et al., 2003: 199) and Gravettian (Boyle, 1990: 256) sites in the region. While the examples discussed above provide insight into the range of treatment of faunal remains in the Aurignacian and Gravettian, they show very little chronological patterning, and as the assemblages probably reflect more than one season of occupation, data on carcass management should be treated with caution (Boyle, 1990: 240).

8. Conclusion

Palaeolithic archaeologists are increasingly citing demographic causes for patterns seen in the archaeological record. While modelling and genetic data provide useful estimates of past population numbers and trends, there still remains a need for the empirical assessment of archaeological data in the investigation of palaeodemography. This study has compared the patterns of relative demographic change generated through the use of three different proxies for the Upper Palaeolithic of Southwestern France. This region was selected for study due to the presence of a well-defined and dated chronological sequence which permitted the study of diachronic change, the exceptional richness of the archaeological record, and the concomitant long history of intensive archaeological research, which minimised the effects of sampling and taphonomic bias.

In contrast to previous studies which utilise the same archaeological proxies (Mellars and French, 2011), the proxies did not show any clear chronological patterning,[1] and frequently presented conflicting demographic signatures. This raises some interesting issues of interpretation. Taking the results shown by the majority of proxies, should, at least in probability terms, be the best way to proceed, although that does not preclude the possibility that the signature generated through the converging proxy is the 'correct' one (see French, 2015). What is pattern and what is noise? One way of assessing the relative value of the regional patterns generated is to compare the results to wider-scale demographic studies (e.g. Bocquet-Appel and Demars, 2000a, 2000b; Gamble et al., 2004, 2005), although these are often based on a single type of archaeological data. While the focus of this study has been documenting relative demographic change rather than explaining it, another possible line of enquiry to select between competing patterns could be the comparison between the patterns generated and the patterns expected. Both group size and population density of ethnographically documented hunter–gatherers are known to vary according to environmental factors (Binford, 2001; Birdsell, 1953, 1958, 1968; Grove, 2009; Johnson, 2014; Layton and O'Hara, 2010; Marlowe, 2005). The comparison between the results generated by each proxy and the expected response of hunter–gatherers to the prevailing climatic and environmental conditions during a given

[1] It is unclear how the results of this current study impact on this previously published study of demographic change during an earlier period in the region. In Mellars and French (2011), a figure of a ten-fold population increase across the Neanderthal-to-Modern Human transition was proposed, based on the convergence in the results of the analysis between the same three proxies used in this study. Does the lack of convergence seen in the data here suggest that this figure is likely an overestimate, or does the lack of a similar pattern in this Upper Palaeolithic dataset reinforce the strength and size of this difference in the size of populations in Southwestern France across the Middle-to-Upper Palaeolithic transition?

period, particularly as it affects the availability of food resources, provides a useful starting point for choosing between competing demographic signatures.

For this dataset, I suggest that the number of sheltered sites and quantities of retouched tools are the most reliable; the former being well-preserved and the latter being robust, subject to limited taphonomic degradation, and largely standardised across sites in both collection methods and subsequent reporting. These suggest relative population increases in the Solutrean, Middle Gravettian, and Upper and Final Magdalenian with relative decreases in the Late Gravettian and Middle Magdalenian. A similar pattern has been documented for the study region using summed probability distributions of radiocarbon dates as a demographic proxy (French and Collins, 2015). Population increase at the regional level is strongly supported for the Middle Gravettian by the high occupation intensity as measured through quantities of retouched tools seen at archaeological sites dated to this phase. The faunal meat weight estimates are deemed to be *a priori* the least reliable proxy, being more susceptible to taphonomic destruction, lacking a fully standardised method of quantification (leading to reduced inter-site comparability), and being based on a smaller sample. These correlate with the proxy data which are obtained most easily from the Palaeolithic archaeological record. Although attributable largely to past regional research trends and trajectories, the difficulties documented with the lack of availability of data from old collections in the Southwestern French Upper Palaeolithic calls into question whether similar palaeodemographic methods can be applied to other, less intensively studied, regions.

Despite an imperfect archaeological record, it is possible to use archaeological data to explore patterns of relative demographic change in the Palaeolithic. Problems of equifinality of interpretation need to be considered, although as discussed above with the case of the Aurignacian and Gravettian sequence, a lack of studies of the long-term fluctuations in the behavioural variables which provide alternative explanations for patterns in the data prevent the empirical testing of competing interpretations. Difficulties of contemporaneity of occupation between sites and limitations of chronological resolution in Palaeolithic contexts also abound. The question remains as to whether these relative estimates are useful for the type of evolutionary and behavioural ecological approaches that currently dominate research agendas. In particular, the forced restriction in this study of the analysis of demographic change across the broad chrono-typological periods, rather than the much shorter sub-divisions, is unfortunately crude, conflating possibly hundreds of human generations. This obscures, or at least confuses, the role of the individual in past population processes, particularly with regard to the role of external stimuli (i.e. local environmental change). Nonetheless, the demographic trends seen in the archaeological record could serve as a starting point for further modelling studies, being used to help select the most likely absolute population estimates, and identify which parameter combinations provide the closest fit with the empirical archaeological data (e.g. Porčič, 2011).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jaa.2015.04.005.

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