Demography and the Palaeolithic archaeological record

Jennifer C. French

McDonald Institute for Archaeological Research, Department of Archaeology and Anthropology, University of Cambridge, Downing Street, Cambridge, CB2 3DZ, UK

Email: jcf35@cam.ac.uk Telephone: +44 (0)1223 338256

Abstract

Demographic change has recently re-emerged as a key explanation for socio-cultural changes documented in the prehistoric archaeological record. While the majority of studies of Pleistocene demography have been conducted by geneticists, the archaeological records of the Palaeolithic should not be ignored as a source of data on past population trends. This paper forms both a comprehensive synthesis and the first critical review of current archaeological research into Palaeolithic demography. Within prevailing archaeological frameworks of dual inheritance theory and human behavioural ecology, I review the ways in which demographic change has been used as an explanatory concept within Palaeolithic archaeology. I identify and discuss three main research areas which have benefitted from a demographic approach to socio-cultural change; 1) technological stasis in the Lower Palaeolithic; 2) the Neanderthal-*Homo sapiens* transition in Europe, and; 3) the emergence of behavioural modernity. I then address the ways in which palaeodemographic methods have been applied to Palaeolithic data-sets, considering both general methodological concerns and the challenges specific to this time period. Finally, I discuss the ability of ethnographic analogy to aid research into Palaeolithic demography.

Key words: Demography, Palaeolithic, hunter-gatherers, behavioural ecology, cultural evolution

Introduction

> *"Un des problèmes les plus irritants de la préhistoire paléolithique est celui qui est lié aux factuers démographiques" (Bordes et al. 1972:26)*

Demographic change has recently re-emerged as a key explanation for socio-cultural changes documented in the prehistoric archaeological record. Within wider research agendas of cultural evolution and cultural transmission theory (Boyd and Richerson 2005; Kuhn 2012; Shennan 2009a and papers therein), demographic change assumes a pivotal causal role in the understanding of variation in a wide range of archaeological material culture (e.g. Eerkens and Lipo 2005, 2007). As part of this evolutionary framework of cultural 'descent with modification,' population dynamics are viewed as the "single most important factor in understanding cultural change" (Shennan 2000:821) and regional demography and culture history are intimately and intrinsically linked. Aided by the increased precision of absolute dating methods, numerous recent studies document population patterns in the Holocene prehistoric archaeological record, exploring the relationships between demography, material culture, and environment (e.g. Armit et al. 2013; Attenbrow 2006; Bocquet-Appel et al. 2009; Crombé and Robinson 2014; Edinborough 2009; Hinz et al. 2012; Kelly et al. 2013; Kuijt 2009; Shennan 2001, 2009b, 2013; Shennan and Bentley 2008; Shennan and Edinborough 2007; Tallavaara and Seppä 2011; Tallavaara et al. 2013; Wicks and Mithen 2014; Williams et al. 2010).

While the primacy played by demography within this evolutionary framework is chronologically universal, the twin complications of the coarse resolution of absolute dating methods and the increase of data palimpsests has resulted in a situation in which the study of Pleistocene demography is largely the domain of researchers in fields other than archaeology. In particular, the work of population geneticists has highlighted the dynamic Pleistocene population history of both our own species and earlier hominins, transforming our understanding of the demography of Pleistocene foragers from a global history of slow growth rates and low population numbers (Hassan 1975 :41–42, 1981), to one of regional variation which saw population bottlenecks (Ambrose 1998; Excoffier 2002; Excoffier and Schneider 1999; Garrigan et al. 2007; Stajich and Hahn 2005), migrations and expansions (Achilli et al. 2005; Beaumont 1999; Jorde et al. 1997; Pereira et al. 2005; Ray et al. 2003), distinct geographical groupings (Fabre et al. 2009; Lalueza-Fox et al. 2011) as well as interbreeding between hominin species (Green et al. 2010; Neves and Serva 2012; Prüfer et al. 2014; Sankararaman et al. 2014; Wall et al. 2013).

Palaeolithic archaeologists are increasingly recognising the dynamic nature of Pleistocene demography, drawing on the results of both these genetic studies and mathematical models of the relationship between population and socio-cultural change (Shennan 2001; Powell et al. 2009). It is now widely acknowledged that processes of ebb and flow and local extinctions and colonisations characterised Pleistocene populations, representing responses to changing environmental and climatic conditions (Dennell et al. 2011; Gamble et al. 2004; Hublin and Roebroeks 2009). Utilising the independent estimates of population produced by other disciplines, demography is increasingly evoked as an explanatory variable for patterns seen in the Palaeolithic archaeological record. However, with some notable exceptions (e.g. Ashton and Hosfield 2010; Ashton and Lewis 2001; Bocquet-Appel and Demars 2000a, 2000b; Bocquet-Appel et al. 2005; Conard et al. 2012; French 2013; Grove 2010; Hosfield 1999, 2005; Mellars and French 2011, 2013; Morin 2008; Straus 2011; Straus et al. 2000), Palaeolithic archaeologists have been reluctant to use their own *archaeological* data to document and assess demographic change.

Archaeologists and anthropologists have long been sceptical of the ability of archaeological data to contribute to the study of Palaeolithic[1] demography, suggesting that none of the palaoedemographic methods used in later periods are applicable to Palaeolithic data-sets (Yellen 1977:100), and reducing any results to “reasonable guesses” (Howells 1960:175). More recent critiques have considered the study of Palaeolithic demography from archaeological data an “inexact science” or “black art” (Kuhn 2012: 82) with specific studies (e.g. Mellars and French 2011) lauded as “courageous” but the methods used dismissed as “rarely reliable” (Dogandžić and McPherron 2013; cf. Mellars and French 2013). The applicability of palaeodemographic methods developed from the study of ethnographic and historical populations to pre-modern (*Homo sapiens*) hominins has also been called into question (Hassan 1981:84), posing problems for the study of demography from the Early and Middle Pleistocene archaeological records.

Despite these reservations, the archaeological record remains the best source of data on the hominin extinctions, replacements, expansions, and migrations that occurred during the ~2.6 million year span of the Palaeolithic; demographic processes which would have impacted considerably on long-term trajectories of socio-cultural and

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[1] In this paper I use the term ‘Palaeolithic’ to refer more broadly to the Pleistocene, recognising that there are continental variants used to describe the archaeological record of this period.

artefactual change. Methods for estimating population size and densities from the Palaeolithic archaeological record are still in their infancy. Nonetheless, the archaeological record has the unparalleled potential to provide both a unique long-term perspective on Pleistocene demography, and direct empirical evidence from which to assess any results generated from the largely theoretical, or ethnographically-derived, models of the relationship between population size and culture which are currently dominating the research agenda (see Collard et al. 2013a).

This paper forms both a timely comprehensive synthesis and the first critical review of current archaeological research into Palaeolithic demography. This review comprises four main sections. I start by considering recent approaches to the study of demography within archaeology as a discipline, before reviewing the literature and analysing the implications of these approaches to our understanding of key features of the Palaeolithic archaeological record. I then move on from viewing demography as a purely explanatory concept, to assess critically the methods that archaeologists use to generate demographic patterns, focusing on the particular challenges of applying these to Palaeolithic data-sets. Finally, I examine the ethnographic record, discussing how, and to what extent, data on the demography of ethnographic hunter-gatherer groups can contribute to the study of Palaeolithic hunter-gatherer populations. While I adopt an explicitly critical stance to the potential pitfalls of studying Palaeolithic demography, the aim is not to imply that all demographic analyses founded on archaeological data are inherently and inescapably unreliable. Rather, the intention is to acknowledge the difficulties involved in studying prehistoric demography, identifying the theoretical and methodological challenges that are priorities for future research.

Archaeological approaches to demography

The study of demography has a long and varied history in archaeology (for summaries see Hassan 1978, 1981; Schacht 1981; Welinder 1979). Prior to the 1980s most studies adopted a Malthusian (1872) or Boserupian (1965) approach, in which population was seen respectively as either a dependent or independent variable in the relationship between food production, intensification, and population growth (e.g. Binford 1968; Childe 1936, 1950; Cohen 1975a, 1975b; Cowgill 1975a; Dumond 1965; Flannery 1969). As part of a wider research emphasis on adaptive explanations and the ecological basis of cultural change, processual archaeologists of the 1960s and 1970s embraced the Boserupian model of population as an independent variable in the process of socio- cultural change (Chamberlain 2006:4). Archaeological studies adhering to the Boserupian model focused on population as a ‘prime-mover’ (i.e. the primary causative factor), specifically population *pressure* caused by an upset in the equilibrium between population size and available food resources (see Bronson 1975; Cowgill 1975a, 1975b; Hassan 1974, 1975). Within this framework, population changes were viewed from the perspective of alterations in human adaptive systems.

Following the advent of Darwinian or Evolutionary archaeology in the 1980s (Dunnell 1978, 1980; see Shennan 2008 for a review), archaeologists have increasingly drawn on human behavioural ecology (HBE) and dual inheritance theory (DIT) to study demography. While both of these adhere to an evolutionary framework, they form two distinct, albeit largely complementary, research traditions, with HBE emphasising the role of natural selection in the evolution of human behaviour, and DIT emphasising the role of changing cultural traditions (Shennan 2008:78-79). Full reviews of these approaches are beyond the scope of this paper (see Bird and

O'Connell 2006 for a review of HBE in archaeology and Shennan 2011, 2012 for DIT), and the focus here will be on the implications of their use to explore and explain past demographic change in the archaeological record.

Human Behavioural Ecology and Life history theory

One of the key developments in palaeodemographic theory in the past thirty years has been the increased consideration of the role of individuals in large-scale population processes. Drawing on ideas from HBE, specifically *life history theory*, several scholars have advocated studying the long-term population trends seen in the archaeological record from the perspective of the decisions of individuals designed to maximise their reproductive success (e.g. Boone 2002; Hammel and Howell 1987; Hill 1993; Read and LeBlanc 2003; Shennan 2002, 2009). Reproductive success does not necessarily correlate with the maintenance of a high birth rate, but instead the adjustment of fertility within optimal fitness-maximising strategies. This involves an adaptive trade-off in resource and energy allocation between off-spring quality and quantity, reflected in variations in birth spacing, age at first birth, parenting strategies and mate selection and, when considering a range of hominins, additional biological factors such as maturation rate and brain and body size. (Borgerhoff Mulder and Schacht 2012:4-6; Winterhalder and Smith 2000). Environmental adaptation plays a key role in HBE, and strategies to maximise reproductive success are flexible and responsive to changes in a group's immediate environment (Shennan 2008:82). Due to this emphasis on environmental adaptations, the use of HBE, both generally and with regard to demography, has focused on forager populations (see Winterhalder and Smith 2000).

This emphasis on the actions of individuals has clear ramifications for how archaeologists think about past populations. When we view the agent of reproductive decisions as the individual rather than the abstract population (as seen in earlier processual studies; e.g. Cohen 1975a, 1975b, 1977; Harner 1970; Smith 1972), we reverse the interpretation of the resultant demographic pattern in the archaeological record: large-scale population trends become the result of multiple individual decisions triggered by personal experience and short-term self-interest, not goals of biological self-regulation designed to maintain long-term equilibrium with the environment (Read and LeBlanc 2003:62; Shennan 2002:110, 2009b:340). However, the poor resolution of the archaeological record conflates multiple human generations into one chronological event, and only permits the study of long-term trends. As such, the demographic picture generated is likely to be false and unrealistically stable (Read and LeBlanc 2003:60; Shennan 2002:118-123). This also affects the geographical scale of study of past populations. A focus on global or continental population patterns is potentially misleading within a life-history framework as it refers to aggregates of populations rather than a population *sensu stricto*, at least as far as concerns reproductive possibilities (Hammel and Howell 1987:142). While a large geographical focus may help compensate for low chronological resolution, a regional perspective is preferred. Thus, while the resolution of the archaeological record may trick archaeologists into envisioning population changes as long-term, global events, such processes occur at the local level on a short-to-medium time-scale. The introduction of life history theory into the archaeological study of demography provides a useful framework to relate the low resolution archaeological record to the behaviour behind its formation.

Dual inheritance theory

Concomitant with the behavioural ecological approach is the increased use of a framework which explicitly links demography with the interpretation of material culture. Drawing on earlier studies (Boyd and Richerson

1985; Cavalli-Sforza and Feldman 1981) archaeologists have investigated the material culture which forms the archaeological record in evolutionary terms (e.g. Collard and Shennan 2000; Eerkens and Lipo 2007; O'Brien and Shennan 2010; Powell *et al.* 2010; Richerson *et al.* 2009; Rosenberg 1994; Shennan 1996, 2000, 2002, 2008, 2009a, 2011; Steele and Shennan 2009). Specifically, cultural changes, including those seen in material culture, are viewed within a framework of *dual inheritance theory* (Boyd and Richerson 1985) which maintains that humans (unlike other animals) have a second, cultural, inheritance system, in addition to the biological, genetic, inheritance system. This system of cultural inheritance is subject to evolutionary processes, and can be understood in ways analogous to that of genetic inheritance.

The system of cultural inheritance is that of social learning and changes are typically envisioned as innovations (Shennan 1996:175, 2002:38, 51). Unlike the biological inheritance system is which genetic information is transmitted only from parent to offspring, cultural transmission can take many forms, cross-cutting generations (i.e. transmission between peers) and often involving multiple individuals (i.e. one-to-many transmission) (Cavalli-Sforza and Feldman 1981:53; Powell *et al*. 2010:140; Shennan 2002:50). There are two main processes which cause variation in cultural traits through social learning; 1) guided variation, in which individuals modify their socially-learnt cultural adaptations through trial and error, and; 2) biased transmission, in which individuals adopt a cultural trait preferentially (Boyd and Richerson 1985; Powell *et al*. 2010:141; Shennan 1996:176). In addition, random, non-selective processes of cultural drift (broadly analogous to genetic drift) can occur, with chance variation impacting the frequency with which cultural practices are copied, irrespective of their inherent properties (Shennan 1996:176). Within this evolutionary framework, changes in the frequencies of different cultural traits in the archaeological record are a result of these various processes of social learning and random variation (Powell *et al.* 2010:141).

This model of cultural evolution has significant implications for the way in which archaeologists theorise the relationship between cultural change and past populations. Within the DIT framework, demography has a considerable impact on cultural evolution and material culture change through the effect of demographic change on both social learning practices and the frequency of random selection processes (Richerson *et al.* 2009:211). Mathematical modelling has demonstrated the prominent influence of population size on rates of innovation and maintenance of cultural traits ('cumulative culture') as well as the impact of social connectivity and transmission networks between populations and levels of population stability (e.g. Henrich 2004; Ghirlanda and Enquist 2007; Ghirlanda *et al*. 2010; Neiman 1995; Riede and Bentley 2008; Shennan 2001, 2006). Similar to the system of genetic inheritance, it is the effective population size (in genetic terms, the breeding population; in cultural terms, the number of 'cultural parents' or those who pass on culture to subsequent generations) rather than the absolute (census) population size which affects the transmission of cultural traits (Shenann 2001:8).

Shennan's (2001) model suggests both that innovations are more likely to occur in larger populations, and that any innovations are more likely to be maintained than in smaller populations, resulting in increased cumulative cultural complexity. Cultural drift (random selection) resulting in the loss of cultural traits and traditions is shown by Neiman (1995) to be negatively correlated with population size. The relationship between population size and cultural change has been famously cited by Henrich (2004), who attributes the loss of cultural traits in Holocene Tasmanian populations to a rapid reduction in population size (Henrich 2006 cf. Fitzhugh and Trusler 2009; Read 2006, 2012). Furthermore, decreases in population size may differentially affect the evolution and maintenance of cultural traits. Simpler technologies, for which the skills required for production and usage are easier to acquire, are more likely to persist than those which require one-on-one learning from a particularly skilled individual (Derex et al. 2013; Henrich 2004:204; Kempe and Mesoudi 2014; Kline and Boyd 2010 cf. Collard et al. 2005; 2013a, 2013b; Read 2012; see also Vegari and Foley 2014), although assessing the skill required to manufacture artefacts found in the archaeological record (and thus their relative complexity) is difficult (Bamforth and Finlay 2008).

Drawing on these studies, Riede (2009:312) has suggested inverting the link between cultural evolution and demography, using changes in material culture as archaeological proxies for past demographic change. However, it is unlikely that human population histories and cultural histories are identical, except in rare circumstances where vertical (parent-to-offspring) transmission of cultural traits is extremely strong (Shennan 2002:64). Nonetheless, the link espoused by DIT between archaeologically-visible material culture and the archaeologically-invisible processes of demographic change provides a firm theoretical framework for the study of prehistoric population patterns using archaeological data.

Demography as an *explanatory* concept in the Palaeolithic

Within the broad frameworks of HBE and DIT, Palaeolithic archaeologists are increasingly evoking demographic change as an explanation for key patterns and events documented in the archaeological record. I identify three main research areas where the application of a demographic approach has changed how archaeologists think about socio-cultural change in the Palaeolithic; 1) technological stasis in the Lower Palaeolithic; 2) the Neanderthal-*Homo sapiens* transition in Europe, and; 3) the emergence of behavioural modernity. In all three cases, demography contrasts with the dominant (but not mutually-exclusive) paradigm in which explanations for these phenomena are based on the perceived cognitive capacities of the hominins in question.

1) Technological stasis in the Lower Palaeolithic

One of the most intriguing features of the Lower Palaeolithic archaeological record is the conservative nature of Acheulean technological industries. Found across Africa and large parts of Eurasia from around 1.6 million to 100,000 years ago [kya] BP, the Acheulean is a hand-axe dominated industry characterised as homogenous and technologically static across its wide chronological and geographical range (Issac 1972; Leakey 1975). The slow pace of technological change and limited diversity seen in Acheulean industries is frequently attributed to cognitive and linguistic constraints (resulting in an ability to innovate) amongst the hominins (*Homo erectus*) who manufactured them (e.g. Binford 1989; Isaac 1972; Mithen 1996). Although geographical and chronological differences are apparent, these are seen to represent ‘variations on a theme’ rather than fundamental alterations in the technological and typological underpinnings of the industry (Lycett and Gowlett 2008; Pettitt and White 2012:171). Nonetheless, it is becoming clear that the Acheulean is less uniform than commonly claimed, particularly at the regional and assemblage/site based level (McNabb et al. 2004; Nowell and White 2010: 70-72).

According to Nowell and White (2010) one of the most puzzling features of the Lower Palaeolithic archaeological record is the contrast between the relative stasis in technology and the concurrent evolution of

Middle Pleistocene hominin life histories. Drawing on ideas from HBE and DIT discussed above, Nowell and White (2010) have argued that the conservative nature of Acheulean industries has a demographic basis. They suggest the Lower Palaeolithic hominin populations were just too small for enduring change and technological advances to take place. The combination of low population numbers and wide dispersal and limited interconnectivity of Lower Palaeolithic groups meant that any innovations were unable to spread, resulting in a lack of cumulative cultural development, and a loss of skills associated with the innovation. In addition, they argue that the short duration of childhood and adolescence amongst Middle Pleistocene *Homo erectus*, would have limited the time individuals had to learn new skills, resulting in a situation where innovation was discouraged and in which the technological basis of Acheulean industries was imprinted early in the cultural learning process (Nowell and White 2010:76).

Hopkinson et al. (2013) take this idea further, emphasising the importance of Lower Palaeolithic metapopulations (the regional 'population of populations') to Acheulean technologies. They argue that in models linking demography and cultural innovation, it is the relationship between the local population and the regional population, rather than gross population size, which is crucial to the spread and persistence of cultural innovations and change (Hopkinson et al. 2013:65; see also Powell et al. 2009). In particular, the longevity of the local populations which comprise the metapopulation, and the social networks which bind them are key; factors which in turn are affected by local population sizes, territorial range and rate of migration and population aggregation and dispersal (Hopkinson 2011). Within this metapopulation model, Hopkinson et al. (2013) attribute widespread technological stasis in the Acheulean not only to small population sizes, but also limited territorial ranges and between-group migration, all of which contributed to short-lived local populations and the decreased likelihood of innovative behaviours being both disseminated and persisting.

Demographic explanations for technological stasis in the Acheulean are particularly persuasive as they explain one of the key contradictory features of the Lower Palaeolithic record: relative stasis and stability at larger chronological and geographical scales, with increased variation at the local level. Small population numbers, widely dispersed social groups, and frequent local group extinctions have all also been proposed to explain the perceived inertia of Middle Palaeolithic Neanderthal lithic industries, compared to those of the later Upper Palaeolithic (Bocquet-Appel and Tuffreau 2009: 296-297; Eerkens et al. 2013:1133; Premo 2012 ; Premo and Kuhn 2010; Hosfield 2005). In particular, Premo and Kuhn (2010) have stressed the importance of local population stability on culture change and diversity in both the Lower and Middle Palaeolithic. Using spatially explicit agent-based modelling, they show that increased rates of local group extinction can depress cumulative cultural change and diversity even when the metapopulation size remains stable, although the severity of this varies according to the level of intergroup cultural transmission and the extent of social networks (Premo 2012).

2) Neanderthal-Homo sapiens transition in Europe

The extinction of the Neanderthals and the subsequent colonisation of Europe by *Homo sapiens* (anatomically modern humans [AMH]) populations remains one of the dominant research agendas in palaeoanthropology. While recent studies have demonstrated that some Neanderthal genetic material is still present in modern populations via inter-breeding between Neanderthals and early *Homo sapiens* (Green et al. 2010; Neves and Sera 2012), it is not the case that Neanderthals evolved into *Homo sapiens*, and their disappearance from the archaeological record ~40 kya BP (Higham et al. 2014) reflects their extinction across their Eurasian geographical range. The Neanderthal-*Homo sapiens* transition is thus one of the most important demographic transitions documented in the archaeological record.

Despite this, research into this transition has traditionally focused on the cognitive differences between the two species which allowed AMHs to prosper while Neanderthals died out (Stringer and Gamble 1993; Wynne and Coolidge 2004; see Villa and Roebroeks 2014 for a review). Nonetheless, as early as 25 years ago, Zubrow (1989) using stable population models, demonstrated mathematically that small demographic differences between the two species could transform into large discrepancies in mortality and life expectancy, with an increment in Neanderthal mortality of 1-2% leading to extinction within as little as 30 generations (~1000 years) (although this model does not take into account recent genetic evidence for inbreeding between the two species). More recently, Sørensen (2011) constructed a model to assess Neanderthal demography relative to changing climatic conditions and resource availability, while keeping birth and death rates constant. Similar to the Zubrow model, small demographic differences, in this case a 1% reduction in death during childbirth and in death by hunting incidences between AMHs and Neanderthals, were crucial, permitting population growth amongst AMHs despite adverse climatic conditions ~45 kya BP. These models both draw upon and reinforce osteological and biological evidence of life history advantages of early AMHs over Neanderthals (Caspari and Lee 2004, 2006; Guatelli-Steinberg 2009; Ramirez-Rossi and de Castro 2004; Smith et al. 2010; Trinkaus 1995 cf. Trinkaus 2012) as well as larger local group sizes amongst AMHs (Aiello and Dunbar 1993; cf. Steele 1996).

It is therefore surprising how few archaeological studies of the Neanderthal-*Homo sapiens* transition have explicitly evoked a causative role of demographic factors (e.g. Pettitt 2000; Wobst 1976). One particularly promising area of research addresses the adaptive advantages of AMHs over Neanderthals within the framework of HBE, using nutritional ecology to consider how differences in diet translate into demographic differences. ‘Nutritional ecology’ refers to the study of the relationship between essential nutrient intake (including both macronutrients (calories) and micronutrients (non-caloric vitamins and minerals)) and its effect on human health (Hockett and Haws 2003). Diversity of diet is linked to lower infant mortality rates and longer life expectancy. Stable isotope data (see Richards and Trinkaus 2009 for a review) and zooarchaeological assemblages suggest that Neanderthals had a very restricted diet, obtaining most of their dietary protein from large herbivores (e.g. Stiner et al. 2000). In contrast, AMHs consumed a diverse range of resources (Drucker and Bocherons 2004). Hockett and Haws (2003, 2005) have linked these findings into a model of Neanderthal extinction and AMH population replacement, suggesting that dietary broadening would have lowered maternal and fetal-to-infant mortality, as well as raising average life-expectancy amongst early European *Homo sapiens* populations, resulting in population increases.

While the study of nutritional ecology provides an archaeologically-visible ‘way in’ to the study of demography, recent research has revealed that plant foods played a much greater role in Neanderthal diets than previously supposed (Buck and Stringer 2013; Hardy 2010; Henry et al. 2014; Revedin et al. 2010) calling into question those studies which attribute the demise of the Neanderthals to high mortality brought about by limited nutritional diversity. A diet based entirely on terrestrial herbivores is also incompatible with estimates of Neanderthal calorific requirements and daily energy expenditure (Aiello and Wheeler 2003; Churchill 2006; Froehle and Schoeninger 2008; Pearson et al. 2006; Sorensen and Leonard 2001). Using an estimate of 5500 calories required per day to sustain a pregnant Neanderthal woman, Hockett (2012) has shown that a diet from which these calories were derived exclusively from terrestrial herbivores would have killed a pregnant Neanderthal through protein poisoning, toxic levels of vitamin A, and the severe under-consumption of carbohydrates and vitamin C. While it is unclear from this example which part of the equation used to generate the calorific requirement estimate is wrong, Hockett's study serves to reinforce the bias in the archaeological record of dietary behaviour and incomplete understanding of various hominin diets. While the impact of nutrition on the fertility and mortality of Pleistocene populations is grounded in firm ecological theory, assessing these archaeologically is undeniably difficult.

Firmer estimates are available for Neanderthal population sizes and densities. While it is often assumed that Neanderthal group sizes and populations were smaller than early *Homo sapiens*, it is only recently that empirical evidence for this has been sought and linked explicitly into debates about the Neanderthal-*Homo sapiens* transition. Genetic evidence of Neanderthal effective (breeding) population sizes shows no clear consensus. Based on evidence from five Neanderthal mitochondrial (mtDNA) genomes, Briggs et al. (2009) postulated a mean Neanderthal effective population of between 268–3 510 individuals (95% higher posterior density interval) and report low mtDNA diversity across the specimens, potentially reflecting a low effective population size over much of their history. Other estimates based on mtDNA range from 5 000–9 000 individuals (Lalueza-Fox et al. 2005) and, combined with a modelling approach, an effective population that ranges from 3 000–25 000 (Fabre et al. 2009), with studies based on nuclear DNA suggesting sizes of between 3 000–12 000 (Green et al. 2006). However, generating absolute (census) population estimates from effective population size is difficult (Hawks 2008). Using a formula from conservation biology, Bocquet-Appel and Degioanni (2013) propose an estimated census population size of 5 000–70 000 Neanderthal individuals.

The Neanderthal-*Homo sapiens* transition is one of the few topics where researchers have also embraced the archaeological record as a source of demographic data. Drawing on a wide range of archaeological data, including faunal remains, site numbers, radiocarbon dates and quantities of lithic tools, several studies have attempted to provide relative estimates of the differences in both absolute population size and density and group size between Neanderthals and early AMHs (Bocquet-Appel and Demars 2000a (cf. Pettitt and Pike 2001); Burke 2006; Conard et al. 2012; Grayson and Delpech 2003; Hayden 2012; Mellars and French 2011, 2013; Morin 2004, 2008). In nearly all instances (cf. Morin 2004, 2008), the Neanderthal-*Homo sapiens* transition is associated with an increase in population density of potentially up to 10 times that seen amongst Neanderthals (Conard et al. 2012; Mellars and French 2011, 2013 cf. Dogandžić and McPherron 2013). Using the order-of-magnitude difference documented by Mellars and French (2011) for Southwestern France, Bocquet-Appel and Degioanni (2013) proposed census population sizes for the region of 80-1,300 Neanderthal individuals, contrasting with an estimate of 795–12 980 AMHs during the Aurignacian (Bocquet-Appel et al. 2005).

The results of these studies suggest that sheer strength in numbers can help explain the demise of Neanderthals and the eventual success of AMHs, without recourse to any perceived cognitive advantages of one species over another. It may simply be the case that Neanderthal populations declined below their Minimum Viable Population (MVP) threshold (the threshold population size below which a species will go extinct; Gilpin and Soulé 1986; Reed et al. 2003; Shaffer 1981), either coincidental to the arrival of AMHs into Europe, and/or abetted by the resultant increased competition for resources. While the fact that both Neanderthals and early

AMHs in Europe lived in broadly similar environments (and likely overlapped for up to ~5000 years; Higham et al. 2014) means that some adaptive advantage of AMHs still needs to be evoked (how exactly did they manage to support greater population densities in the same environments?), the increasing number of demographic studies of this transition can help to identify these potential adaptive differences, while recognising that it is small but cumulative effects of changes in demographic variables (fertility, mortality) which translate into long-term archaeologically-visible population trends.

3) Emergence of Behavioural Modernity

Perhaps the most well-known example of a demographic approach to the Palaeolithic archaeological record is that which applies notions of innovation and cumulative culture to the appearance of evidence for 'behavioural modernity'. While the concept of 'behavioural modernity' remains contentious and ambiguous (d'Errico 2003; d'Errico and Banks 2013; Henshilwood and Marean 2003 (and comments therein); Nowell 2010) it broadly refers to a suite of behaviours which are typically (but not necessarily exclusively; Zilhão 2007) associated with Late Pleistocene AMHs, and which are taken to indicate the presence of modern-level linguistic and cognitive abilities. These are identified in the archaeological record through the presence of such objects and behaviours as deliberate burials, complex lithic and hafting technologies, personal ornamentation, pigment use and 'symbolic' art and artefacts (e.g. Henshilwood and Marean 2003; McBrearty and Brooks 2000; Mellars et al. 2007). The appearance of these behaviours in the archaeological record was originally envisioned to have occurred ~40–35 kya BP with the advent of the European Upper Palaeolithic, coincident with the arrival of the earliest AMHs in Europe (Mellars 1973, 1990; Mellars and Stringer 1989; White 1982). Evidence of these behaviours, which contrasted greatly with those seen in the earlier (Neanderthal) Middle Palaeolithic record, were viewed as a dramatic and sudden change, resulting in the term 'Human Revolution' being applied to the initial appearance of behavioural modernity in the archaeological record. The concurrent appearance of both anatomical and behavioural modernity led to the equation of biology and culture, with the absence of similar features in the Neanderthal archaeological record reflecting their lack of the necessary cognitive abilities (e.g. Mithen 1996).

Over the past 25 years, increased knowledge of the archaeological records of other regions of the world, particularly Africa, has questioned the uniqueness of the Upper Palaeolithic 'revolution'. The African Middle Stone Age, chronologically contemporary to the European Middle Palaeolithic, and associated with AMHs, shows many of the behaviourally modern elements previously considered unique to the European Upper Palaeolithic. The evidence from Africa suggests that the appearance of these behaviours occurred gradually in a piece-meal fashion from ~ 300 kya BP (McBrearty 2007; McBrearty and Brooks 2000). Nonetheless, the earliest convincing evidence for modern behaviour dates to ~164 kya BP, at the site of Pinnacle Point, South Africa (Marean et al. 2007) and the earliest evidence for symbolic behaviour dates to~75 kya BP at Blombos Cave, South Africa (d'Ericco et al. 2001; Henshilwood et al. 2004; Henshilwood 2007) with possible earlier dates of ~90–100 kya BP in the Near East (d'Errico and Vanhearen 2007). As such, there is an apparent time lag between the appearance of modern human biology and modern human behaviour in the archaeological record. In addition, instances of 'modern behaviour' amongst Neanderthals are cited (e.g. Zilhão 2007; Zilhão et al. 2010), and research has demonstrated an increase in the number and diversity of putative 'modern' behavioural elements across the chronological span of Neanderthal occupation of Eurasia (Langley et al. 2008). The resultant situation is one in which behavioural modernity is not necessarily a species-specific phenomenon, and in which different markers of modern behaviour emerged at different times. The question still remains as to why evidence of behavioural modernity appears in the archaeological record when and where it does, especially in instances where the equation of modern anatomy and modern behaviour is a matter of debate, rather than a given (Nowell 2010).

Drawing on DIT frameworks, Shennan (2001) proposed a demographic basis for the emergence of behavioural modernity. In Shennan's model, the emergence of behavioural modernity is explicitly linked to population size, with demographic growth and larger population networks providing the impetus both for the increased occurrence and maintenance of behavioural innovation, resulting in greater cumulative cultural complexity. This model was later expanded by Powell and colleagues (2009) who also argued for a demographic basis for the emergence of behavioural modernity, stressing the importance not only of population size and density but also the degree of interaction and migration of the constituent sub-populations on the accumulation of cultural traits (cf. Vaesen 2013). Based on genetic estimates of regional population size, Powell et al. (2009) provided estimates for the critical effective population necessary for the accumulation of modern behavioural traits, noting that population density at the start of the European Upper Palaeolithic was similar to that found in sub-Saharan Africa ~45 000 years earlier, where behavioural modernity first emerged. This model has the advantage of explaining several key features of the archaeological record of behavioural modernity, including the time-lag between its initial emergence and its wide-scale presence, as well as the geographical and chronological variation in the first appearance of such behaviour (see also Richerson et al. 2009). Furthermore, as it does not rely on inferred cognitive capacities as the explanatory variable, changes in population size and connectivity can be used to assess incidences of modern behaviour associated with earlier Neanderthal populations.

Other researchers have considered whether demographic change explains specific patterns of the emergence of behavioural modernity, focusing on both the Australasian (Brumm and Moore 2005; Langley et al. 2011; O'Connell and Allen 2007) and South Asian (James and Petraglia 2005) archaeological records. Langley and colleagues (2011), for example, note a decrease in the evidence for complex 'modern' behaviours in the archaeological record of Sahul corresponding with reduced and fragmented populations during the Last Glacial Maximum. Hovers and Belfer-Cohen (2006) have also suggested a role of small populations and repeated population crashes in the sporadic occurrence of 'modern' behavioural traits in the Middle Palaeolithic Neanderthal record, positing a situation where behaviours and technologies were repeatedly invented as demographic instability never permitted the retention of cultural knowledge or the accumulation of the skills required for the manufacture and use of innovative technologies. While we should resist the temptation to replace one prime mover for the emergence of behavioural modernity with another (d'Errico and Banks 2013), it is clear that a demographic approach to this research question has considerable utility. While the reality is likely somewhere between the dichotomy of behavioural modernity emerging as a result of "get[ting] smart or just get[ting] together" (Culotta 2010), a demographic approach has the advantage of permitting both the accommodation of local historical trajectories into any model of behavioural change, and being more archaeologically testable than explanations based on proposed cognitive or mental capacities (e.g. Klein and Steele 2013). It is to this issue of the archaeological testability of demographic hypotheses that we now turn.

The application of palaeodemographic *methods* to the Palaeolithic archaeological record

DIT and HBE have provided vital frameworks for the study of archaeological demography. Yet the application of these approaches, particularly DIT, to Palaeolithic data is not unproblematic. It is not enough simply to acknowledge the conceptual link between cultural change and population change; how, for example, do we measure and quantify rates of change and innovation in material culture? Studies of ethnographic hunter-gatherer groups focus on the diversity and complexity of their tool-kits (Collard et al. 2005, 2011, 2013a, 2013b; Henrich 2004; Read 2008). These measures have been applied to archaeological hunter-gatherer data-sets from the terminal Pleistocene and Holocene (Bettinger and Eerkens 1999; Edinborough 2009; Eerkens et al. 2013; Fitzhugh and Trusler 2009; Riede 2008), as well as cladistic analyses constructing phylogentic trees documenting the evolution of specific material culture traits (Buchanan and Collard 2007; O'Brien and Lyman 2003; O'Brien et al. 2001, 2014). Within DIT, documenting patterns in material culture relies on measures of dispersion and variation, rather than describing the average tendency of artefact assemblages (Eeerkens et al. 2013). Measuring such changes with the majority of Palaeolithic datasets is difficult, and, with few exceptions, studies linking changing material culture and population are often restricted to comparing broad artefact typologies (e.g. Bocquet-Appel and Tuffreau 2009). In particular, the Lower and Middle Palaeolithic records do not lend themselves to fine-grained quantitative analysis of cultural transmission (Smith et al. 2009:175), as they primarily represent aggregates of behaviour. It is especially challenging to infer the means of cultural transmission between individuals (Mesoudi and O'Brien 2009; Premo 2014) and researchers studying the same archaeological record have reached different conclusions about the type of cultural transmission which produced the assemblages in question (e.g. compare Nowell and White 2010 and Lycett and Gowlett 2008 for the Acheulean (Lower Palaeolithic)). These difficulties have led Richerson and Boyd (2008:302) to suggest that archaeologists should play to disciplinary strengths of the study of long-term change, rather than attempting to fit micro-evolutionary approaches directly to their data.

In addition, Collard et al. (2013a) have recently claimed that the empirical ethnographic evidence supporting the relationship between population size and cultural evolution for hunter-gatherers is ambiguous. Unlike among small-scale food producers (Collard et al. 2013c; Kline and Boyd 2010), other variables, including adaptation to changing environmental conditions and risk of resource failure, have a greater effect than demography on the structure and complexity of hunter-gatherer tool kits (Collard et al. 2005, 2011, 2013b; Read 2008, 2012). They warn that "more caution is needed" (Collard et al. 2013a) by Palaeolithic archaeologists citing population size as an explanation for patterns seen in the archaeological record. Overall, DIT and cultural evolutionary models in Palaeolithic contexts function at present primarily as broad explanatory frameworks, rather than robust methodologies for the study of the relationship between demography and material culture. Finding ways in which to reconcile these frameworks with our data is a clear priority for the study of Palaeolithic demography.

Leaving aside these methodological difficulties, the majority of studies of Palaeolithic demography based on evolutionary frameworks have two fundamental shortcomings; 1) they rarely address the causes of population changes, and; 2) they rarely provide empirical evidence that the population change evoked as part of the explanation for patterns seen in the archaeological record *actually occurred*. The rest of this review will focus on this latter point. While the models derived from other fields provide a useful starting-point for the study of Palaeolithic demography, to assess their validity we need to acquire independent, archaeological, evidence for prehistoric demography (Shennan 2011:1078). While assessing demographic patterns from archaeological data is far from easy, as Hopkinson et al. (2013:70) rightly point out, it is a no more difficult task than providing evidence for the cognitive abilities which frequently form the main competing explanation.

Demography and prehistoric demography

It is useful at this point to reiterate the basis of demography. Three demographic variables (measured as rates) are the immediate causes of all population change past and present; 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). Demographic change is the result of variation in at least one of these variables, which cause further changes in the size, density, and growth rate of the population (Daugherty and Kammeyer 1995:11).

As fertility, mortality, and migration govern population change demographers need to know their rates and what causes them to alter (Weeks 1999:70). Unfortunately, data on these variables are unavailable from the archaeological record. Prehistoric demographic analysis (palaeodemography) is thus restricted to the study of the results of changes in these three parameters; namely, *relative* chronological and geographical changes in population density, distribution, and size, with little recourse to the specific demographic variations that caused these changes[2] (Beaton 1991). As such, Palaeolithic demography primarily involves documenting population trends, rather than producing population estimates, concentrating on trends in census (i.e. total) population sizes, rather than the effective population sizes crucial to DIT (although relative estimates could be made assuming that the effective population is approximately ¼ of the census population; Shennan 2001:8). This enforced focus on the outcome of variation in demographic variables is also difficult to explicitly reconcile with the HBE framework and the role of individual decisions in demographic change.

The four most common methods used to study demography from archaeological data are listed in Table 1 and discussed below. While the emphasis is on the application of these to Palaeolithic data-sets, many of the debates surrounding the use of these methods are chronologically universal, and in the absence of up-to-date summaries (see Hassan 1978, 1979, 1981; Paine 1997; Schacht 1981; Welinder 1979), some general discussion of these approaches is included where appropriate. Similarly, I have chosen not to consider the use of osteological evidence in archaeological demography, as this has been the topic of several recent reviews (Bocquet-Appel 2008a, 2008b; Chamberlain 2006, 2009; Monge and Mann 2007).

The nature of palaeodemographic evidence

Regardless of the method used, two factors complicate all attempts to use archaeological data to study demography. Of these, the most fundamental is the reliance on proxy data; the archaeological material itself contains no direct demographic information (see Chapman 1999). As such, archaeologists require some form of theoretical 'leap' to move from the observed pattern in the archaeological record to an understanding of past demography, usually following a principle of uniformitarianism (Fritz 1972). The methods listed in Table 1

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[2] Although some estimates of changes in fertility and mortality rates have been (questionably) 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 such parameters can be modelled (Sørensen 2011; Surovell 2000).

provide the means to convert the archaeological proxies into meaningful statements about demographic change. While the assumptions behind these approaches are plausible, the extent to which they are valid in the present (and hence applicable to the past) is largely unconfirmed (e.g. Levinson 1979). Part of the problem is that modern day demography is based on observation rather than experiment (Daugherty and Kammeyer 1995:79), providing little impetus to examine the inferred relationships between population and the proxies used by archaeologists. In addition, all of these approaches suffer from the problem of equifinality; multiple valid explanations can be evoked to explain the patterns seen in the data. For example, different rates of artefact accumulation between sites could reflect occupation by groups of different sizes, but could also reflect cultural changes in consumption or varying lengths of occupation (e.g. Heizer 1960: 93; Hiscock 1986; Ross 1985:82-83). Differentiating between the possible explanations and demonstrating conclusively that the pattern in the proxy data reflects past demographic change remains one of the greatest challenges of palaeodemography. For hunter-gatherer populations, such as those present during the Palaeolithic, the most frequently cited alternative explanation for patterns generated through the use of the methods listed in Table 1 is a change in mobility strategy or land-use patterns (e.g. Attenbrow 2006).

The other fundamental difficulty is what is termed ‘the contemporaneity problem’ (Schacht 1984). This refers to the practice of considering remains dated to the same general period as contemporary, despite it being unlikely that they are strictly contemporary. This problem results from the use of data in accumulated form (Ammerman et al. 1976) which makes it hard to assess whether the material represent a discrete occupation episode or a palimpsest of past activity; whether the occupations were simultaneous or sequential. In demographic terms, this distorts estimates of past populations by combining centuries or millennia into a single time phase (Freter 1997), ignoring elements of change within the defined periods, and forcing a reliance on the equation of ‘populations’ with certain classes of material culture. This problem of (lack of) chronological precision is one of the primary obstacles within palaeodemography, and means that any demographic data generated is difficult to reconcile with both DIT and HBE frameworks (for attempts to overcome the contemporaneity problem see; Ammerman et al. 1976; Grove 2012; Hill 1970; Plog 1975; Schacht 1981).

While these difficulties are common to all palaeodemographic analyses, they are particularly pertinent when dealing with the Pleistocene archaeological record. The range of cultural material available as proxy data is more restricted and problems of data resolution and occupation palimpsests are more pronounced than for later prehistoric periods (Conard 2001). The wide margins of error associated with any chrono-metric date and the applicability of ^{14}C dating only after ~40 kya BP (Higham 2011), coupled with the long-standing importance of generalisation with Palaeolithic archaeology (Hopkinson and White 2005), forces an increased reliance on typologically-derived relative chronological sequences, making it even more difficult to ascertain contemporaneity of occupations. Nonetheless, these problems are reduced if we are primarily interested in the study of patterns of relative, long-term, population change and if a multi-proxy approach is adopted, comparing and contrasting the results generated from each.

Site counts and ‘dates as data’

The number and distribution of archaeological sites is commonly used as a demographic proxy following the assumption that variations in these data reflect proportional fluctuations in the relative size and distribution of past populations. This approach is well-suited to application to Palaeolithic contexts. Archaeological ‘sites’ are defined by the presence of a chronological distinctive artefact type (cf. Smith and Sharp 1993), which are typically robust and survive well in the archaeological record. As such, while the ideal situation is to produce maps of site numbers and distributions based on radiometrically defined time-slices from archaeological deposits (Petraglia et al. 2009; Straus et al. 2000), in the absence of absolute dates, or if the data came from survey rather than excavation, sites can still be included and dated by reference to artefact typologies. The use of typology as a way of assigning sites to chronological periods both permits the extension of the approach to those stages of the Pleistocene which are difficult to date radiometrically, and limits taphonomic bias relative to time-depth through the use of virtually indestructible lithic artefacts as diagnostic markers (Bocquet-Appel et al. 2005:1664).

The use of site counts as a demographic proxy has been applied to Palaeolithic data sets at both the regional (David 1973, 1985; Demars 1996, 1998; French 2013; Mellars and French 2011; Schmidt et al. 2012; Smith 1966; Straus 2011; Straus et al. 2000) and continental level (Anderson and Faught 2000; Bocquet-Appel and Demars 2000b; Bocquet-Appel et al. 2005; Lahr and Foley 2003; Petraglia et al. 2009; van Andel et al. 2003), using the archaeological records of both AMHs and earlier hominin species. To accommodate for the uneven lengths of any periods under consideration, site counts are frequently standardised and expressed as a value of number of sites/1000 years. The European Upper Palaeolithic (~40 –10 kya BP) has proven particularly amenable to this approach, with long histories of research in key areas (for example, the refugium zone of Southwestern Europe (France, Iberia)) enhancing the representativeness of site numbers and distribution as proxies of past populations (Mellars and French 2011; Schmidt et al. 2012; Straus et al. 2000). While the majority of studies are restricted to using site counts to assess relative chronological differences in demography, Bocquet-Appel and colleagues (Bocquet-Appel and Demars 2000b; Bocquet-Appel et al. 2005) have used these data to arrive at absolute estimates for metapopulation sizes across the European Upper Palaeolithic. Drawing on ethnographic data from hunter-gatherers, they calculated a demographic density (per 100km^2) for four periods of the Upper Palaeolithic (Aurignacian, Gravettian, Glacial Maximum and Late Glacial) by backprojecting a reference density for the Late Glacial with inter-period growth rates based on the numbers of archaeological sites. Absolute estimates were then obtained by multiplying the demographic density with the perceived territory size generated through modelling the geographical distribution of sites (Bocquet-Appel et al. 2005). While there are undoubtedly difficulties with the use of ethnographic data in Palaeolithic contexts, the combination of ethnographic and archaeological data used by Bocquet-Appel and colleagues has produced the most well-founded estimates of absolute population numbers for the Palaeolithic to date.

Nonetheless, there are several methodological difficulties with this approach. These include; 1) questions about whether the inclusion of non-habitation sites (e.g. burials, rock-art locations) is appropriate for assessing past population changes (Bird and Frankel 1991; e.g. compare the criteria adopted by Smith and Sharp 1993 and Straus et al. 2000); 2) the influence of under-or-over-weighting of sites of varying sizes if all sites, from isolated find-spots to large habitation sites, are treated as equal (Bocquet-Appel et al. 2005: 1658) and the potential for differential preservation of sites of varying sizes and functions (including differences between sheltered and open-air sites); 3) the impact of sampling and fieldwork bias on the known number and distribution of sites; 4) the differential visibility and recognisability of diagnostic artefact types, and the potential that distinctive or visually impressive types (e.g. Solutrean points of the European Upper Palaeolithic; Straus et al. 2000) may inflate site numbers for a given period; 5) that the use of typological markers restricts our study to population changes between chrono-typological periods, obscuring any likely changes within these periods, and ; 6) how to accommodate geographical areas and periods where chronologically diagnostic artefacts are lacking (e.g. Holdaway et al. 2005; Kuzmin and Keates 2005). By far the most pertinent difficulties as far as Palaeolithic data-sets are concerned are problems of chronological control and the aforementioned 'contemporaneity problem' (Schacht 1984), with sites that date from the same period of often multiple millennia plotted on maps and treated as if they represent an accurate 'snapshot' of past population distributions.

One popular method which reduces this problem of poor chronological control is the use of summed probability distributions of radiocarbon dates as a demographic proxy ('dates as data'; Rick 1987). This approach is based on the same assumption as the use of site counts, with relative changes in the frequency and distribution of ^{14}C dates argued to reflect variations in past population sizes and densities (Riede 2009). The validity of this assumption is enhanced in regions with long and intensive research histories and for which a large number of ^{14}C dates are available (Shennan and Edinborough 2007; Williams 2013), as potential biases caused by research focuses, intensity and budgets are well known, if frequently underestimated (Crombé and Robinson 2014; Williams 2012; van Andel et al. 2003). The exact nature of the relationship between radiocarbon dates and population is frequently assumed to be linear and uniform throughout time (cf. Peros et al 2010) although this remains untested.

While archaeologists have most extensively applied the 'dates as data' approach to Holocene prehistoric archaeological records (Armit et al. 2013; Barrientos and Perez 2005; Blockley 2005; Bocquet-Appel et al. 2009; Crombé and Robinson 2014; Hinz et al. 2012; Johnson and Brook 2011; Kelly et al. 2013; Martínez et al. 2013; Munoz et al. 2010; Neme and Gil 2009; Peros et al. 2010; Riede 2009; Shennan 2009b, 2013; Shennan and Edinborough 2007; Shennan et al. 2013;Tallavaara and Seppä 2011; Tallavaara et al. 2010; Wicks and Mithen 2014; Williams et al. 2010; Woodbridge et al. 2012), it has also been applied to Pleistocene datasets, most prominently those of the European Upper Palaeolithic (Anderson et al. 2011; Bamforth and Grund 2012; Blackwell and Buck 2003; Blockley and Gamble 2012; Blockley et al. 2000; Buchanan et al. 2008; Collins 2012; Fiedel and Kuzmin 2007; Gamble et al. 2004, 2005; Graf 2009; Kuzmin 2009; Kuzmin and Keates 2005; Meeks and Anderson 2012; Schmidt et al. 2012). Attempts have also been made to apply similar approaches to earlier records, most noticeably Bocquet-Appel and Demars' (2000a) study of Neanderthal demographic contraction and AMH expansion in Europe (but see Pettitt and Pike 2001). Despite the increasing use of complex Bayesian models to manage large databases of radiocarbon dates, the limits of radiocarbon dating (currently ~ 50-40 kya BP; Higham 2011) restrict the use of the 'dates as data' approach to only the later stages of the Pleistocene. In any case, it is inadvisable to conduct meta-analyses of radiocarbon dates without the prior application of criteria to assess their reliability, particularly with Palaeolithic dates (e.g. Pettitt et al. 2003).

Two main issues hamper the use of site counts and radiocarbon dates as demographic proxies. The first of these is taphonomic. Surovell and colleagues (Surovell and Brantingham 2007; Surovell et al. 2009) have demonstrated that the positive curvilinear distributions regularly observed in these proxies in the archaeological record also occur in natural paleontological and geological contexts (see also Ballenger and Mabry 2011; Johnson and Brook 2011 cf. Riede 2009). The findings of their studies suggest that any trends should be treated with caution and could instead be interpreted in terms of increased taphonomic loss with time-depth, unless some form of 'correction curve' is applied (Surovell et al. 2009). To prevent any patterns simply reflecting a bias against older sites in the archaeological record, Surovell and colleagues advocate their comparison with the underlying geological formations of the study region, or using the distribution of more geologically-protected cave and rock-shelter sites as a check against the frequency distributions of open-air sites and any radiocarbon dates which come from them (e.g. Kelly et al. 2013).

The second main issue is the aforementioned problem of equifinality. Past human behaviours —whether dependent or independent of population fluctuations— could also impact on the number and distribution of archaeological sites and radiocarbon dates. As mentioned earlier, for hunter-gatherer groups, the most cited alternative explanation for variation in these proxies is a change in mobility strategy and land-use patterns, with an increased signature interpreted as representing periods of higher mobility (e.g. Attenbrow 2006; Niekus 2005/2006; Tallavaara et al. 2010:253). This could relate to differences in overall group mobility strategy which impact how often hunter-gatherer groups move home bases and the number of non-residential sites they generate (e.g. Binford's (1980) continuum of 'logistic' and 'residential' mobility), or seasonal/annual population aggregations and dispersals following the 'fission-fusion' pattern well-documented amongst ethnographic hunter-gatherers (Aureli et al. 2008; Layton and O'Hara 2010). Ways of looking at changing patterns of mobility include considering such additional factors as the size of archaeological sites, seasonality of occupation, quantity and diversity of associated artefactual remains, and extra locational data, such as elevation and spatial distribution (Bocquet-Appel et al. 2005:1658; Conkey 1987; French 2013; Perreault and Brantingham 2011; Wadley 1987).

Site size

The most common of these additional factors is that of site size, following the assumption that there is a positive correlation between the size of the site and the number of people who inhabited it (Ammerman et al. 1976; DeRoche 1983; Plog 1975; Schacht 1981:125; Welinder 1979:34 cf. Schreiber and Kintigh 1996). Studies of later prehistoric and historic periods incorporate both relative and absolute population and group size estimates based on the area and number of dwelling structures present (Brown 1987; Casselberry 1974; Casteel 1979; Cook and Heizer 1968; Curet 1998; Davies 2010; DeRoche 1983; Haviland 1969; Hill 1970; Kolb 1985; Kramer 1980,1982; Kuijit 2000; LeBlanc 1971; Longacre 1976; Milisauskas 1972; Milner 1986; Naroll 1962; Odell 1980; Phillips 1972; Porčić 2011, 2012; Postgate 1994; Read 1978; Storey 1997; Sumner 1979; Thompson 1971; Wiessner 1974). Due to the rarity of dwelling structures in the Palaeolithic archaeological record and the difficulty of distinguishing between habitation and non-habitation space at sites (Yellen 1977), the focus here will be on the use of overall site size as a demographic proxy.

Palaeolithic archaeologists have used the relationship between site area and number of individuals as a proxy measure for group size, investigating both inter- and intra-site chronological variations (Burke 2006; French 2013; Hayden 2012; Mellars 1973; Mellars and French 2011, 2013; White 1985). For example, Mellars and French (2011) noted that in Southwestern France final Neanderthal (Châtelperronian) sites were on average markedly smaller than those associated with early AMHs (Aurignacian) (means of 64.7m^2 and 243.8 m^2 respectively). They interpreted this difference as evidence of smaller living groups of Neanderthals compared to early AMHs in the region. Several of the estimates used in their study came from the same site, strengthening the interpretation of group size influencing site area, as smaller areas of occupation were documented during the Châtelperronian despite room for expansion.

Several difficulties with this approach have led to the use of site size as a demographic proxy having limited application to Palaeolithic contexts. The primary difficulty is defining the limits of the site, which is usually determined by the extent of the spatial distribution of material culture. This can be hard to ascertain, especially when the site has not been excavated in its entirety, or when the estimate is based on survey data (Fletcher 1981:102; Newell 1973; Phillips 1972). This problem is compounded by the need to make the data comparable between sites, meaning that the often lower-quality data on site size from older excavations form the basis of the comparison, limiting the use of higher-quality spatial data from more recently excavated sites. Site size estimation is also hampered by the problem of occupation palimpsests. It is frequently unclear 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. In other words, large sites could be the result of the single occupation of a large group, or successive (re)occupations by smaller groups. In contrast, small sites could only feasibly have been occupied by small groups. Thus, while there is some ambiguity involved in correlating group size and site size as far as larger sites are concerned, the assumption that small sites reflect occupation by small groups is reasonably sound. This is especially so where the site area is either spatially constrained or remains small, despite the potential for occupation of a greater area. As such, estimates of site size for the Palaeolithic are much more secure for cave/rock-shelter sites than for open-air sites, where the lack of spatial constraints and the increased occurrence of horizontal displacement of artefacts (Lenoble et al. 2008: 108) make estimates much cruder (although the occupation and use of spaces in front of formal dwelling areas (including caves/rock-shelters; White 1985) is common and can hamper size estimates (LeBlanc 1971; O'Connell 1987; Wiessner 1974)). The difficulty of accurately determining site areas has led to many estimates of Palaeolithic group sizes being based on osteological data, particular for pre-modern hominins (Aiello and Dunbar 1993; Burke 2006; Mithen 1996; Steele 1996). Recently, Grove (2010) has developed a method to estimate group size for both archaic hominins and *Homo sapiens*, using a spatial model of archaeological site distribution combined with an estimate of population density based on body mass. He notes a general trend of increased group size throughout time, which accelerates at the advent of the European Upper Palaeolithic (~40 kya BP), combined with general increases in population size and density.

Issues of interpretation also complicate the link between population and site size. The specifics of the relationship between site size and number of individuals are ambiguous, although Hamilton et al. (2007a) have recently proposed an allometric relationship (i.e. the area required per person changes as site area increases) between the two variables for hunter-gatherers. Similarly, variations in the area of archaeological sites can also be interpreted in terms of mobility either referring to the total duration of occupation, the anticipated duration of occupation or the frequency of re-occupation (Kelly et al. 2005; Kent 1991, 1992; Kent and Vierich 1989; Yellen 1977). It is logical that the amount of refuse generated by a group would increase to some degree with an increased duration of residence (regardless of the absolute size of the group), and that, where no geographical barriers exist, the likelihood of the habitation area expanding is similarly increased, due to a desire to maintain a distance between different activity areas. Likewise, successive re-occupations of the same site are liable to expand the settlement limits, as groups shift the central zone of occupation laterally to avoid the debris from previous occupations. One way of examining this is to combine data on site size with data on the number of sites; we may be looking at chronological changes in mobility rather than group size or overall population density if there are more sites, but these are on average smaller. Conversely, a reduction in both site numbers and site sizes provides stronger evidence for a reduction in relative population density. However, the aforementioned problem of contemporaneity of occupation again comes into play, as a regional population utilising a series of sites sequentially would look very similar archaeologically to a population that was large enough to occupy all sites simultaneously (Grove 2010:403). While the broad intuitive trend that more people generally take up more residential space holds for hunter-gatherers (Hamilton et al. 2007a) several scholars have demonstrated the impact of other factors on site size, including kinship ties between group members (Binford 1991; Fletcher 1991; Whitelaw 1983, 1991), risk of predation (Gould and Yellen 1987) and subsistence base (Hamilton et al. 2007a), all of which may also have affected Palaeolithic hunter-gatherers.

Accumulations research

The use of quantities of material culture (‘accumulations research’; Gallivan 2002; Kohler and Blinman 1987; Ramenofsky et al. 2009; Varien and Mills 1997; Varien and Ortman 2005; Varien and Potter 1997) as a demographic proxy relies on the assumption that there is a positive correlation between the amount of material discarded at a location and the number of people who inhabited it (Ammerman et al. 1976:31). Accumulations research employs models based on the use and disposal of a given class of occupation residue to calculate rates of accumulation (often expressed as the amount of material/area or volume unit, for a given length of time (e.g. Attenbrow 2006; Neme and Gil 2009)) to examine variation in relative population numbers. Attempts have also been made to use accumulations research to estimate absolute population numbers, based either on sophisticated ‘discard equations’ (Schiffer 1975, 1976:59, 1987; see for examples Gallivan 2002; Kohler and Blinman 1987; Pauketat 1989; Varien and Potter 1997), or calculation of the calorific value of the faunal remains at a site and the number of individuals this could feasibly sustain (Ascher 1959; Cook 1946; Glassow 1967; Wheat 1972). The use of discard equations to obtain absolute population estimates relies on accurate data on such variables as the use-life of artefacts and the time span over which the material accumulated. As this information is only available in rare archaeological instances (e.g. Varien and Potter 1997), and never for the Palaeolithic, the rest of the discussion is limited to the use of accumulations research for the comparative analysis of relative population numbers.

One of the main advantages of accumulations research is that it can be applied to both site-based and landscape studies. Studies of the Lower and Middle British Palaeolithic have adopted this approach, using both biface and levallois densities from well-mapped river terrace sequences to examine changing population at a regional scale (Ashton and Hosfield 2010; Ashton and Lewis 2001; Hosfield 1999, 2005). Artefact densities were calculated per square kilometre/100 000 years and adjusted to take into account biasing factors including differential rates of quarrying and urban growth across the different terrace areas. The most recent analysis, focusing on the Solent River system, postulates population peaks between Marine Isotope Stage [MIS] 12 and 10, followed by a decline during MIS 9 and 8 (Ashton and Hosfield 2010). The application of accumulations research to the Middle Pleistocene archaeological record has been particularly profitable, demonstrating how long-term demographic patterns can be extracted from coarse-grained palimpsest datasets in secondary deposits, although the re-working of artefacts from higher to lower deposits is a significant problem which can potentially skew the demographic signature (Ashton and Hosfield 2010).

Accumulations research has also been applied to site-based studies, exploring regional population trends in the Middle and Upper Palaeolithic. Meignen et al. (2006) compared the lithic artefact densities/m^3 of deposit, adjusted for the estimated length of occupation, at an early Middle Palaeolithic site (Hayonim Cave, Level F and base E) and a Late Middle Palaeolithic site (Kebara cave, units XI-IX) in the Levant, suggesting, based on both increased artefact densities and an increase in site numbers, population increase across the Middle Palaeolithic in the region. Increases in quantities of lithic artefacts have also been used to argue for population increase across the European Middle-Upper Palaeolithic transition in both Southwestern France (Mellars and French 2011, 2013) and the Swabian Jura, Southwestern Germany (Conard et al. 2012), although in the latter case, the study did not take into account the different lengths of the chronological phases in question. Adjusting for the length of phases, Mellars and French (2011) documented a mean of 9.7 retouched tools/m^2/1000 years for the final Neanderthal (Châtelperronian) in Southwestern France contrasting with a mean of 17.6 retouched tools/m^2/1000 years for the initial AMH (Aurignacian) occupation.

The main difficulties with accumulations research are well documented and not restricted to their application to Palaeolithic contexts. Most crucial is the nature of the relationship between the two variables. While the logic of a relationship between the number of people and the amount of occupation residue is sound, the specifics are ambiguous, and while most studies assume a linear relationship between the two variables (e.g. Kohler and Blinman 1987; Marsden and West 1992) this assumption is largely untested. Furthermore, the number of people is not the only variable which affects the amount of material discarded; factors such as the length of occupation affect the amount of material that are incorporated into the archaeological record. For example, Moncel and Rivals (2011) have used lithic material density at sites as part of their study into the length of Neanderthal occupations and overall mobility strategies (see also Sullivan 1992).

The palimpsest nature of most Palaeolithic deposits means that distinguishing individual episodes of occupation is usually impossible, and accumulations research is often used in Palaeolithic contexts as a measure of ‘occupation intensity’ where inter-site differences in the amount of cultural material are interpreted in terms of either varying population or varying occupation lengths/frequencies with low densities of material associated with short (or rare) occupations and high densities with long (or frequent) occupations (e.g. Conard et al. 2012). One way to choose between these competing explanations is to examine the evidence from other demographic proxies. For example, Mellars and French (2011) demonstrate that the increase in lithic density at sites in Southwestern France across the Middle-Upper Palaeolithic transition is accompanied by a similar increase in the numbers of sites, suggesting that decreased logistical mobility amongst AMHs cannot explain the increase seen in lithic densities (see also Ross 1985:87). Other forms of evidence for chronological differences in mobility and settlement strategies can be examined, and their impact on any estimates of lithic artefact densities assessed, including the ratio of local: non local lithic material, frequency of artefact retouch and prevalence of cortex found at the sites being studied (Amick 1996; Barton et al. 2011; Close 2000; Kelly and Todd 1988; Moncel and Rivals 2011; Riel-Salvatore and Barton 2004; Roth 2000; Sellet 2006; Surovell 2009; Thacker 2006).

At a more fundamental level, questions still exist as how best to conduct accumulations research. While researchers have used both volume and area to quantify rates of accumulation, a frequent lack of knowledge of rates of sedimentation (e.g. rock falls) and erosion both within and between sites plagues the use of volume to calculate artefact densities. The question also remains as to what type of occupation residue should be examined. Accumulations research was developed using ceramics (e.g. Cook 1972); an artefact type which cannot be modified and reworked to the same extent as the lithic technology which dominates the Palaeolithic archaeological record (Dibble 1984; Rolland and Dibble 1990; Schott 1989). Differential degrees of retouching of lithic artefacts will affect their quantities in the archaeological record, independent of differences in the number of individuals using and manufacturing them. Furthermore, within the broad category of lithic artefacts, decisions still need to be made as to what types of artefacts to quantify. Due to lack of systematic excavation and collection of all but the most diagnostic and recognisable forms until the latter half of the 20th century, researchers have typically limited their analysis to bifaces (Ashton and Hosfield 2010; Ashton and Lewis 2001; Hosfield 1999, 2005) or formal retouched tool classes (French 2013; Mellars and French 2011, 2013), ignoring unretouched elements such as flakes which were undoubtedly also used by people in the past (see Holdaway and Douglass 2012). Conard et al. (2012) found that lithic densities calculated using all remains, including microdebitage, were artificially inflated for those sites which were recently excavated due to improvements in excavation and recovery strategy, skewing the demographic signature. When only pieces $\geq$ 2cm were analysed the values for these sites were comparable to the others in their study region of the Swabian Jura, Southwestern Germany (Conard et al. 2012: 240). In addition, several behavioural variables affect the quantity of lithic artefacts found in assemblages independent of population, including changes in artefact use and function, changes in location of discard and the effects of variable raw material supplies on manufacture, use and discard (see Attenbrow 2006: 28-29). Data on these variables are often lacking, and further than recognising them as a potential source of bias, their impact is difficult to assess (see French 2013).

Furthermore, lithic artefacts are just one (albeit the dominant) part of the Palaeolithic cultural repertoire. Organic remains are often poorly preserved in Palaeolithic contexts and similar quantitative data on other cultural material, including burnt bone and charcoal is thus frequently lacking (Conard et al. 2012). Aided by the excellent preservation offered by the limestone-dominated caves and rock-shelters of Southwestern France, Mellars and French (2011, 2013) used quantities of ungulate remains (expressed as estimates of meat weight (kg) and deemed to represent food debris; White 1953) as part of their analysis of occupation intensity across the Middle-Upper Palaeolithic transition in the region. While data were available from fewer sites, these results complemented those found in the analysis of retouched tools, with a mean meat-weight of 84.6 kg/m^2/1000 years found at Neanderthal (Châtelperronian) sites and 152.8 kg/m^2/1000 years found at AMH (Aurignacian) sites. However, similar to lithic artefacts, the use of faunal remains as a demographic proxy needs to accommodate numerous biasing factors, including variation in the intensity of exploitation and processing of carcasses, differences in body-part transportation and variations in the rate of storage of faunal remains.

Indirect approaches

Although reliant on proxy data, the above three methods are the most direct approaches available to study demographic patterns from the archaeological record. Due to some of the problems with their application and use, archaeologists have also employed indirect approaches, inferring population trends from the perceived cultural responses to population change. The advantage of the types of data employed in these indirect studies is that they are often ratio or proportion data, circumventing some of the effects of taphonomic bias (Surovell and Brantingham 2007:1876). However, extra inferential steps are required to move from the data to estimates of demographic trends (Kuhn 2012: 82). As all palaeodemographic evidence comes from proxy data, to aid the verification and the interpretation of results, it is particularly important to compare any patterns generated from indirect data on cultural responses to those seen in other lines of evidence.

The use of indirect approaches in Palaeolithic contexts has focused on the relationship between hunter-gatherer populations and their environment and resource base. These studies draw on the much-cited, but difficult to calculate, factor of environmental carrying capacity ("the maximum population that a given region can sustain, if one assumes that a particular set of resources are being exploited with a given technology" ; Glassow 1978:39) (see Bayliss-Smith 1978; Brush 1975; Dewar 1984; Hassan 1978; Hayden 1975; Jochim 1976; Zubrow 1971, 1975), as well as elements of HBE, particularly *optimal foraging theory* (Belovsky 1988; Smith 1983). The most prominent example of this approach is that of Stiner and colleagues (Stiner 2001, 2009; Stiner and Munro 2002; Stiner et al. 1999, 2000, 2008 see also Munro and Atici 2009), who, in a series of papers, argue that changing patterns in the use of small game by hunter-gatherers act as a 'demographic barometer' (Stiner et al. 1999:193) for changes in human population density. Predator-prey dynamics between humans and small game mean that changes in human population density influence both the rates of contact between humans and their prey, and the availability of small game as a food resource. Stiner and colleagues ranked small prey according to handling costs and their resilience to over-harvesting by humans. The relative ratios of high-ranked tortoises (easy to catch but with populations sensitive to predation) to low-ranked partridges and hares (fast and difficult to catch, but resilient to human predation) in a faunal assemblage reflect changing human population density. A greater reliance on slow-moving species is only sustainable under conditions of low and dispersed populations, with an increase in the exploitation of fast-moving species reflecting increasing population densities, as the need to meet protein requirements forced foragers to broaden their diet to include species with high handling costs. Increased diversity of small game assemblages has been used to argue for increases in population density from the Middle to Upper Palaeolithic in Italy, Israel and Turkey (Stiner 2001, 2009; Stiner et al. 1999, 2000, 2008), as well as population decreases within the Natufian period (13–10 kya BP) in the Levant associated with the onset of the Younger Dryas (Stiner and Munro 2002).

Stiner and colleagues argue that changing proportions of small game in faunal assemblages provides a much better indicator of changes in human population density than similar data on large ungulates, as small species vary more in their population resilience and predator avoidance characteristics, as well as having similar body sizes making estimates of dietary yield more comparable (Stiner et al. 1999:190, 2000:56, 2008). Nonetheless, ungulates constituted the bulk of the diet of most Palaeolithic hunter-gatherers, and their relative abundance would also have affected human population densities, even if this exact impact is difficult to quantify. Drawing upon earlier ideas of a 'Broad Spectrum Revolution' (Binford 1968; Flannery 1969) which saw hunter-gatherers diversify their resource base during the late Pleistocene as a possible response to population growth, Marín-Arroyo (2009) used a mathematical model to simulate the interaction between humans and four ungulate species during the Magdalenian in Northern Spain. Taking into account human foraging behaviour and topography, Marín-Arroyo concluded that the dietary diversification seen in the archaeological record was best explained by an increase in human population density rather than climatically-induced changes in resource availability. However, these two variables are often difficult to differentiate. In his study of the Middle-Upper Palaeolithic transition in Southwestern France, Morin (2008) argued that climatically-induced reduction in species diversity in the Early Upper Palaeolithic (Aurignacian), seen in the faunal assemblage at the site of Saint-Césaire, would have triggered declines in human population densities in the region. Within this decreased diversity, the increased reliance on reindeer, a famously fluctuating resource in terms of seasonal availability, would have exacerbated this decrease in population density. However, while the proposed link between hunter-gatherer population density and species diversity of the resource base is based on ethnographic data, the relevance of patterns seen in the continental North American ethnographic examples to the coastal-influenced landscape of late-glacial Southwestern France is not examined. Furthermore, Morin provides no additional independent evidence for population decrease in the Aurignacian, and it is questionable how far results based on the analysis of a single site can be extrapolated to regional population density estimates.

Taking data on assemblage composition and diversity one step further, Discamps (2013) produced environmental carrying capacity estimates for the Middle and Early Upper Palaeolithic of Southwestern France applying an ungulate biomass index to archaeozoological assemblages. Chronological variations in the ungulate biomass index (calculated through comparing the abundance of steppic taxa (Bison, Horse) with forest and tundra taxa (Red deer, Roe deer, Reindeer) were compared to the number and distribution of hyena dens to assess the impact of ungulate biomass fluctuations on large predators, with a close correlation seen between low periods of ungulate biomass and reduced hyena populations, and vice-versa. The number and distribution of hyena dens as a proxy for hyena population size is not hampered by the potential impact of shifting mobility and land-use strategies seen in the use of site counts as a proxy for human populations. The correspondence between the population of this large predator and reconstructed environmental carrying capacity suggests that prey availability was a key factor for the Neanderthal and AMH populations which also inhabited the region during this period. Based on ungulate biomass estimates by Delpech (1999), Langlais et al. (2012), have argued for a similar correlation between increased resource availability and increases in hunter-gatherer population density during the Middle Magdalenian (18–16 kya) in the same region.

The size of faunal remains has also been used to infer relative changes in Palaeolithic human population density. Decreases in the size of individuals of a given species are argued to reflect increasing human population densities and more intensive exploitation of the species due to pressure on food resources, as human preferences for larger individuals during times of low resource pressure exert considerable impact on the size and sex structures of the remaining prey population (Klein and Cruz-Uribe 1983, 2000; Klein and Steele 2013; Stiner 1999; Stiner et al. 2000; Straus et al. 1981). Non-dietary aspects of faunal assemblages have also been used as a palaeodemographic proxy. At the cave site of Grotte XVI in Southwestern France, Grayson and Delpech (2003) used declining cave bear abundances across the Middle-Upper Palaeolithic transition to argue for increased human group size and/or occupation length as Early Upper Palaeolithic (Aurignacian) groups out-competed cave bears for occupation of the cave. While the authors reject extrapolation of this finding as evidence of increased population densities across the region, the hypothesis of increased group size at the site during the Early Upper Palaeolithic is supported by similar increases in average lithic and faunal assemblage sizes from nearby sites.

By far the biggest difficulty of using faunal data as an indirect proxy for demography is demonstrating that any differences in species size and consumption by humans are independent of changes brought about by climate or environmental change (see discussions in Klein and Cruz-Uribe 1983; Stiner et al. 2000). One obvious way in which an environmental explanation could be discounted is if the data showed the opposite pattern than that predicted by ecology (e.g. Stiner 2001:6994). In addition, all archaeozoological assemblages are anthropogenic and any estimates of carrying capacity based on these are approximate. Many of the approaches discussed above also suffer from the same problem of equifinality which hampers other palaeodemographic methods. In their study of chronological variation in the ratio of high-ranked to low-ranked small game at the Natufian site of Hayonim Cave, Israel, Stiner and Munro (2002) were unable to distinguish between the competing explanations of changes in group size or changes in occupation length, instead referring to changes in "site occupation intensity" defined as a combination of group size, length of stay and frequency of site visits. Furthermore, the attribution of dietary diversity to increased population densities contradicts the nutritional ecology model discussed earlier in which dietary diversification is a cause rather than a consequence of population growth (Hockett and Haws 2003, 2009), although this could be a result of the latter model's consideration of plant, as well as faunal, resources. Nonetheless, the relationship between food resources and hunter-gatherer demography provides a theoretically firm, if often difficult to quantify, avenue of research into Palaeolithic populations.

Lessons from hunter-gatherer ethnography

Finally, it is worth considering how, and to what extent, data on the demography of ethnographic hunter-gatherers can contribute to the study of Palaeolithic populations. There is a degree of circularity in the use of ethnography analogy to interpret and verify population trends seen in the archaeological record, as the results derive from the use of the methods described above, the assumptions of which were conceived largely on the basis of ethnographic data (e.g. Naroll 1962). Nonetheless, the search for cross-cultural demographic patterns amongst ethnographic hunter-gatherers can potentially help Palaeolithic archaeologists interpret the results generated from palaeodemographic methods, and to formulate hypotheses against which to test their data. Concerns about the uncritical application of data derived from modern foragers to the interpretation of prehistoric foragers are well-known, particularly those which highlight the contrast between the marginal environments and global contexts in which modern foragers live, and the Palaeolithic 'world of hunter-gatherers' (Freeman 1968; Kelly 2013: Chapter 10; Wobst 1978; Wylie 1985). There are undoubtedly differences between Pleistocene and post-Pleistocene hunter-gatherers (Foley 1988), and it is clearly both difficult and fundamentally flawed to attempt to establish a proto-type from any ethnographic group as a model of Pleistocene foragers. However, it is arguably equally flawed to ignore the structural basis of hunter-gatherer population dynamics as documented through cross-cultural analysis, particularly in view of the uniformitarian nature of demographic processes. Nonetheless, the use of ethnographic data as an interpretive tool to aid Palaeolithic demography is less suited to the archaeological records of pre-modern hominins, due to the effect of potential life history differences on fertility and mortality (Robson and Wood 2008).

As with archaeological populations, data on specific demographic parameters amongst ethnographic hunter-gatherers are rare (e.g. Blurton-Jones et al. 1992, 2002; Headland 1989; Helle and Helama 2007; Hill and Hurtado 1996; Hill et al. 2007; Howell 1979; Yengoyon 1972) and are biased towards those which have an clear socio-cultural component (e.g. childhood mortality and infanticide practices and mobility; Acker et al. 1975;

Denham 1974; Divale 1972; Hayden 1972; Kelly 1992; Morales 1987; Schrire and Steiger 1974). The ability of the ethnographer to obtain demographic information is hampered by factors including cultural restrictions on informants which prevent individuals accurately answering questions, the lack of equivalent translations for demographic terms in native languages, and difficulties of estimating the ages of people who do not recognise time by the calendar year (Blurton Jones et al. 1992:164; Kelly 2013:167; Turnbull 1972:284). Nonetheless, the available data on specific demographic characteristics permit a sense of the range of variation found across hunter-gatherer groups (Kelly 2013: Chapter 7). Data on total fertility rate (the average number of births women who survive the reproductive span will bear) suggest a wide range of fertility rates amongst foragers, ranging between 2.6 and 8.0 (Kelly 2013: Table 7.5; Pennington 2001:195). Life expectancy at birth is also wide-ranging, from 37 years among the Ache of Paraguay to 21–24 years among the Agta of the Phillippines (Gurven and Kaplan 2007; Pennington 2001:194). Projecting simulations by Pennington (2001) based on the observed range of ethnographic forager fertility and survival rates to the past suggest that periods of rapid growth and decline would have characterised prehistoric hunter-gatherer populations. However, with small sample sizes and limited data, understanding the causes behind demographic variation remains difficult, particularly with regard to those, largely environmental, variables that archaeologists hope to address. One notable exception is the work of Helle and colleagues (Helle and Helama 2007; Helle et al. 2008) who examined the impact of temperature change of the population dynamics of three Sami groups in Northern Finland for the period 1722–1850 AD. Contrary to expectations, they demonstrated that variations in annual mean temperatures had no significant impact on birth and mortality rates (Helle and Helama 2007), although it possibly affected the birth sex ratio (Helle et al. 2008).

In order to grapple with the issue of relative population change amongst Palaeolithic foragers it is more useful to consider the outcome of variation in these demographic processes; group size and population density. Group size and population density are the best studied aspects of hunter-gatherer demography, on which a large corpus of quantitative, cross-cultural data are available. A full review of these parameters is outside the scope of this paper (see Binford 2001; Johnson 2014; Kelly 2013, Chapter 7) and the focus here will be summarising the relationship(s) between hunter-gatherer group sizes, population densities, and archaeologically discernible cultural and environmental variables.

Three nested types of hunter-gatherer groups are widely recognised: the family group, the local group/band and the regional group/tribe. Attempts to quantify the number of individuals which comprise these units have traditionally focused on the ‘magic numbers’ of 25 people in a local group and 500 in a regional group/tribe (Birdsell 1953, 1958, 1968, 1970; Lee and DeVore 1968; Martin 1973; Wilmsen 1973). Computer simulations by Wobst (1974,1976) suggest a regional group size of 175–475 individuals as the minimum viable human breeding population size for hunter-gatherers; an estimate close to the ‘magic number’ of 500. Recent cross-cultural studies also suggest average hunter-gatherer local group sizes of 28–30 people (Hill et al.2011; Marlowe 2005), as well as a scaling ratio of approximately 4 in the sizes of the nested levels of hunter-gatherer group types (Hamilton et al. 2007b). Nonetheless, the validity of these magic numbers as group size estimates should not be assumed in all contexts, particularly as they are likely influenced by different factors, with local group size related to resource availability and procurement roles and the regional group size related to reproductive strategies. The most comprehensive study of cross-cultural patterns of hunter-gatherer group sizes

(Binford 2001), demonstrates variation based on a wide range of interacting variables. Binford's Group 1 (local group) and Group 2 (regional group) will be the focus of discussion here.

According to Binford (2001:229) mobility costs act as the ultimate limiting factor on hunter-gatherer group sizes. This relates to food availability and assumes that in the absence of intensification, the larger the group, the greater the demand on the food supply. The larger the group, the greater the number of moves needed per year to meet subsistence needs (Binford 2001:234; Kelly 2003:52). Group sizes are overall larger amongst sedentary or logistically mobile hunter-gatherers than those who are residentially mobile. However, the impact of mobility on group size is not straightforward and also depends on the group's subsistence base and the aspect of mobility being measured (see also Grove 2009). For example, groups primarily exploiting terrestrial animal resources move greater residential distances annually and make a greater number of residential moves than those reliant on plant or aquatic resources (Binford 2001:275). Binford (2001:278) suggests a threshold of 400 km/annum travelled, below which groups making residential moves reduce their local group size with annual distance moved, and above which local group size increases.

While mobility is difficult to measure archaeologically, this variable interacts with those that are more discernible from the archaeological record, including diet. Group sizes are generally largest amongst foragers primarily dependent on terrestrial animal resources and smallest for those with a plant-based diet. The relative frequency of different group sizes also varies between subsistence bases, with plant-based groups associated most often with small local group sizes, and larger local group sizes more common amongst groups dependent on aquatic or animal resources (Binford 2001:252–3). As resource availability is strongly conditioned by the environment, differences in the effective temperature [ET] and environmental productivity (primary biomass) of the region also impact group size. Local group size and effective temperature are positively correlated up to a threshold of 11.53^{o}C (latitudes above 35^{o}) after which group size decreases as the ET drops (Binford 2001:263). There is also a trend towards larger group sizes as net above-ground productivity increases. This trend varies depending on the primary food source of the group, with the local group sizes of hunter-gatherers following a plant-based diet more strongly correlated with environmental productivity than those reliant on aquatic or animal resources (Binford 2001:265). Local group sizes are also largest amongst groups heavily dependent on food storage (Binford 2001:261) , and other factors that are difficult to ascertain from the archaeological record, including division of labour, extent of polygny, and ranking are also shown by Binford to impact on group size.

At a wider scale of analysis, the combined population of these local groups is used to calculate the regional population density. Since Birdsell's (1953, 1958, 1968) pioneering studies of Australian aboriginal populations it is widely accepted that hunter-gatherer population density is heavily determined by environmental factors, particularly as they relate to food availability (Belovsky 1988; Hassan 1981:7). Population density varies according to habitat type, with the highest density seen in temperate and tropical coastal environments, and the lowest in semi-desert and Arctic environments (Layton and O'Hara 2010). Marlowe (2005) has shown a correlation between population density and environmental productivity (expressed as primary biomass; kg/m^2), which levels off at a primary biomass of ~30 kg/m^2. As habitat type and environmental productivity condition the available food resources, there is a clear relationship between hunter-gatherer population density and subsistence base, with the lowest population densities found amongst groups primarily dependent on terrestrial animal resources, and the highest amongst those focusing on aquatic resources (Binford 2001:380–383).

However, population density can also affect the subsistence base exploited. For example, as population density increases, dependence on terrestrial animals decreases to the extent where no documented groups living at densities greater than 9.1 persons/100km^2 are primarily dependent on animal resources (Binford 2001: 381). Hunter-gatherer population density also varies with mobility strategy, so that, regardless of subsistence base, logistically mobile and sedentary groups live in higher population densities than residentially mobile groups, with the population density threshold of~ 32–35 persons/100km^2 between the two strategies (Binford 2001: 313). Total distance moved annually and average distance per residential move are also inversely correlated with population density (Binford 2001:312).

Cross-cultural patterns in hunter-gatherer group size and population density can aid archaeologists by providing a series of expectations about how these demographic variables change under different environmental conditions and subsistence strategies. However, the relationships between group size and population density, and the interacting variables affecting them, are complex and difficult to untangle. The relationship between mobility and demography is particular complicated, especially as it is often unclear which is the dependent and the independent variable. Both demography and mobility are affected by changes in environment and subsistence base. Amongst hunter-gatherers, mobility is often seen as a response to changing resource availability and distribution (Halstead and O'Shea 1989; Low 1990:236-8), with demographic change a likely result of resource fluctuations. The nature of ethnographic data on demography can also cause problems for archaeologists. This relates to the small scale of hunter-gatherer societies and the short time perspective enforced by the limits of ethnographic fieldwork. The small scale of forager societies means that they are highly subject to annual population fluctuations through stochastic error (Headland 1989:62). Furthermore, forager societies are characterised by annual and seasonal variations in population cohesion and dispersal ('fission-fusion'; Aureli et al. 2008; Harpending and Davies 1977; Layton and O'Hara 2010; Lee 1976; Mauss and Beuchat 1906). This constant state of flux of all ethnographically documented hunter-gatherer populations (Turnbull 1972: 289) precludes the assumption that any observed short-term demographic pattern is a reliable indicator of the population at any point other than the field work period. While anthropologists frequently adopt the use of stable population models to extrapolate longer-term population trends (e.g. Blurton Jones et al. 1992; see Howell 1979), archaeologists applying these results to Palaeolithic data-sets need to consider both the accuracy of the ethnographic data, and the best way to link this short-term data to the long-term demographic trends extrapolated from the archaeological record.

Conclusion: The future of Palaeolithic demography

The demography of Palaeolithic populations has been described as "one of the most critical and elusive of archaeological signatures" (Pike-Tay 2000:65). A society's demographic parameters affect other aspects of its peoples' lives (Cox 1976:2; Poston and Bouvier 2010; Weeks 1999:6–7), and an understanding of prehistoric demography is crucial to the understanding of the societal and artefactual change which dominates archaeological research agendas. Aided by results from genetics and computer modelling, Palaeolithic archaeologists are increasingly recognising the importance of demographic change, both to the lives of the individuals they study, and to the formation of the resultant archaeological record. Within evolutionary frameworks of HBE and DIT, demographic change has been cited as a key variable in the understanding of such important palaeoanthropological questions as when and why modern behaviour emerged, and why technological innovations were so rare amongst Lower Palaeolithic populations.

Despite this, proper consideration of exactly how elusive the archaeological signature of Palaeolithic demography is has, until now, been limited. As Bocquet-Appel and Demars (2000b:552) remind us, there are two recurring problems with palaeodemography: the quality of the sampling of data is never sufficient, and the uniformitarian assumptions linking the data and demographic interpretation are always bold. These problems are heightened in the Palaeolithic. Nonetheless, as discussed in this review, there are several excellent examples of the application of palaeodemographic methods to Palaeolithic data-sets, ranging from the Lower Palaeolithic of the British Isles to the terminal Pleistocene in the USA, permitting an understanding of relative population fluctuations both chronologically and geographically. Furthermore, while demography may be elusive compared to other archaeological variables (e.g. diet), it is arguably less so than others, such as cognitive and linguistic changes, which have long been serious subjects of enquiry from Palaeolithic data.

There are still many difficulties with conducting palaeodemographic research with Palaeolithic archaeological data. Foremost among these is how to assess the success of any palaeodemographic endeavour. How can we tell if the reconstruction of relative demographic change is accurate? This is, of course, impossible without written records with which to compare our archaeological reconstructions. The adoption of a multi-proxy approach to Palaeolithic demography is one way in which the accuracy of results can be assessed. If multiple palaeodemographic proxies reveal the same trend, the validity of the trend is strengthened. However, difficulties arise when the proxies do not match up and other factors specific to the archaeological record in question (data availability, preservation at archaeological sites) must be evoked to assess which proxy is 'correct' (French 2013). Ethnographic data can also be used to assess the accuracy of demographic reconstructions from Palaeolithic data. Cross-cultural analysis shows strong patterning in both group size and population density in hunter-gatherer societies with regard to such archaeologically-discernible variables as environment and subsistence base. The extent to which any Palaeolithic data correlate or converge with the expected ethnographic pattern provides a solid starting point for assessing whether demographic change is a valid interpretation of the patterns seen in the proxy data.

Perhaps the most crucial development required for a greater understanding of Palaeolithic demography is an improved ability to differentiate between the competing explanations for changes seen in the data used as demographic proxies. There is often little data available on the long-term fluctuations of the behavioural variables cited as alternative explanations, and as such, the palaeodemographer is limited to inferences based on 'snap-shots' of behavioural differences seen across their study period and/or region. Improving this requires increased diachronic data on such variables as raw material economies, lithic reduction sequences, faunal acquisition strategies and site function. In particular, the complex inter-dependent relationship between hunter-gatherer group sizes, population density and mobility (Binford 2001; Grove 2009; Kelly 2003), highlights the critical importance of finding ways to disentangle and identify the impact of these variables on hunter-gatherer societies, and how best to study these from the archaeological record remains a priority for Palaeolithic palaeodemography. The improvement and further development of Palaeolithic palaeodemography thus relies on the combined efforts of archaeologists from various specialisms and the availability of those data not only integral to the methods discussed in this review, but also those relevant to those factors which complicate the automatic equation with changes in the proxy data with population change.

This review has focused largely on *how* archaeologists study demography for the Palaeolithic archaeological record, with an emphasis on using archaeological data to document relative long-term fluctuations in population size and density. As a result, little attention has been paid to the important question of *why* any documented demographic changes occurred, including whether any changes were the result of natural population increase/decrease or migration. While understanding the reasons behind population change is the ultimate aim of palaodemography, if archaeologists want to continue to use demography as an explanatory concept in the Palaeolithic, they need first to engage more with the potential of their own data for palaeodemographic research, making increased effort to address the methodological challenges discussed in this paper.

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