Archaeology, demography and life history theory together can help us explain past and present population patterns

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Abstract

Population matters. Demography is both a cause and a consequence of human behaviour in other important domains, such as subsistence, cooperation, politics and culture. Demographers interested in contemporary and recent historical populations have rich data at their fingertips; the importance of demography means many interested parties have gathered demographic data, much of which is now readily available for all to explore. Those interested in the demography of the distant past are not so fortunate, given the lack of written records. Nevertheless, the emergence in recent years of a new interest in the demography of ancient populations has seen the development of a range of new methods for piecing together archaeological, skeletal and DNA evidence to reconstruct past population patterns. These efforts have found evidence in support of the view that the relatively low long-term population growth rates of prehistoric human populations, albeit ultimately conditioned by carrying capacities, may have been due to 'boom-bust' cycles at the regional level; rapid population growth, followed by population decline. In fact, this archaeological research may have come to the same conclusion as some contemporary demographers: that demography can be remarkably hard to predict, at least in the short term. It also fits with evidence from biology that primates, and particularly humans, may be adapted to environmental variability, leading to associated demographic stochasticity. This evidence of the fluctuating nature of human demographic patterns may be of considerable significance in understanding our species' evolution, and of understanding what our species future demographic trajectories might be.

Introduction

Population patterns are fundamental to human history. In the last 200 years the key process has been the 'demographic transition' [1]. Economic and social changes led to decreasing mortality, while fertility continued at the previous high levels for some time before eventually decreasing. The result of that intervening period has been a wave of global population increase that started in Britain and has spread across the world as the conditions for decreased mortality have become increasingly widespread.

In the context of the political and economic history of the last 200 years the demographic patterns can be seen as long-term features with massive inertia, but archaeological time-scales are much longer and can potentially tell us about multiple demographic events connected with changes in human adaptations. Indeed, his recognition of this was at the heart of Childe's [2] concept of the Neolithic and Urban Revolutions (cf. [3]). The only graph in his book was one of the population of Britain, 1500-1850, showing the upswing in population between 1750 and 1850 associated with the Industrial Revolution, which 'facilitated the survival and multiplication of the species concerned'. He went on to suggest that it was possible to 'discern in earlier ages of human history other "revolutions". They manifest themselves in the same way as the "Industrial Revolution" — in an upward kink in the population curve'. In other words, these new strategies were successful in natural selection terms for those who adopted them. Binford's [4] argument about the agricultural revolution was rather different. He proposed that populations that had become sedentary as a result of exploiting plant resources at the end of the last Ice Age were effectively forced into cultivation as their population expanded, at the expense of diminishing returns for increased effort, but his argument was more in keeping with Ester Boserup's [5] emphasis on 'population pressure' as a problem that needed a solution, rather than that the population growth associated with a strategy was an indicator of its success.

Neo-evolutionists like Service [6] argued that one of the problems posed by larger populations, especially larger group sizes, was solved by the development of 'managerial elites' to organise them. In a more dystopian vein, Carneiro's 'circumscription theory' [7] proposed that societies whose room for expansion was limited in some way would eventually feel pressure on resources that would lead to warfare between different groups and the ultimate victory of a single group that would incorporate the others in a new form of organisation.

Such population 'prime mover' arguments fell out of favour when it was pointed out that the populations of foraging societies had apparently been conditioned by density-dependent mechanisms determined by the carrying capacity of their resources for thousands of years, so it had to be explained what had suddenly changed. Given that even low rates of exponential growth lead to massive increases in population over timescales that are very short by archaeological standards, population pressure, in the sense of density-dependent equilibrium at carrying capacity, must always have been present and therefore could not be an explanation for specific developments like the origins of agriculture (e.g. [8, 9]). Of course, this does not mean that population size and political centralisation may not sometimes be linked (see [10]).

Archaeological demography today

In Childe's time the evidence for the 'upward kinks' in the population curve that characterised his revolutions was thin to say the least but in the 85 years since it is notable that archaeologists

have until recently paid relatively little attention to the detailed documentation of demographic patterns, despite the ongoing centrality of population-centred accounts of change in prehistory. Indeed, many archaeologists have thought that tracing population patterns with archaeological evidence was an insuperably difficult task. The papers in this volume are represent of a renewed interest in demographic patterns and processes and their relation to cultural change on the part of archaeologists that has developed over the last 25 years, together with an associated recognition of the importance of testing models with data. There are several reasons for this renewed interest and all of them are reflected in this issue.

On the theoretical side, a major one has been the growing awareness on the part of archaeologists of developments in ecological evolutionary demography, and life history theory in particular. These have revealed the detailed mechanisms at the level of the individual woman and the individual family that affect fertility and the successful recruitment of children to the next generation. A major influence on archaeological perceptions of these mechanisms was the late Jean-Pierre Bocquet-Appel's idea of the Neolithic Demographic Transition (NDT [11], anticipated by [12]). By analogy with the modern demographic transition, he argued that the development of agricultural modes of existence led to a major shift in human fertility-mortality schedules. In contrast to the modern transition, this was led by changes in fertility rather than mortality because increased female energy levels resulting from decreased mobility and the increased availability of carbohydrates, led to higher fertility rates. But this would not be sufficient in itself unless it also resulted in increased recruitment. In fact, it seems that selection in humans strongly favours parental investment in existing young children over further fertility [13]. Kaplan et al.'s Tsimane study [14] showed that 'transition to the next birth is affected by both energy stores and whether there is an existing living infant to invest in.' So farming must also have improved recruitment as well, perhaps through decreased risk and better weaning foods, as well as better maternal energy balances. In keeping with this, ethnographic studies point to improvements in both fertility and recruitment with increased sedentism and involvement in horticultural/agricultural activities (e.g. [15]. In other words, agriculture enabled a shift in the quality-quantity trade-off in the costs and benefits of reproduction, increasing not just the number of children born but also the number that could be successfully raised. However, this sedentary existence created new infectious disease risks that may also have led to life histories in which there was a greater payoff to allocating more of a woman's available energy to immune function and reproduction and less to growth and maintenance, explaining the often commented apparently paradoxical association of farming with population increase on the one hand and evidence of more disease and smaller achieved height on the other [16].

Regardless of whether archaeological data have sufficient time resolution to provide information at the micro-level of life-history decisions (see below), life history theory provides the theoretical underpinning for understanding the larger patterns in prehistory that archaeology can tell us about. Population growth, for example, becomes an indicator not of population pressure, as the 1960s view had it, but of a successful shift in the balance of trade-offs towards increased fertility and recruitment based on the availability of increased resources, whether as a result of subsistence innovations, as in the case of the NDT, or environmental change. The long-term growth rate is an indication of the adaptive success of a population's subsistence strategy in the prevailing conditions. Moreover, while locally a population will tend to reach a carrying capacity or ceiling, where birth and deaths are in Malthusian equilibrium, if space is available expansion can continue through emigration, as it did in the case of the

European colonisation of the New World and that of Europe by early farmers of Anatolian ancestry [17]. However, it is better to see this in term of population 'pull' rather than population 'push'. In fitness terms it is an opportunity not a threat, because those who adopt the strategy will have increased reproductive success compared to those who do not. Importantly, because of their behavioural flexibility and the cultural nature of their adaptations, humans can expand into new environments relatively easily, unlike other primates. Indeed, this may often be easier than intensifying exploitation by means of increased labour inputs on the lines of the Boserup model.

If Bocquet-Appel's work on the demography of the origin and spread of farming was one source of a new interest in population patterns (e.g. [18]), another has been a growing concern with the historical impact of past climate change on human populations and its role in civilizational collapse (e.g. [19]). From a different direction altogether, the ongoing twenty-year old debate about the relationship between population size and the rate of cultural evolution has also had an important influence on research, represented here by several papers. This debate arose for two main reasons. First, the mathematical formulation of cultural transmission processes by Cavalli-Sforza and Feldman [20] and Boyd and Richerson [21], which had been considered irrelevant by the processual archaeologists of the 1960s to 80s, showed that transmission processes could have a major impact on patterns of cultural change and stability. Second, recognition of the piecemeal nature of cultural developments in the late Pleistocene [22] undermined existing cognitive-genetic explanations of the increased technological complexity of the Upper Palaeolithic and Late Stone Age. The impact of population fluctuations on cultural transmission provided an alternative [23]. Archer's paper in this volume [24] makes a major advance in addressing this problem empirically by showing that in late Pleistocene Africa the incidence of backed stone artefacts (components of complex tools/weapons) is associated with inferred higher population densities themselves affected by climate change. Conversely, Lundström et al.'s study of final Palaeolithic demography in southern Scandinavia [25] points to a link between low population levels and cultural loss, while Strassberg and Creanza's overview [26] shows ways forward in addressing the different results and conclusions of different studies of the cultural complexity-demography relationship.

All the topics mentioned above may be regarded as theoretical drivers of the new interest in palaeodemography, but the availability of new sources of information and the development of new techniques has also changed perceptions. Thus, Bocquet-Appel tested his NDT hypothesis by showing how information about the age-at-death distribution of buried individuals from excavated cemeteries could be used to show that samples from cemeteries of Neolithic farmers, in contrast to those of Mesolithic foragers, contained high proportions of juvenile individuals, an indication that the populations from which they came were growing (see [27]).

Of great importance here has been the explosion of ancient genomic DNA studies. These have frequently revealed massive shifts in the genomic composition of populations in different parts of the world implying that significant migrations must have taken place, raising the question of why these might have taken place. In doing so they have given support to other lines of demographic argument. Thus, ancient DNA analyses have shown that the initial spread of farming into Europe was the result of the expansion of a population of Anatolian ancestry [17], as noted above, resulting from their adoption of farming, in keeping with Bocquet-Appel's model and also with his cemetery evidence of growing populations. Vanderlinden and Silva in

this volume [28] contribute to further understanding the way in which farmers and farming expanded into Europe by integrating information on speed of spread and population growth to show that it must have been a density-dependent dispersal process, even if many of the details remain to be understood.

Finally, and more internal to their discipline, archaeologists have improved the resolution of their time scales through the use of techniques such as dendrochronology and the use of Bayesian methods incorporating contextual information to narrow the time intervals that can be derived from radiocarbon dates. Thus, when your units of time last for a millennium it is easy for populations to appear in equilibrium with their environments when this is not in fact the case (see below).

All these different considerations have come together in, on the one hand, providing new questions whose answers depend on patterns in population history, and on the other new tools to address them, aided by a general explosion in the availability of archaeological data. A major battle within the discipline, especially in the last decade, has focussed on the reliability of one of those tools and data sets: the use of summed radiocarbon date probabilities (SPDs) and related measures such as kernel density estimates (KDEs) as a proxy for changing relative population sizes through time. These have the advantage over more traditional measures such as site counts that they provide better chronological resolution and that the chronological subdivisions over which data are aggregated are not determined by archaeologists' artefact typologies. They are also very generally available, in ever-increasing quantities. Their disadvantages include the possibility of artefacts in the patterns resulting from the radiocarbon calibration curve, biases of various kinds in the selection and collection of samples, and the more general taphonomic problem affecting all such proxies that sites of some periods may have been preferentially destroyed or be more difficult to find than others.

These debates have led to the continuing development of statistical tools to test the significance of claimed patterns of population rise and fall [29], and also to increasing comparison of inferences made on the basis of independent lines of evidence, for example pollen evidence for human impact on the landscape. These approaches and the contributions they can make to the understanding of long-term history and to justifying the validity of the methods themselves are strongly represented in this issue (e.g. [30-33]). For example, as Arroyo-Kalin and Riris [30] put it in their study of regional population patterns in Amazonia, ''simply put, the size of human populations bears on how novel human niches are formed, how traditions of material culture evolve, why people intensify food production, and how new languages diversify within a language family.' Of importance in a different way, Robinson et al. [34] show that the correspondence between radiocarbon and dendrochronological patterns in an area where both are available validates the use of summed radiocarbon probabilities as a demographic indicator of population collapse in areas where these are the only available data source. The paper by Timpson et al. [35], together with the associated software, represents the latest methodological development in the statistical analysis of summed radiocarbon probability distributions by identifying the maximum number of change points in a population trajectory that can be justifiably inferred from the information in a given dataset, and the dates at which they occurred, using a continuous piecewise linear model. This innovation avoids the danger of over-interpreting the positive and negative departures from given growth models that exist with current methods.

However, these radiocarbon-based approaches are not the only recent method for obtaining reliable population estimates for prehistory. The so-called 'Cologne Protocol' developed by Zimmermann and colleagues and represented here by the papers of Schmidt et al. [3] and Lundström et al. [25] takes a rigorously defined spatial approach at different scales, producing successive snapshots of scale-dependent population patterns that aim to estimate absolute and not just relative population densities. Moreover, like Timpson et al. [35], Schmidt et al. provide the computational tools to make their methods available; it can be anticipated that they will be widely taken up.

Populations in flux

What these methods have generally revealed when applied at the regional scale is evidence of population fluctuations, often very considerable ones. When farmers arrived in the various regions of Europe, for example, populations did not gradually rise to a new carrying capacity and stay there: the initial farming 'booms' were followed by 'busts'. This was a surprise, because it contradicted assumptions of equilibrium that had been taken for granted on the basis of the coarse time-scales noted above. In some cases they could potentially be accounted for by adverse climate change (e.g. [36]), but by no means always. It is here that such empirical findings lead to theory again and to issues that remain to be resolved.

Early computer modelling studies [37] showed that there was no guarantee that populations would grow smoothly to an equilibrium size in accordance with the logistic growth equation. Potentially, they could overshoot and end up oscillating. The oscillations could even increase in range, resulting in extinction. Moreover, demographic studies of present-day forager groups showed that they were expanding at very fast rates, incompatible with evidence that over the long term hunter-gatherer populations were at very low levels, the so-called 'forager population paradox', discussed here by French and Chamberlain [38] and Tallavaara et al. [33]. The former also draw attention to another paradox in archaeological demography. Age-at-death distributions in living populations are U-shaped, with larger numbers of deaths in the youngest and oldest age groups. Cemetery populations generally have too many prime age adults for normal attritional demographic processes. Biases created by preservational factors or the exclusion of certain age groups from an archaeologically recognisable burial clearly have a potential role here. However, Keckler [39] showed by simulation that in a population history where growing populations are intermittently hit by what he called 'decimation events' the element of catastrophic mortality introduced by the crashes would produce the observed cemetery patterns of larger than expected proportions of adults. A saw-tooth pattern of oscillations around a carrying-capacity would also result, and given the episodic short-lived nature of these decimation events would have the interesting and counter-intuitive consequence that populations would be growing most of the time.

Tallavaara and Jørgensen's paper addresses the important question of whether we can get at such short-term growth rates archaeologically. They show that population growth rates derived from archaeological data are on average an order of magnitude lower than those derived from ethnographic data or from the documented historical demography data of recent centuries. They argue that this arises because of the time-averaged nature of the archaeological record, which does not provide us with the resolution to identify changing growth rates but rather is telling us about longer term changes in mean population size that reflect changing carrying capacities mostly affected by environmental productivity. McLaughlin et al.'s study of Atlantic

Iberia provides a very good example of this, using a variety of lines of evidence to show how a series of environmental fluctuations was linked to lagged population changes, while the formation of new maritime environments after 8.2 kya provided productive resources that had not previously existed, whose exploitation led to major population growth. In a similar vein, Timpson et al. show that the phase of rapid population growth in the South American Arid Diagonal was associated with expansion into a new niche. The following phase, on the other hand, corresponds to an effective equilibrium lasting 4,000 years. As the authors point out, this does not mean there were no short-term fluctuations over this period but the evidence available does not provide any support for them.

As these papers suggest, these days there is an increasing appreciation of the importance of facing up to the time-averaged nature of the archaeological record for many if not most of the topics that interest archaeologists. In particular, rates of change in both cultural and biological phenomena are inversely correlated with the length of time over which they are measured [40]. These and related problems affecting inferences about long-term changes in patterns of human activity are addressed by Bevan and Crema in their paper [41]. Measurement of rates depends on the scale of scale of chronological resolution available to us. This is why radiocarbon date distributions are so important because they provide the highest level of resolution generally available, so long, of course, as they really are a proxy for what we are trying to measure.

In the light of the conclusion of Tallavaara and Jørgensen [33] that archaeological temporal resolution is not generally good enough to tell us about instantaneous growth and decline rates, it is interesting that Porčić et al.'s [32] calculation of a growth rate for incoming farming populations in the Central Balkans over ~200 years produces estimates of well over 1%, entirely compatible with ethnographic rates and resulting from the much higher carrying capacity made possible by farming. It was immediately followed by a rapid drop, down to half the peak level within 200 years, before rising equally rapidly to another peak. The reasons remain unclear in this case, as Porčić et al. acknowledge, and this is true of many other such examples. Are we seeing an oscillating pattern of overshoot and undershoot, mass emigration to the onward-moving agricultural frontier, the impact of disease, rapid over-exploitation of soils whose nutrients had been able to build over millennia and thus a carrying capacity crash, or something else? This is a major area for further research in understanding both the mechanisms that produce such fluctuations and also their social and economic consequences.

As the resolution of the record and the sample size of sites decreases, which tends to be more and more the case as you go further back in time, the more Tallavaara and Jørgensen's [33] claim holds true. Indeed, there comes a point where the archaeological record is being averaged across phases of major environmental change and therefore across different carrying capacities. However, one of the important results of the Schmidt et al. paper [3], and in keeping with French's earlier research [42], is that we now have mutually-confirming lines of archaeological evidence with sufficient resolution to identify regional population fluctuations across a period of 30,000 years. Moreover, this is in keeping with the genomic record for episodes of Palaeolithic population replacement, though Loog [43] rightly cautions us about the problems involved in using genetic data to inform about changing population sizes. Of course, as we have seen, the ethnographic and simulation studies mentioned above strongly suggest that the real pattern is one of short-term fluctuations around a mean value determined by environmental productivity. However, in future we can potentially bridge the gap between the two by means of simulation,

aided by the fact that the environmental record is increasingly high resolution well back into the past, even when the archaeological record is not.

However, we also still need more work on explaining why specific carrying capacities are what they are. One example of the issue is pointed out by Schmidt et al. [3] and emerges from their spatial approach. In the case of the first farmers in Central Europe a variety of lines of evidence confirm that regional populations grew to a peak and then declined, but even at the peak it seems that there were areas whose temperature, precipitation and soil conditions were ideal for their farming system, i.e. they were exactly the same as areas that were extensively occupied, but remained empty. What was it about the day-to-day and year-to-year processes of subsistence and social relations that led to births and deaths coming into equilibrium when they did?

Or maybe equilibrium conveys the wrong impression. Puleston et al.'s [44] simulation study used a detailed bottom-up population ecology model to examine the way a carrying capacity emerges from the operation of low-level processes. They modelled an age-structured population with given vital rates, age-related calorific needs and labour capacity colonising a new area with a given area of agricultural land with a given potential, examining the relationship between the total calorific needs of the population and the total calories available as the population grew. In contrast to the standard logistic model, which assumes that an equilibrium is reached, with growth rates gradually slowing down and population slowly levelling off, what emerges is very different. Exponential population growth continues at the maximum rate then comes to a sudden stop as the food ratio, the total food calories available divided by the total required, drops below unity. This leads, without warning, to a transition phase in which fertility rates and probability of infant survival suddenly drop and mortality rates sharply increase, heralding the beginning of an indefinite Malthusian phase of reduced fertility, increased mortality and varying degrees of hunger. The higher the fertility and the lower the mortality in the growth or copial phase, when quality of life is high, the greater the shock in terms of reduction in fertility and life expectancy as the limit suddenly hits. Importantly, the transition is not the result of any new external stimulus but of the endogenous processes in the model. Moreover, the Malthusian phase can result in deleterious social effects, like warfare, that exacerbate already poor conditions. At first sight the observation mentioned of unused areas at the population peak of Central Europe's first farmers appears in conflict with the assumptions of this 'invisible cliff' model but that does not mean that its bottom-up modelling approach is not a productive one to explore further. Indeed, even in the case of the Central European farmers it is striking that the later phase of population decline has evidence of massacres in several regions [45].

Archaeology, demography and life history theory

This recent archaeological work therefore proves Malthus was right. In his 1798 'Essay on the Principle of Population', he predicted that rapid human population growth would continually outgrow its resource base, leading to inevitable boom-bust cycles of population growth followed by decline, with mortality crises and drops in fertility levelling the population whenever it grew beyond environmental carrying capacity or when carrying capacity declined. As a result, human population growth over the long-term was very low, though not zero. Our behavioural flexibility and reliance on culture meant that we were sometimes able to partly escape from this 'Malthusian trap' by migrating into new environments – our species very successfully colonised

almost the entire globe while we were largely hunter-gatherers. Indeed, the rapid population growth rates during colonisation episodes that have been revealed in some of these papers confirm the reproductive success of such dispersal strategies [46]. We have also been able to occasionally increase environmental carrying capacity by developing new ways of capturing energy from the environment, which had particularly significant influences unleashing long-term population growth after the development of agriculture and the industrial revolution.

Can the past tell us anything useful about the future? Are we doomed to a Malthusian cycle forever, or was Malthus mistaken to think that our species will be caught perpetually in such a trap? This debate has raged pretty much since Malthus' time without resolution [47, 48]. So far, human populations have continued to grow very dramatically since the Industrial Revolution – global population has more than doubled in just the time the authors of this article have been alive – but predictions are repeatedly made that global population numbers will crash, or at least that population growth will soon slow down. Population growth rates are in fact now declining, having peaked in the 1960s, though population momentum means global population size is likely to grow significantly at least into the near future; most predictions suggesting a peak of around 9-10 billion later this century [49, 50].

These models, however, hinge on what will happen to fertility in the near future. Global fertility has now declined to just 2.3 children per woman, from levels of perhaps 6 children per woman on average before the demographic transition. Yet, fertility has proved rather difficult for demographers to predict. Implicit assumptions underlying the demographic transition model have tended to suggest that fertility should decline continually from high pre-transition levels to around 2 children per women, and then hover around that figure, maintaining populations in equilibrium (in low mortality populations, fertility of around 2 children per women will maintain constant population size). But once it began to decline, fertility dropped quickly to low levels in Western Europe, falling below replacement levels in some populations between the two world wars, but then rebounded to produce the 'baby boom' of the 60s [51]. Later in the 20th century, fertility rate dropped to very low levels, just over one child on average per women in some countries, but then seemed to rebound in the populations with the very highest levels of economic development in the 21st century (in northern Europe ([52] but see [53] for an alternative explanation). Very recently, however, northern Europe has seen unexpected sudden drops in fertility [54].

These significant fluctuations in fertility may suggest a break from Malthus' model in that, in pre-Malthusian time, he suggested it was largely mortality crises – caused by food shortages, epidemics and warfare – which resulted in 'depopulation'. While the archaeological record provides some evidence of, for example, warfare in support of this model, it is better on the whole at providing information on aggregate population growth and decline rates than mortality levels or patterns. Demographic records from the more recent past provide clear evidence of mortality rates which can fluctuate quite substantially over time, however, because of such mortality crises [55]. Since the Industrial Revolution, we have achieved remarkable success in reducing mortality rates and in preventing such crises, to the point that our mortality profiles are now so different from those of pre-demographic transition populations that Burger [56] has suggested these profiles appear to be from entirely different species. This might suggest that future mortality crises are unlikely, though perhaps should not be discounted, given the anthropogenic change which now appears to be wreaking havoc on our environment.

Fertility seems to have become more variable during the demographic transition, however, as suggested by the patterns in Europe described above. Most demographic projections now regard changes in fertility as more likely to drive slowing population growth and ultimately produce global population equilibrium, rather than increases in mortality.

But should we expect global population to permanently stabilise with births and deaths roughly in equilibrium? On archaeological timescales, the Industrial Revolution was very recent, so we could be in the middle of just another boom/bust cycle right now – it is not necessarily the case that the Industrial Revolution allowed us to escape the Malthusian trap, and we may continue to experience boom/bust cycles of population growth into the future. Ultimately, what pre-transition fluctuations in mortality and post-transition fluctuations in fertility may indicate is that demographic patterns in our species are hard to predict, at least in the short term. In other words, they are stochastic. This fits with models using life history theory from biology, which suggest that primate life histories in general, and perhaps human life histories in particular, are adapted to variable environments, meaning that demographic patterns will likely vary with environmental stochasticity [57]. It has even been suggested that human reproductive patterns, which allow rapid population growth, enable us to 'colonise' new environments very successfully [46], even if rapid population growth must inevitably be followed by population decline as we hit the ceiling of carrying capacity in new environments.

Comparative work with primates suggests the factor which might be particularly important in allowing our species not just to cope with environmental variability without risk of extinction, but to flourish and become the world's most successful primate: this factor might be our habit of 'pooling energy budgets' when it comes to raising offspring [58]. Human mothers can maintain high fertility rates because they do not have to bear the costs of reproduction alone [59]. Our species engages in substantial intergenerational transfers, meaning both the grandparental and child generation contribute help to the parental generation in raising children [60]. However, these patterns of helping do show some variation between and within populations [61, 62]; they may partly be a response to environmental variability, but may also contribute to different demographic schedules [63], perhaps providing an explanation for variation in the archaeological record in terms of differential distribution patterns across apparently similar contexts. Further comparative work, such as detailed work which compares the life histories of humans with other great apes [64], might help elucidate further the similarities and differences between the 'colonising ape' which has been demographically successful and those ape species which have not (though admittedly current population declines among ape populations are complicated by anthropogenic destruction of their habitats).

This view of our life history helps explain something which might otherwise appear puzzling to a biologist: humans are large mammals, with characteristically 'slow' life histories, meaning growth is slow, reproduction starts late, and reproductive events are relatively rare. The boom-bust cycles of population growth, which appear to characterise human populations at the centennial scale, are more common in 'fast' species such as small mammals whose life history typically involves fast growth, early reproduction and large numbers of offspring, which results in rapid population growth [65]. Slow life history strategies in contrast are typically expected to have low population growth, and density-dependent mechanisms which keep population size tracking environmental carrying capacity. But slow life histories may also be favoured in environments which are highly variable and so which involve significant periods of population

decline, even if overall, population growth over the long term is positive [57]. However, this perception of a difference may also be a matter of scale: the booms and busts of populations of mammals with slow life histories may occur over much longer time-intervals and need an archaeological vision to be perceived, suggesting further dialogue between archaeologists and biologists may be fruitful in understanding the evolution of human life histories.

Returning to the future demography of our species, if we are adapted to environmental variability, and if our demography is similarly variable in tracking environmental shifts, perhaps we should not expect any stabilisation in global population in the near future. But perhaps this is also not necessarily a bad thing, if environmental stochasticity is exactly the condition under which we are adapted to thrive.

Conclusion

The innovative archaeological research which has recently shed light on the demographic patterns of our species in deep history provides support for one of the earliest and most influential models in demography: Malthus' 'pessimistic' prediction that human populations were condemned to an inevitable oscillation between population growth and population decline around a density-dependent ceiling. Overlaid on Malthus' pessimism, however, is the observation that population growth rates, in the long-term, were positive, as human populations repeatedly escaped from the Malthusian trap through migration to new environments and increasing the carrying capacity of existing environments by developing new methods of exploiting them that lifted the Malthusian ceiling, even if only temporarily in some cases. We may even owe our species' success partly to adaptations which allowed us to thrive under such stochastic conditions, leading to optimism about the future of human populations, especially if future population fluctuations are driven more by shifts in fertility than mortality. Questions remain, however, about the history, and potential future, of our species. Is our behavioural (including cultural), and demographic, flexibility the result of these boom-bust cycles or the cause of them, or both? What do these fluctuating environmental conditions mean for our ability to understand and manage risk and unpredictability? Closer cooperation between archaeology and evolutionary demography might help elucidate some of these questions, combining a detailed understanding of demographic mechanisms and the evolutionary principles behind them with a longer term perspective on what has happened to populations in different places at different times and the reasons for it.

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