The Palaeolithic – the earliest and longest period of human (pre)history – was a time of substantial demographic upheaval. Throughout the Palaeolithic, both our evolutionary ancestors (hominins) and members of our own species (*Homo sapiens*) variously lived and died, interbred, migrated, speciated, and became extinct in a context of frequent and substantial Pleistocene climatic changes. Palaeolithic populations were dynamic, but this dynamism is rarely acknowledged. The Palaeolithic is a mere footnote in most global overviews of humanity’s demographic history; overviews that contrast Pleistocene hunter-gatherers with their more demographically interesting agricultural successors, and that seldom move beyond brief descriptions of their small population size, low density, and slow long-term growth rates (e.g. Biraben 2003; Livi-Bacci 2017). It was, however, during the Palaeolithic that both the biological and social foundations of the human propensity for rapid population growth and range expansion – the former of which continues apace into the twenty-first century – were laid (Kramer 2019).

Encompassing ~3 million years globally, knowledge of Palaeolithic demographic variation is vital to understanding both humanity’s long-term population history and the substantial social and cultural developments that occurred during this period, including the origins of art and symbolism and the colonisation of an increasing array of new environments. The importance of demography to human societies should not be underestimated. Changes in population size and density play key roles in the development and variability of material culture, settlement patterns, social institutions, and languages (e.g. Acerbi *et al.* 2017; Bromham *et al.* 2015; Kempe & Mesoudi 2014). The balance of kin and non-kin in a person’s social network – a network partially determined by the age and sex composition of the population – influences the degree of cooperation and information exchange among individuals and families, and decisions about who to marry and have children with (David-Barrett 2019; Kramer & Greaves 2011; Migliano *et al.* 2017). Demographic processes are also central
to human evolution. Evolution is driven by the propagation of genes through a combination of natural selection and genetic drift; variables that are determined by the survival (mortality), fertility, and dispersal (migration) of individuals (Gage et al. 2012; Metcalf & Pavard 2006). Demographic variation shaped all of human history: the Palaeolithic is no exception.

This book weaves together archaeological, palaeoanthropological, and genetic data, interpreting these with reference to ethnographic data on recent hunter-gatherers and demographic models of extant subsistence-level societies, to develop a demographic prehistory of European Palaeolithic populations between 1.8 million and 15,000 years ago. Three questions lie behind this demographic prehistory: (1) What were the key population limiting factors, and controls and constraints on fertility and mortality experienced by Palaeolithic populations, and how did they vary chronologically, geographically, and between hominin species? (2) What is the relationship(s) between demography, sociocultural change, and climatic/environmental change in the Palaeolithic? (3) What are the implications of these demographic patterns for our understanding of Palaeolithic societies and evolutionary transitions?

The demographic prehistory of Palaeolithic Europe comprises four stages: visitation, residency, expansion, and intensification (Table 1.1). It is a prehistory that is the product of multiple species of humans, all of whom, with the exception of Homo sapiens, are extinct by the end of this nearly two-million-year period (Figure 1.1). It is a prehistory that is both biological and social; one in which, within the physiological constraints on fertility and mortality, social relationships provided the key for enduring demographic success. Most importantly, it is a prehistory concerned with the big picture of human evolution but which is firmly grounded in the day-to-day realities of Palaeolithic people – their families, their children, the way they lived and died.

DEMOGRAPHY AND PALAEODEMOGRAPHY

It is important at the outset to be clear as to what exactly demography is. Throughout this book, I use the term ‘demography’ in two ways; (1) to refer to the composition of a particular population (‘the demography of . . .’), and (2) to refer to the discipline of demography (‘the scientific study of human populations and their change’; Billari 2015: S11). Definitions of key demographic terms that recur throughout this book are listed in the Glossary.

The main aims of demography are to document, forecast, and explain changes within, and variations between, the size and structure (composition) of human populations. The three key demographic variables are fertility, mortality, and migration. To allow comparison between populations these
Table 1.1 Summary of the basic structure of the European Palaeolithic archaeological and palaeoanthropological records, their correspondence with geological and climatic schema and the four demographic stages of the European Palaeolithic.

<table>
<thead>
<tr>
<th>Demographic stage</th>
<th>Archaeological subdivisions</th>
<th>Date range (years ago, approximate)</th>
<th>Pleistocene subdivision</th>
<th>Marine Isotope Stages (MIS) (after Lisiecki &amp; Raymo, 2005)</th>
<th>Hominin(s) present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visitation</td>
<td>Lower Palaeolithic</td>
<td>1.8 million – 300,000</td>
<td>Early-Middle</td>
<td>63–9</td>
<td>Homo erectus; Homo georgicus (?)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Denisovans</td>
</tr>
<tr>
<td>Residency</td>
<td>Middle Palaeolithic</td>
<td>300,000–40,000</td>
<td>Middle-Late</td>
<td>8–3</td>
<td>Homo neanderthalensis; Denisovans</td>
</tr>
<tr>
<td>Expansion</td>
<td>Middle-to-Upper Palaeolithic transition</td>
<td>50,000–35,000</td>
<td>Late</td>
<td>3</td>
<td>Homo neanderthalensis; Denisovans (?)</td>
</tr>
<tr>
<td></td>
<td>Early Upper Palaeolithic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intensification</td>
<td>Mid-to-Late Upper Palaeolithic</td>
<td>35,000–15,000</td>
<td>Late</td>
<td>3–2</td>
<td>Homo sapiens</td>
</tr>
</tbody>
</table>
variables are measured as rates; the number of events in a given time period, divided by the number of people at risk of experiencing that event. Population change is a result of variation in one or more of the variables of fertility, mortality, and migration which cause further differences in population size, density, and/or growth rate(s). Thus, in order to understand population changes, demographers need to know about these variables and what causes them to alter. The relationship between fertility, mortality, and migration forms the ‘basic demographic equation’ where populations alter through time due to a combination of natural increase (the imbalance between the number of births and deaths) and net migration (the imbalance between the number of people moving into a population (immigration) and the number of people moving out (emigration)). The relative importance of the variables of fertility,
mortality, and migration to population change is not constant. For example, prior to the Industrial Revolution, mortality was the driving force behind population change. In contrast, fertility is the main driver of population change in most twenty-first-century nation states (Livi-Bacci 2015).

‘Palaeodemography’ refers to the demographic study of prehistoric populations (i.e. those societies for which no written records exist; Bocquet-Appel 2008). While palaeodemography and demography have similar aims, differences in data availability and quality mean that the two research areas contrast in several key ways.

Detailed information about the demographic variables of fertility, mortality, and migration is available for most present-day populations through censuses and vital registration forms, such as birth, death, and marriage certificates. From these, demographic parameters, including population structure, age-specific fertility and mortality rates, and population growth rates are calculated. By definition, no equivalent direct demographic data exist for non-literate prehistoric populations. Instead, palaeodemographers derive their data from other sources; sources that only indirectly inform on past demographic processes and parameters. Palaeodemographic data will never be as reliable or as complete as demographic data proper and we should adjust our expectations accordingly. In particular, given this lack of direct data, palaeodemography typically focuses on the study of long-term (millennial) relative changes in population size and density in contrast to the shorter-term (decadal) analysis of the full range of underlying demographic variables that characterises the present-day discipline.

The palaeodemographic database comprises fragmentary information from multiple disciplines, including archaeology, biological anthropology, genetics and palaeogenetics, and ethnography. Most palaeodemographers embrace this diverse range of data and advocate a multidisciplinary and multi-proxy approach to prehistoric demography. One reason for this is that no one disciplinary body of data, or methodological approach, informs on all aspects of past demography, with different datasets varying in the temporal and spatial scales at which they provide demographic information. A fuller understanding of demographic processes and behaviours in prehistory thus depends on the integration of data from multiple sources.

The other key reason for a multi-proxy, multidisciplinary approach is the indirect nature of palaeodemographic data itself. As these data contain no inherent demographic information, numerous assumptions and theoretical leaps about the relationship between the data and the targeted demographic variables are required. Issues of equifinality also abound, with some proxies more susceptible than others to alternative, but often equally valid, interpretations, both demographic and otherwise. The consideration of multiple types of data provides a form of cross-check, aiding to overcome the limitations of each proxy and strengthening palaeodemographic interpretations by differentiating...
between competing explanations for the patterns seen in the data. This multi-proxy, multidisciplinary approach to palaeodemography is taken in this book, and how palaeodemographic measures are inferred from archaeological, biological anthropological (osteological), and genetic data are explained in Chapter 2. The challenges of reconciling different proxies, combined with the fragmentary and indirect nature of palaeodemographic data, should not, however, be underestimated. Criticism of the methods and results of palaeodemographic research is long-standing, both from its practitioners and from those outside the field (e.g. Bocquet-Appel & Masset 1982; Petersen 1975).

PALAEOLITHIC PALAEODEMOGRAPHY: KEY ISSUES AND A FRAMEWORK FOR STUDY

Palaeolithic palaeodemography has been subject to some especially strong criticism (e.g. Dogandžić & McPherron 2013; Kuhn 2012: 82). Data quality features heavily in these critiques. Problems with chronological precision and accuracy that plague all palaeodemographic studies are particularly pronounced in the Palaeolithic. Furthermore, most established palaeodemographic methods were developed for the more sedentary societies of later prehistory and are either unsuitable or require some modification to be applied to Pleistocene contexts and their typically sparser archaeological records (French 2016).

As with many other areas of Palaeolithic research, a common response to this sparse record is to look to the richer corpus of demographic data on extant hunter-gatherers to inform on Pleistocene demography. Demographic data from ethnographically documented hunter-gatherer populations are important tools in Palaeolithic demographic research. Ethnographic data play a key role in both the development of models of Palaeolithic demography (e.g. Binford 2001) and the generation of absolute estimates of Palaeolithic demographic variables, including population size, density, and fertility and mortality rates (e.g. Bocquet-Appel et al. 2005; Cucart-Mora et al. 2018; Maier & Zimmermann 2017). Most archaeologists are well-versed in the problems and pitfalls, both methodological and theoretical, of using data from living populations to inform on past populations (e.g. Wobst 1978). Elsewhere, I have detailed the challenges specific to their use in palaeodemography (Page & French 2020). Two of these challenges are particularly important for the demographic prehistory presented in this book, both with regard to the use of ethnographic data to inform on Palaeolithic populations, and the reconstruction of Palaeolithic palaeodemography more broadly.

Demographic Uniformitarianism

Demographic uniformitarianism refers to the assumption that demographic processes, and the mechanisms underlying these, are unchanged between the
past and the present (for a review of this concept, see French & Chamberlain 2021). Demographic uniformitarianism was defined most clearly by Howell, who describes it as the premise that:

> the human animal has not basically changed in its direct biological response to the environment in processes of ovulation, spermatogenesis, length of pregnancy, degree of helplessness of the young, and rates of maturation and senility over time . . . the demographically relevant biological processes of our species are constant in our genetic composition, subject only to variation in response to environmental forces, and that the species has not undergone any significant intra-species evolution since its first appearance as Homo sapiens. (Howell 1976: 26)

Importantly, demographic uniformitarianism does not assume that demographic behaviours have remained the same throughout history, nor that specific parameter values derived from recently observed populations are directly applicable to the past. Rather, demographic uniformitarianism assumes that the basic biological processes relating to fertility and mortality are similar between past and present, that they respond to environmental stimuli in the same way, and that these similarities act as constraints of, and impose limits on, demographic behaviours. The relevant biological processes listed by Howell are more specifically known as life history parameters. Life history parameters structure the timing of key developmental events in an organism’s lifetime and are shaped by natural selection. Given their evolutionary constraints, human life history parameters – and subsequently, patterns of age-specific fertility and mortality – vary in predictable and limited ways. As such, the assumption of demographic uniformitarianism is well accepted.

However, the uniformitarian assumption is only strictly applicable to members of our own species, Homo sapiens, who have a distinctive life history pattern comprising a long gestation period, long childhood, late age at first reproduction, and relatively few children – a life history pattern that likely evolved in response to lowered mortality risks (Smith & Tompkins 1995: 262–3). The other – non-sapiens or archaic – Pleistocene hominins who inhabited Europe during the demographic stages of visitation and residency, exhibited biological and developmental differences from Homo sapiens. The extent of these differences is subject to ongoing debate and is difficult to quantify, but we can safely assume that the life history pattern that characterises Homo sapiens emerged within the Homo clade (Robson & Wood 2008). A key turning point in hominin life history occurred with Homo erectus, with a shift towards the slow life history of Homo sapiens (Antón et al. 2014). Later archaic hominins (e.g. Homo heidelbergensis, Homo neanderthalensis) likely had a pace of development within the Homo sapiens range but nonetheless subtly different (e.g. Rosas et al. 2017; Thompson & Nelson 2011). In addition to their effects on patterns of
age-specific fertility and mortality, life history differences, combined with other related biological and cognitive differences (such as body size, energy expenditure, and brain size), would also have had important implications for population structure and living group size and composition, with attendant repercussions for the evolution of social behaviours such as alloparenting and intergenerational cooperation (Kramer 2019).

Demographic uniformitarianism underpins all research into prehistoric demography. The assumption of uniformity in demographic processes between past and present provides the methodological basis for ageing and sexing human fossils and clear theoretical checks on reconstructions and interpretations of past demographic trends and processes. Where palaeodemographic data do not match up with expectations derived from the uniformitarian assumption (as is usually the case), the assumption helps us to identify the reason(s) for this. The non-applicability of a strict principle of demographic uniformitarianism to the archaic hominins of the Early and Middle Pleistocene has resulted in some fierce and long-standing debates as to the demographic profiles and regimes of these populations. As demographic uniformitarianism provides the justification for the use of estimates of population characteristics and model parameters derived from recent populations to supplement the sparse prehistoric demographic database, it is particularly important to use these data critically in research on the early inhabitants of Europe. We return to the challenges of palaeodemographic research in the absence of the uniformitarian assumption in Chapters 4 and 5.

The ‘Forager Population Paradox’

As many scholars have noted, there is a stark contrast between the observed population growth rates of recent hunter-gatherers and those estimated for Pleistocene hunter-gatherers based on back-projections of known global population sizes (Hill & Hurtado 1996; Pennington 2001). Pleistocene hunter-gatherers could not have grown at the same rate(s) as those recorded among extant foragers. Were this the case, the global population would have reached certain sizes at earlier dates than we know it did. Recent hunter-gatherers have population growth rates averaging 1 per cent per annum (Hamilton et al. 2007); if sustained, this growth rate would result in a population-doubling time of just seventy years, or a ~20,000-fold increase in size over one millennium. To correspond with known estimates of global population size, Palaeolithic hunter-gatherers must have had a long-term growth rate of near zero (stationary populations). Blurton Jones (2016) has termed the contrast between the growth rates of recent hunter-gatherers and Palaeolithic foragers the ‘forager population paradox’.

A hypothesis of stationary, or near-stationary, Palaeolithic populations necessitates an explanation as to the fertility and mortality schedules that made this possible. In the 1960s and 1970s, prevailing models assumed that
this near-zero per cent growth was deliberate, with populations exerting conscious group-level controls on demographic behaviour, regulating growth to ensure that population size never exceeded the carrying capacity of the local environment (Birdsell 1968; Hassan 1975; Hayden 1972). Infanticide (the deliberate killing of babies) was considered to be the primary mechanism used to curtail prehistoric population growth (Divale 1972). Other proposed solutions to the forager population paradox include very low fertility caused by a high prevalence in the Pleistocene of fertility-reducing sexually transmitted infections (Pennington 2001) and very high mortality rates due to increased incidences of violence and warfare (Hill et al. 2007).

However, no single factor can adequately account for near-zero long-term population growth. Furthermore, modelling studies extrapolating from demographic data on recent hunter-gatherers indicate that long-term population stationarity requires a combined fertility and mortality schedule outside, or at the extreme limit of, the known range of human variation, violating the principle of demographic uniformitarianism (Blurton Jones 2016; Hill & Hurtado 1996; Pennington 2001). It is possible that Palaeolithic hunter-gatherers – especially archaic or non-sapiens populations – were demographically different from any recorded human population, but the most parsimonious solution to the forager population paradox, at least as far as past Homo sapiens populations are concerned, is much more banal: it is a product of the contrast between the scales (both spatial and temporal) at which archaeological and ethnographic data are calculated and analysed and of assuming that the uniformitarian assumption applies to demographic parameter values, rather than mechanisms.

Simulations indicate that multiple phases of sustained population growth, followed by sudden population crashes or local extinctions best account for long-term near-zero population growth rates (Boone 2002; Keckler 1997). The regularity and severity of these crashes need not be uniform, but reductions in population size at intervals of 50–100 years could result in long-term zero population growth among populations with demographic profiles within the range of extant foragers (Blurton Jones 2016: 215). A similar saw-tooth pattern of rapid population growth and decline likely also characterised Palaeolithic hunter-gatherers. This pattern provides a more plausible explanation for the long-term trend of near-zero population growth than steady-state equilibrium achieved by the multigenerational balance of fertility and mortality. Genetic data support this scenario, indicating several notably sharp reductions in population size and subsequent population bottlenecks throughout the Pleistocene (e.g. Posth et al. 2016). Peaks and troughs of this frequency are, however, impossible to document at the chronological resolution available for the Palaeolithic archaeological record. Prehistoric growth rates calculated from paleodemographic data are mean values viewed over millennia, recording only the longer term and slower time-averaged rate across crash and recovery cycles. Growth rates of ethnographic foragers represent instantaneous per
annual measures of population change along this continuum of growth and decline. It is therefore not surprising that calculated Palaeolithic growth rates are not the same as those of recent foragers; they are not directly comparable nor can growth rates from recent foragers be taken as realistic long-term estimates for either the population from which they derive or prehistoric hunter-gatherers.

The contrast embodied within the forager population paradox between the long-term stability and slow growth vs. the shorter-term dynamic population fluctuations that occurred during the Pleistocene has important implications for the search for factors that controlled and constrained Palaeolithic populations (known as population limiting factors). The traditional focus on long-term growth viewed Palaeolithic populations within the Malthusian paradigm (see Chapter 2) in which populations were kept in balance with the environment, likely through a combination of moderate mortality and moderate fertility, aided by deliberate regulation. If we switch the focus to the shorter-term, the possibility of intense population growth and crashes indicate periods of much higher fertility and/or lower mortality, followed by lower fertility and/or higher mortality. The search for factors controlling and constraining Palaeolithic populations must take these shorter-term fluctuations into account. Palaeolithic population reductions were likely caused by a combination of stochastic (random) processes (to which small populations are particularly susceptible) and catastrophic events (Gurven & Davison 2019; Hamilton & Walker 2018) that greatly increased mortality and/or greatly decreased fertility. Within this framework, some little-considered causes of mortality, such as diseases and accidents, gain significance, and with them the notion of the relative demographic importance of people of different ages and sexes to the long-term persistence of a population. The role of fertility in population growth is also given greater weight. Earlier assumptions of deliberately maintained stationary populations paid more attention to mortality than to fertility as a means of curbing population growth, as the former is easier to manipulate than the latter in the absence of effective contraception. However, the physiology of female reproduction is an important limiting factor on population growth across mammalian species and similarly played a key role in the overall pattern of long-term low rates of Palaeolithic population growth. This physiology is nonetheless highly responsive to socio-environmental conditions, and factors including diet, workload, and mobility can all have rapid and marked effects on fertility, and subsequently, on short-term population growth (Ellison 2003).

Human Behavioural Ecology as a Framework for Palaeolithic Palaeodemography

The reconstruction of Palaeolithic populations and the assessment of the factors that controlled and constrained fertility and mortality requires the use of multiple lines of evidence from various sources. Ethnographic data provide a valuable tool but the direct application of demographic estimates and models from ethnographic populations to Palaeolithic populations is inadvisable, not least due to the forager...