



REVIEW ARTICLE

Reconstructing prehistoric demography: What role for extant hunter-gatherers?

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Abstract

Demography is central to biological, behavioral, and cultural evolution. Knowledge of the demography of prehistoric populations of both *Homo sapiens* and earlier members of the genus *Homo* is, therefore, key to the study of human evolution. Unfortunately, demographic processes (fertility, mortality, migration) leave little mark on the archeological and paleoanthropological records. One common solution to this issue is the application of demographic data from extant hunter-gatherers to prehistory. With the aim of strengthening this line of enquiry, here we outline some pitfalls and their interpretative implications. In doing so, we provide recommendations about the application of hunter-gatherer data to the study of demographic trends throughout human evolution. We use published demographic data from extant hunter-gatherers to show that it is the diversity seen among extant hunter-gatherers—both intra- and inter-population variability—that is most relevant and useful for understanding past hunter-gatherer demography.

KEYWORDS

demography, fertility, hunter-gatherers, life history, prehistory

1 | INTRODUCTION

Demography and evolution are intrinsically intertwined. Evolution is driven by the propagation of genes, which is determined by the key processes of survival (mortality), fertility, and dispersal (migration) of individuals.^{1,2} Demographic trends influence the age- and sex-structure of a society, altering the balance between kin and non-kin within individuals' social networks,³ with consequences for cooperation, parental investment, and information exchange.^{4–6} Demography further influences the development and variability of human culture, through its recognized role in trait transmission and cumulative culture.^{7,8} Knowledge of the demography of prehistoric populations of both *Homo sapiens* and earlier members of the genus *Homo* thus has the potential to offer vital insights into human evolution across multiple domains.

Our knowledge of demography in prehistory, however, faces one fundamental obstacle: the lack of direct data. Fertility, mortality, and migration leave little mark on the archeological and paleoanthropological records. Researchers studying the outcome of variation in these demographic processes (changes in population size, density, and growth rate) have met with more success, but are largely limited to the comparison of relative changes in these measures.⁹ Furthermore, most established paleodemographic methods^{10–14} have limited applicability to the Pleistocene contexts (~2.6 million to 12,000 years ago¹⁵) that constitute much of prehistory. Genetic data (from both ancient and living populations) inform on some elements of prehistoric demography, notably interbreeding between different hominin taxa, and estimates of effective population sizes,^{16,17} but address a limited range of demographic questions, and ancient DNA sequences are comparatively rare.

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A common solution to this lack of direct data is to look to the richer corpus of demographic data on extant hunter-gatherers. Demographic data from recent ethnographically-documented hunter-gatherer populations are important tools in prehistoric demographic research. Ethnographic data play a key role in developing frameworks of prehistoric demography (e.g., Reference 19) and providing absolute values of prehistoric demographic variables (population size, density, and fertility and mortality rates) for use as descriptive statistics and/or input parameters in formal demographic models.^{20–24} While certainly not complete, nor without its own issues (something we return to below), compared to the archeological and paleoanthropological records, a mass of quantitative data on fertility, and to a lesser degree, mortality, and migration, are available for multiple hunter-gatherer populations. Here, we examine critically the wider relevance and application of demographic data from extant hunter-gatherers to prehistory (with a particular focus on the Pleistocene). The explicit aim of this paper is to highlight key theoretical and methodological considerations in both producing and using hunter-gatherer demographic data to study prehistoric demography. Consequently, our main goal is to communicate these considerations beyond evolutionary anthropology, and address our colleagues in archeology and paleoanthropology, who may be unfamiliar with the relevant literature and prevailing approaches.

We highlight five pitfalls faced by researchers working with past and present hunter-gatherers, and thus applicable to both anthropologists and archeologists. These pitfalls are not new, and we are not the first to recognize them. However, our analysis suggests that these pitfalls are not clearly communicated beyond disciplinary confines (Box 1). Reasons for opaqueness are miscommunication of methodology, assumptions which conflict with wider biological principles, and the uncritical application of single group demographic values or “hunter-gatherer” averages to the past. This has important implications for our understanding of prehistoric demography. We draw on data from extant hunter-gatherers to argue that the between and within-population *variability* in demographic variables seen among extant hunter-gatherers is best equipped to provide insights into past hunter-gatherer demography. Through the lens of human behavioral ecology (HBE) these data allow us to examine how hunter-gatherers today react to selective pressures, providing the tools with which to identify parallels in prehistory.

2 | PITFALL ONE: NOT RECOGNIZING THE LIMITATIONS OF HUNTER-GATHERER DEMOGRAPHIC DATA

While the demographic data produced by biological anthropologists and demographers working with hunter-gatherers are more complete than prehistoric sources, these data are far from infallible. The specific challenges of data collection and accuracy vary between populations, but some problems are universal despite (but lessened by) the extensive efforts of anthropologists. Foraging groups are often non-literate and do not keep their own records. To create a full record of births,

deaths, and migration, fieldworkers conduct detailed self-reported genealogies. However, self-reports rarely produce a fully accurate demographic record; recall bias is common, leading to an underreporting of births, miscarriages, stillbirths, and infant mortality due to either forgetfulness, a lack of cultural recognition of a “birth” or simple miscommunication.^{6,25} Taboos may further exacerbate inaccuracies. For example, the Agta use nicknames to refer to their in-laws since it is forbidden to use their names. As different nicknames are used, reconciling different genealogies can be challenging.²⁶ Self-reporting is also an issue for aging; hunter-gatherers often have a very different, or no concept of calendar time, thus, no clear idea of how old they are.²⁷ Precise estimates of ages are fundamental to the construction of an accurate demographic record, and the subsequent study of life history. Obtaining accurate age estimates is the major challenge of hunter-gatherer demographic studies (Box 2).

Researchers face two further key issues. First, hunter-gatherer population sizes are small (~800–1,000 individuals^{28,29}) and are especially vulnerable to stochastic (random) demographic variation. In terms of long-term growth or decline, in a large population, individual events are “averaged” out, while in smaller groups this random variation has disproportionate influence; patterns of growth and decline are far more extreme and volatile in small populations.^{30,31} Consequently, in a small population an extremely low or high fertility rate may be the outcome of the size of the sample. HBE frequently explore whether a behavior is adaptive³² and a surprisingly low fertility rate can be interpreted as the product of maladaptive behavior. This may be the case. However, we must also consider that a fertility rate is the product of a random collection of individual events, reflective of the study population, and data collection protocols (i.e., few births occur in the population during data collection). Furthermore, small sample sizes are one reason why data on older age mortality is lacking in comparison to data on fertility rates and pre-adult (age 16 and below) mortality in hunter-gatherers. As the cohort ages more individuals die, and the sample at risk of death becomes smaller. With small populations, the sample size at older ages is likely too small to accurately estimate mortality rates (i.e., when the mortality rate is less than $1/n^{18,33}$). Given the importance of age-specific mortality rates in human evolution, demography and life history models³³ (see pitfall two) researchers working on prehistory should pay attention to the sample sizes from which key figures arise, acknowledging the large confidence intervals around the mortality estimates.

The relatively short timeframe of ethnographic fieldwork introduces further uncertainties. Demographic ethnographies vary in the length of data collection, from years to decades, but primary fieldwork is usually limited to periods of months. Such short fieldwork periods are problematic due to the fission-fusion nature of hunter-gatherers; where over time individuals either join a group (fusion) or leave (fission) and spilt the group.³⁴ Such trends cause researchers with limited observation periods to question who actually belongs in a household, camp, or wider group. During our first visits with the Agta, we frequently found an absence of “teenagers” in some parts of the population. One potential interpretation of this pattern is that particularly high past infant and child mortality rates had occurred, distorting the

BOX 1 Glossary

Age-specific fertility: The number of live births occurring to a particular age group of women per year. It is often expressed per 1,000 women. Age groups used are often a single year, or 5-year groups.

Age-specific mortality: A count of deaths in a particular age group (numerator). The denominator is the number of total persons in that age group. It is algebraically independent of mortality events at all other ages.

Cohort: A group of people who experienced the same demographic event during a particular period of time.

Cumulative probabilities of mortality (l_x): In a life table the l_x column is headed by the radix (the root or full population, represented by 100,000, 1,000, 100, or 1). This number decreases over time as individuals die, therefore, it represents the survivors from the radix by age.

Delayed-returned hunter-gatherers: settled, hierarchical, or “complex” societies with food storage.

Demographic uniformitarianism: the assumption that basic demographic processes, and the mechanisms underlying these, are unchanged between the past and the present.

Growth rate: The ratio of growth in a given period to the mean population during that period.

Human behavioral ecology (HBE): An adaptive approach to human behavior, based on the premise that individuals optimize behavioral strategies to particular ecological contexts.

Immediate return hunter-gatherers: groups who are largely egalitarian and consume their resources daily rather than store goods.

Infanticide: The deliberate killing of infants, usually shortly after birth.

Life expectancy (e): The length of time expected before death, from any stated time after an initiating event. Given by the “ e ” column of a life table, with e_0 denoting *life expectancy from birth* (the average number of years a newborn is expected to live), while e_x denotes *age-specific life expectancy* (expectation of life from age x).

Life tables: a tabular description of age and sex-specific mortality trends that express the likelihood of a mortality event occurring at a specific time interval as well as cumulative trends.

Maximum lifespan: the definition of maximal lifespan is contentious—there is no single age that some individuals reach and have no chance of surviving—here it is more useful to think in terms of “life endurance” or the age at which 10% of the initial cohort remain alive.¹⁸

Median lifespan/age at death: The age at which half the initial cohort is dead.

Natural fertility populations: Fertility that exists in the absence of parity-dependent fertility control. Thus, natural fertility populations can demonstrate behavior that limits fertility (such as post-partum sex taboos), providing this behaviour is not designed to reach an ideal completed family size (e.g. four children). From an HBE perspective, and here, this term is often used to refer to populations who lack modern forms of contraception.

Stable population: A stable population is one which has an unchanging age structure. A stable population may still be growing (or shrinking), however, each age group must be changing by the same amount. A stable population, which is not growing nor shrinking is called a stationary population. Stable populations are always closed to migration.

Total fertility rate (TFR): The number of children a woman would have if she experienced the age-specific fertility rates for the period in question throughout her reproductive life. The TFR is by default considered a period measure but can also be reported at the total *cohort* fertility rate (or completed family size), which is the TFR for a real cohort of women reported after reproductive cessation.

Yearly probability of death (q_x): Stemming from l_x , it measures the proportion of people reaching a given birthday within a calendar year who die before their next birthday.

social and demographic composition in a particular area. However, in the Agta case, young adults frequently visited distant camps because of exogamous marriage rules, enabling individuals to avoid marriages with relatives by looking further afield.²⁶ It is highly likely then that individuals frequently go unreported, individuals who might share particular characteristics such as age and sex, as these structure mobility patterns.³⁵ Consequently, the structure of the population reported by the ethnographer will always be, in part, a product of their data collection.

Anthropologists are well aware of the difficulties of precise demographic data collection among hunter-gatherers, but this awareness is frequently lost outside the field. Our first recommendation is for researchers to evaluate data critically in and of themselves, before considering their applicability to prehistoric contexts. For instance, how many individuals were included in the study, and how long were they studied for? What methods were used to account for errors in fertility and mortality reports as well as aging? If the sample size is small and/or individuals were studied for a short time period

BOX 2 An issue of aging in hunter-gatherers

Researchers have long been aware of the necessity and difficulties of aging populations without accurate birth records or concepts of time similar to the researchers. Early work relied on “guesstimates,” based on how old the researcher personally considered an individual to look.³⁶ However, this is problematic since physical appearance trajectories vary substantially across populations; in many foraging populations adults frequently look much older than they chronological age based on researchers' expectations. To improve accuracy, Howell³⁷ used steady-state models to match existing (western) life tables to the demographic trends of a foraging population, which stipulate the proportions of individuals expected in each age group. This method is problematic, however, since it assumes stable populations (an unrealistic assumption) and forces hunter-gatherer demography onto western schedules, hiding the diversity the research is seeking to explore.³⁸ To overcome these issues, Hill and Hurtado³⁸ developed a regression method using relative age lists; based on a few individuals of known ages, it was possible to age the remaining individuals in the population based on their relative age rank and “age difference” between individuals. However, this method does not account for the uncertainty in age estimates, which is inherent in this form of aging, particularly important when the error in the age difference between individuals is cumulative.²⁷ Recent work utilizes a Bayesian method, which inherently takes the uncertainty of age estimates into account by producing a *distribution of possible ages* for each individual, ultimately increasing the reliability of the estimates.²⁷ Future ethnographic work can capitalize on these methodological improvements. In the meantime, researchers should be aware of the methodologies used and the consequence this has on the estimate's quality.

additional sources should be gathered. Such results cannot be taken at face value. Data based on longitudinal fieldwork have advantages because of continual data collection, but due to time and funding constraints are only available for a few groups (e.g., Dobe!Kung,³⁹ Hadza,⁴⁰ Ache,³⁸ and San Ildefonso Agta^{41,42}). Below we highlight the importance of the diversity of hunter-gatherer populations. Constructing an image of prehistoric demography based on two or three foraging groups, who reside in a limited range of environments is inadvisable; balancing data availability and data suitability is challenging but paramount.

3 | PITFALL TWO: THE INCORRECT INTERPRETATION OF DEMOGRAPHIC PARAMETERS

Part of the critical evaluation of ethnographic data includes understanding the demographic measures used; measures which are often (understandably) unfamiliar to paleoanthropologists and archeologists. In the absence of this familiarity, there is a clear risk of applying ethnographic data to prehistoric contexts in ways which are at best misleading, and at worst, at odds with key biological and demographic principles. Examples of such misunderstandings exist in the literature, several of which have gained the status as truisms of prehistoric hunter-gatherer demography.

One notable example is the assumption that very few (if any) prehistoric people lived to be old.^{40,43} The frequent lack of older (aged 40+) individuals in skeletal assemblages, particularly, although not exclusively,⁴⁴ those of archaic hominins^{45,46} lends some support to this position. However, other factors could explain this apparent absence (Box 3). At least as far as prehistoric *H. sapiens* hunter-gatherers are concerned, the assumption of societies with very few old people is unlikely, and in disagreement with both life-history

theory and contemporary demographic data, as well as violating the key principle of demographic uniformitarianism (Pitfall four).

Life history schedules are the outcome of differential investment of time into the competing aspects of growth, maintenance, and reproduction. Primates have particularly “slow” life histories (i.e., take longer to reach maturity and produce fewer offspring) compared to other mammals of similar body size because their average adult lifespans are around 2.5 times longer.⁴⁷ *H. sapiens* further extend this “slow” pattern; we have an extremely long development, including a prolonged juvenile period for intellectual and social development.⁴⁸ This is possible because even in hunter-gatherers with little access to medical care, the mean survival after age 45 is 20.7 years. Thus, it is not uncommon to reach 65–70 years, 20–30 years longer than other non-human great apes.^{49,50} In the!Kung, Ache, and Hadza between 29 and 36% of women survive past the age of last birth, compared to less than 6% of chimpanzees.⁵¹ An unusual feature of human life history is the presence of post-reproductive women, a period of hominin life history, which arguably evolved to help mothers successfully reproduce.⁵² Furthermore, given the allometric relationship between body, brain, and longevity⁴⁷ the predicted longevity of *H. habilis* (52–56 years) and *H. erectus* (60–63 years)⁵³ falls well beyond the cessation of reproductive function long before the appearance of *H. sapiens*.¹⁸ Humans, then, have many interconnected features that rely on a “slow” life history strategy, which is incompatible with a maximum life span of 40 years.

Similarly, while mortality rates among recent hunter-gatherers are high⁵⁸ this does not exclude the possibility of a long life. This common misunderstanding is likely, at least in part, caused by demographic unfamiliarity, confusing life expectancy at birth (e_0), median lifespan/age at death, with maximum lifespan, and cumulative probabilities of mortality.⁴⁰ Among many hunter-gatherers, both median age at death and life expectancy at birth are low. Across a range of hunter-gatherers median e_0 falls at 25.9 years (Table S1, Figure 1), with a range of 16–50.4 years

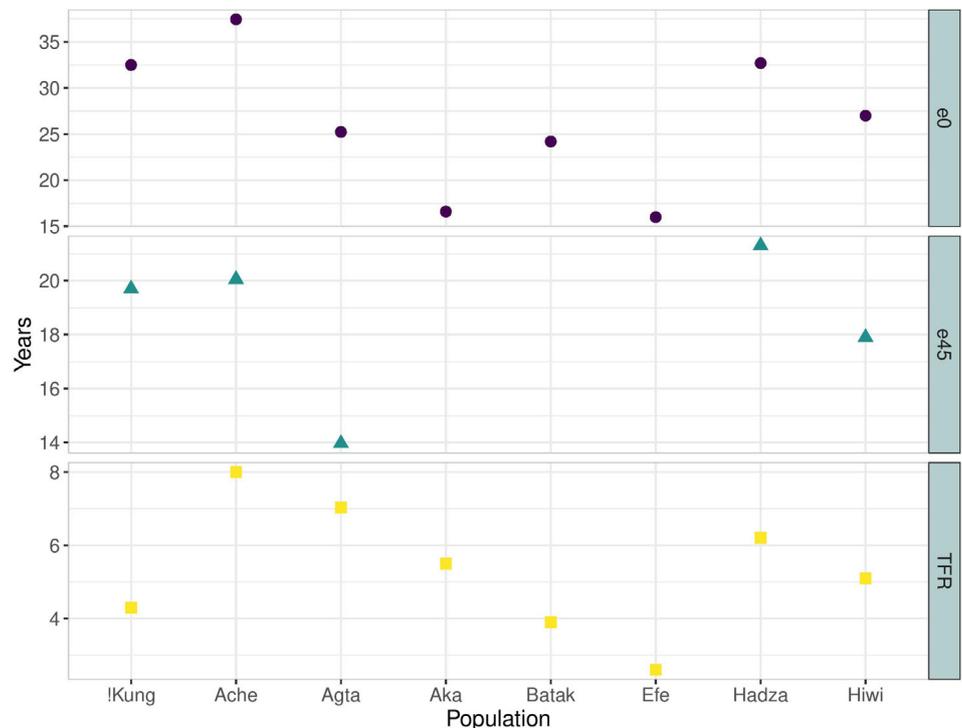
BOX 3 Where are the old people in prehistory?

One common feature of many prehistoric skeletal assemblages is the lack of older (aged 40+) individuals. Whether this is an accurate representation of longevity in this past is a long-standing debate in skeletal paleodemography,⁵⁴ and if not, how do we explain their absence from the archeological record?

The most likely explanation is methodological. It is difficult to produce accurate age-at-death estimates from adult skeletons. The age of adults is determined through the study of macroscopic and microscopic markers for dental and skeletal degeneration and wear, the accuracy of which are heavily disputed.⁵⁵ The particular inability to discriminate between older ages (i.e., distinguishing a 50-year-old from a 70-year-old), means that the age of many older individuals is frequently underestimated when binned into a terminal age interval.⁵⁶ Poor preservation may also be a factor: the increased loss of calcium means that the bones of older individuals are less resistant to disintegration, reducing the likelihood of their survival compared to those of younger adults.⁵⁷ Cultural factors, such as differential burial practices for older adults, are also important. In the case of mobile prehistoric hunter-gatherers, it is possible that older individuals were “left behind” when they could no longer maintain a high level of mobility, and their remains subsequently not recovered by archeologists.⁴⁴

Overall, a combination of methodological, preservational, and cultural factors best explain the apparent lack of older individuals in prehistoric skeletal assemblages, especially those of *H. sapiens*. The persistence of this pattern into later prehistorical periods (e.g., the famous Libben Site, OH, 800–1100 AD)⁴³ provides further support for this position; being too recent (in evolutionary terms) to accommodate such substantial biological changes within the human lineage as is implied by these age-at-death distributions.⁵⁸

FIGURE 1 Demographic parameters for a range of foraging populations. e_0 = life expectancy at birth, the average number of years a newborn will survive, e_{45} = life expectancy at age 45, the average number of years an individual aged 45 is expected to survive. Further parameters and reference information can be found in Table S1. Aka, Batak, and Efe are all missing e_{45} values [Color figure can be viewed at wileyonlinelibrary.com]



(interquartile range 22.03–32.55 years).^{37,40,42,50,59–62} This does not mean that hunter-gatherers are *most likely* to die aged 20–30 years; quite the opposite is true. The human mortality hazard curve is typically U-shaped, a product of high mortality hazards in early and later life.⁵⁰ The particularly low e_0 is a product of very high infant and juvenile mortality rates; survival rates to age 15 are commonly around ~45–55% (i.e., measures of life endurance or expectancy are not independent measures as they subsume infant, child, and other mortality rates). For

instance, Figure 1 demonstrates that while the Agta and Hiwi have e_0 values of 24.3⁴² and 27⁵⁰ years, respectively, they simultaneously have e_{45} (the average number of years an individual aged 45 is expected to survive) values of 13.7 and 17.9 years. e_0 tells us little about adult life expectancy or life endurance.

For information about the likelihood of surviving to a particular age (l_x), and thus a sense of the life endurance, one must turn to life tables. Life tables of recent foraging populations^{38,42,63} and cross-

cultural analyses⁵⁰ collectively indicate that many hunter-gatherers live into their sixth decade and longer. Combined, both ethnographic data and life history theory refute the assumption that recent and prehistoric hunter-gatherers rarely lived to be old, an assumption that is compounded by a general unfamiliarity with demographic parameters. We recommend that researchers familiarize themselves with demographic methods for measuring population dynamics (see Reference 64 for an introductory guide), exploring the difference behind a range of parameters (for instance, the difference between the yearly probability of death, q_x , the cumulative measure of mortality to a particular age, l_x , and age-specific life expectancy, e_x), and the interpretative consequences of these differences.

4 | PITFALL THREE: OVERLOOKING THE DIFFERENCES IN DEMOGRAPHIC SCALES IN PREHISTORIC AND EXTANT HUNTER-GATHERERS

The contrasting scales of ethnographic fieldwork and prehistoric inquiry introduce further difficulties. These difficulties primarily manifest in discussions of the growth rate of prehistoric hunter-gatherer populations. Throughout prehistory, global hunter-gatherer populations experienced near-zero net growth.⁶⁵ If hunter-gatherer populations were growing at a long-term greater rate than this, the global population would have reached specific sizes earlier than we know it did. However, no recent hunter-gatherers have a growth rate of near-zero; the mean hunter-gatherer growth rate is ~1% per annum.²⁸ Long-term population growth rates of near-zero would require a combined fertility and mortality schedule outside of or at the extreme limit of the known range of human variation,⁴¹ violating the assumption of demographic uniformitarianism described further below.

Blurton Jones terms this contrast between the growth rates of prehistoric and extant hunter-gatherers the “forager population paradox.”⁵⁹ The best explanation for this discrepancy is the different scales at which archeological and ethnographic data are analyzed, which means that the growth rates generated are not directly comparable. Prehistoric growth rates of ~0% are mean values viewed over millennia, the combined result of multiple cycles of rapid population growth, followed by local extinctions,⁶⁵ likely caused by a combination of stochastic processes and catastrophic events.^{66,67} Growth rates of ethnographic foragers on the other hand, represent real per annum measures of population change somewhere along this continuum of growth and decline. In fact, many recent foragers for whom we have growth rate data were experiencing a phase of rapid population recovery at the time of data collection following previous crashes at the hands of colonial forces.³⁸ It is therefore not surprising that calculated Pleistocene growth rates are not the same as those of recent foragers, nor can growth rates from recent foragers be assumed to be realistic long-term estimates for either the population from which they derive or prehistoric hunter-gatherers.

The lack of recognition of these different scales led earlier researchers to search for population control mechanisms to explain how prehistoric populations maintained long-term near-zero growth rates.^{68–70} These mechanisms were envisioned as deliberate group-level controls that ensured population size never exceeded environmental carrying capacity. Infanticide is a mechanism, which continues to be cited,^{70–76} and in our experience, discussed at archeological conferences and workshops, as crucial to curtailing past population growth. This narrative has become an “accepted truth” but is unlikely for multiple reasons, which we will highlight here with the example of female-biased infanticide.

Female-biased infanticide has been pinpointed as particularly important for population control; since females are the limiting factor in reproduction, population growth rates are reduced more by removing females than males.⁷⁷ Beyond some specific examples,^{78–80} female-biased infanticide has not been extensively reported among hunter-gatherers, nor is a stated or observed sex preference in parental investment. The highest rates of infanticide originate from ethnographic reports from Arctic hunter-gatherers,⁸¹ however, such reports have been called into question, and were likely exaggerated³⁵ (for a fuller discussion see Reference 6). Furthermore, the requirement for population reduction among hunter-gatherers is questionable; hunter-gatherers today and historically have rarely strained at the limits of their resources.^{59,82} Finally, there are theoretical reasons why explanations based on group level processes should be questioned. Infanticide is documented in a wide range of the world's populations and may be in an *individual's* best interest.⁸³ However, infanticide as a direct means of population regulation invokes the idea of what is in the *group's* best interest, which is more problematic. Wynne-Edwards⁸⁴ argued that groups of individuals who restricted their fertility would “out-perform” groups who did not. Theoretically, groups of selfish “breeders” would die out while the cooperative “restrictors” would survive, but it requires two rare conditions; a) that the groups die faster than individuals for the effect to be greater than that of individual selection and; b) that individuals from the selfish group cannot migrate into the cooperative group and overrun it, a condition particularly unlikely in mobile hunter-gatherers.⁸⁵ Thus, it is unlikely that individuals, past or present, systematically conduct female-biased infanticide *due to* a need to regulate the population size.

The endurance among archeologists and paleoanthropologists of the “infanticide as population control” hypothesis is another example of the gulf between researchers studying past and present hunter-gatherers. Furthermore, the lingering effects of a focus on deliberate population control have seen greater weight given to mortality than fertility in discussions of prehistoric demography, as the former is considered easier to manipulate than the latter in the absence of effective contraception (the perceived greater visibility of mortality than fertility in archeological contexts is likely another contributing factor [although this perception is often inaccurate⁸⁶] as is the under-investigation of women and female domains in archeology⁸⁷). However, it is vital to look at *both sides* of the demographic equation. We return to the topic of fertility in Pitfall five.

5 | PITFALL FOUR: UNCRITICALLY APPLYING DEMOGRAPHIC UNIFORMITARIANISM TO ARCHAIC HOMININS

Demographic uniformitarianism refers to the assumption that basic demographic processes are unchanged between the past and the present. This does not mean that demographic behaviors have remained the same throughout history, but that the biological processes are similar, responding to variations in the social and natural environment in the same way, and that these similarities act as constraints and impose limits on demographic behaviors.⁸⁸ The principle of demographic uniformitarianism underpins all research into prehistoric demography, providing the rationale for the use of demographic data from recent populations as a tool for the analysis of past populations.^{55,89}

The uniformitarian assumption is only strictly applicable to members of our own species, *H. sapiens* (the earliest known specimen of which dates to ~300,000 years ago⁹⁰). The biological and developmental differences between *H. sapiens* and prehistoric archaic hominins are subject to on-going debate and are often difficult to quantify.⁴⁹ A key turning point in hominin life history occurred with *H. erectus*, with a shift toward the slow life history described in Pitfall 2.⁹¹ Later archaic hominins (e.g., *H. heidelbergensis*, *H. neanderthalensis*) likely had a pace of development within the *H. sapiens* range but nonetheless subtly different.^{92–94} These differences mean that we cannot take for granted demographic profiles analogous to those seen among recent hunter-gatherers.

One line of evidence that suggests possible important demographic differences between recent hunter-gatherers and archaic hominins is group composition. Cross-culturally, ethnographically documented hunter-gatherers live in residential groups composed of a high proportion of non-kin.^{95,96} However, there is some compelling evidence for high genetic relatedness within groups of archaic hominins, especially Neanderthals.^{97,98} Notably, this contrasts with the available evidence for group composition among early European *H. sapiens* who's within-band relatedness is similar to that seen among ethnographic hunter-gatherers.⁹⁹ These differences in residential composition have important implications for social networks, cooperative ties, mobility, and groups sizes, potentially highly divergent from what is documented in hunter-gatherers today.^{5,96,100}

Given the possible differences in group composition, the direct transfer of group size values from ethnographic hunter-gatherers to non-*H. sapiens* prehistoric hunter-gatherers are both inadvisable and uninformative, especially the application of the median group size of 25–30 individuals²⁹ regardless of hominin species or geographical context. This median value has been applied to a wide range of time periods (from the lower Paleolithic to Mesolithic), localities (Western Europe to South Africa) as well as hominin species (*H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*).^{101–105} This is problematic since group sizes are influenced by multiple factors, including mobility, diet, and ecological settings.^{19,35} There are good reasons why the cross-cultural average group size is ~25–30 people. This number of people

represents a good compromise between the lower and upper viable limits of local group size—small enough not to deplete resources quickly, and to allow for group cohesion, while simultaneously containing enough active food producers to ensure the groups' continued survival.^{28,35} However, the documented variability in forager group sizes, and the possible differences in prehistoric group composition discussed above should cause us to pause before applying this median value to all past hunter-gatherers. The application of a given group size requires justification based on an understanding of what drives variability in these traits in recent populations, and the applicability of these trends to the prehistoric comparison. While absolute estimates of prehistoric group sizes are important and unfortunately difficult to generate (see References 106 and 107 for recent examples of novel approaches), taking an average value from the ethnographic literature is not the answer. Our null hypothesis should be that prehistoric hunter-gatherers were similarly, if not more, variable than current hunter-gatherers, given the longer chronology, the wider range of environments inhabited, and multiple *Homo* species.

6 | PITFALL FIVE: ASSUMING THERE IS SUCH A THING AS “THE” HUNTER-GATHERER DEMOGRAPHY

Defining who is, and who is not a “hunter-gatherer” is not an easy task, primarily due to the range of variability within and between populations. Evidently, “hunter-gatherer” is primarily an economic category describing groups who lack the domestication of plants or animals. However, since the earliest ethnographies, most hunter-gatherers have derived some of their diet from non-foraged sources. Thus, strict adherence to the “absence of domestication” definition of hunter-gatherers would eliminate most known populations.¹⁰⁸ Rather, how hunter-gatherers have been defined throughout the 19th and 20th centuries was often based on ideology or modeled on a few of the best studied groups.¹⁰⁹ Hunter-gatherers were originally defined as male-dominated patrilocal bands,¹¹⁰ later an emphasis was placed on mobility and egalitarianism as hunter-gatherers became the “original affluent societies.”¹¹¹ More recently, they were defined by their marginalized role within globalized world-systems.¹¹² In seeking to develop universals by which to understand the foraging way of life, anthropologists have been too quick to stress the homogeneous nature of the categories, and in doing so risk painting an unrealistic image of hunter-gatherers. Such an approach systematically and arbitrarily reduces the diversity within and between populations because hunter-gatherers are not discrete entities.

Given the degree of inter-population diversity in lifeways of hunter-gatherers, resulting in the often arbitrary nature of subsistence classifications, which groups provide the most appropriate data for reconstructing prehistoric demography? While it is evident that groups which only farm have less relevance, the distinction between the most “relevant” hunter-gatherer population is less clear. Given the cross-cultural range in different types and degrees of foraging (fishing, hunting, gathering³⁵), it is difficult to establish a proportion of time

foraging that all would agree was “enough” to be a hunter-gatherer. This is harder still when there is significant intra-population variation, something we discuss below. Some argue that we should “give extra weight to those with less contact” to gain insight into Pleistocene foragers, given the radical impact contact with agriculturalists and/or pastoralists has had on extant foragers.²⁹ We do not, however, consider this the best strategy for demographic research if it means using the parameters from a single population.

First, limiting our inferences about demography to the dynamics of one population, risks reducing human diversity down to a very specific ecology and context. What if the “least contacted” lived in a vastly different ecology to that being modeled? Further, while not intentional (in particular, it is not the focus of Reference 29, discussed more below) it implicitly suggests that contact is the main source of variation between hunter-gatherers. For instance, approaches which seek the least contacted foragers assume that prior to contact, the hunter-gatherer adaptation was static and uniform. This is untrue. The archeological record shows marked geographical and temporal variability in response to changing selective pressures^{113,114} as well as interbreeding between a variety of hominin species.^{16,115} It is important to consider the period in prehistory under demographic reconstruction (as suggested by Reference 29, as well as degree of technological innovation). An additional concern is the emphasis on recent contact, that is, since anthropological documentation, while overlooking the contact, which occurred long before. The archeological, linguistic, and genetic record is rife with evidence of significant amounts of interaction and trade between hunter-gatherers and non-hunter-gatherers.^{116–119} It is unclear how one could remove these influences, which necessarily have shaped hunter-gatherers' behavioral strategies since their occurrence. Consequently, it is not possible to distinguish a more “real” or modal foraging group; rather there are many forms of hunter-gathering possible.

Hunter-gatherers, therefore, are not an immutable concept that can be used as an explanatory variable.³⁵ Using the example of total

fertility rate (TFR), we demonstrate below why taking the average hunter-gatherer parameter is particularly problematic when attempting to reconstruct fertility in prehistory. We selected fertility as a case study for two reasons. First, as identified in Pitfall three, the role of fertility in prehistoric demographic change is frequently overlooked (although estimates of fertility measures are increasingly common^{21,120}). Second, data from recent hunter-gatherers indicate the key role of physiological constraints on reproduction in explaining variability across multiple fertility measures,^{39,121} and ultimately demographic trends more broadly. These constraints, such as energy balance and availability, are equally applicable to prehistoric contexts, and crucially, their proxies (e.g., mobility, diet) are directly inferable from the archeological record.⁸⁷

6.1 | Case study: Variability in extant hunter-gatherer TFR

Hunter-gatherers are reported to have a relatively low TFR of 5–6.¹²² The “relatively” is in reference to other natural fertility populations as well as the biological maximum fertility.¹²³ Bentley, Jasienska, and Goldberg (1993) found that the TFR of agriculturalists was significantly higher than non-agriculturalists (hunter-gatherers and horticulturalists combined). Yet, they did not find a significant difference between hunter-gatherers and agriculturalists when hunter-gatherers are no longer grouped with horticulturalists¹²²—do hunter-gatherers, then, have low fertility? The main reason for this lack of difference is the extreme variation in TFR. In Bentley and colleagues' sample, while the mean TFR is 5.6 for hunter-gatherers and 6.6 for agriculturalists, the *SD* (σ) of TFR was 1.39. A high *SD* indicates the mean (or median) does not accurately represent the wider range of values. Given this *SD* and a sample size of 5–11 hunter-gatherers, this analysis does not have the power to detect a 1.1 change in TFR the majority of the time. Thus, while agriculture is predicted to be associated with

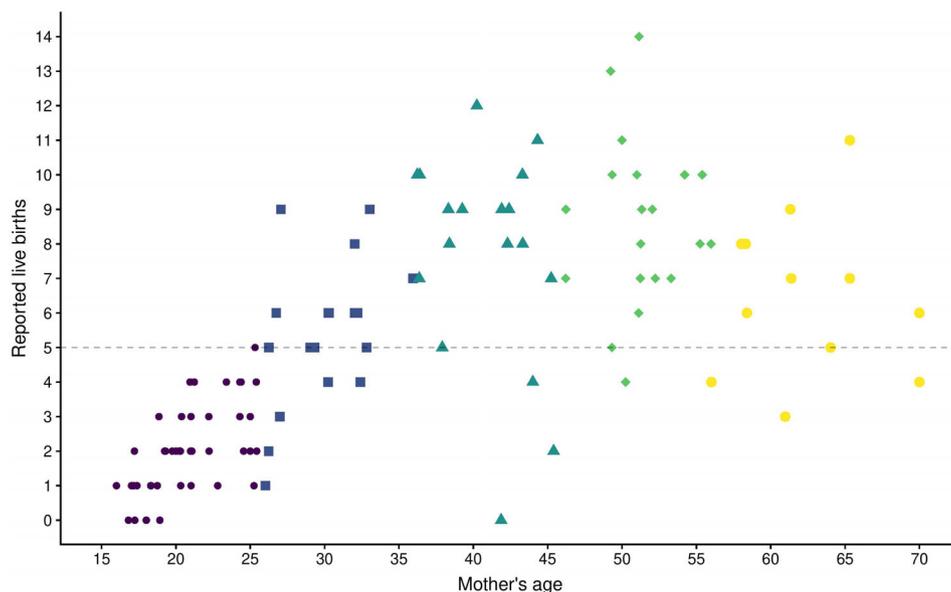
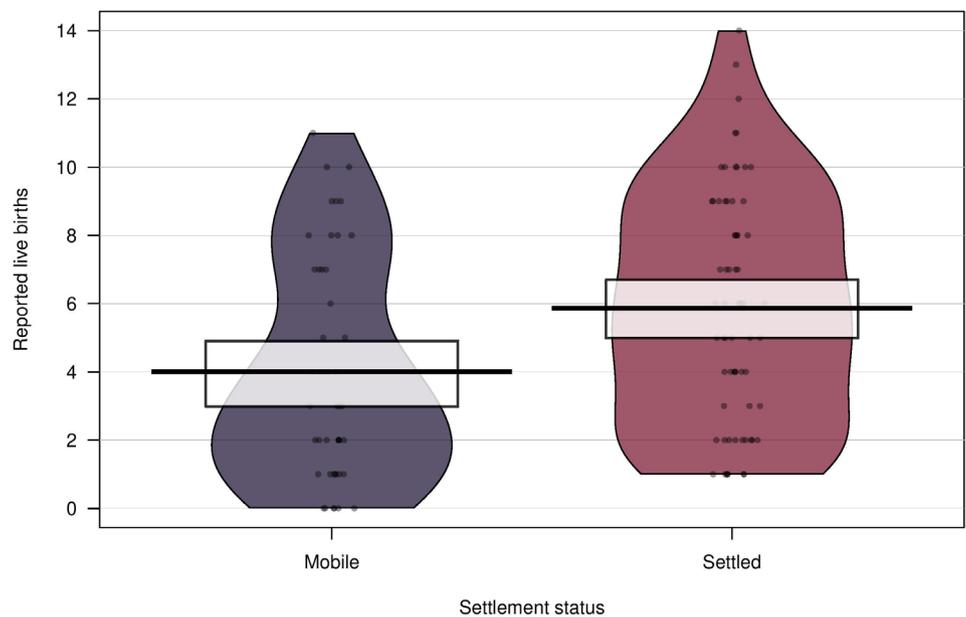


FIGURE 3 The relationship between the reported number of live births and degree of settlement. Settled mothers are those who never moved camps over a 2-year period, while mobile mothers moved camp at least once. The points are the raw data, the colored area is the density curve showing the data distribution, the line is the mean of each group, and the white band is the 95% CI around the mean [Color figure can be viewed at wileyonlinelibrary.com]



increased fertility and population expansion,¹²⁴ Bentley and colleagues conclude they cannot use average TFRs to make predictions about fertility levels based on *subsistence technology alone*, a point which had been previously made.^{61,125} Figure 1 (Table S1) reveals the diversity in the TFR reported in hunter-gatherers, ranging from 2.6 to 8.5, highlighting the issue of variation within this 5–6 average.

The Efe, a Pygmy population who reside within the Congolese jungle, had a reported TFR in 1987 of only 2.6,¹²⁶ while to the south of the continent the Dobe!Kung (Namibia), who reside in the Kalahari savannah, had a TRF of 4.3–4.7 during the 1960s.^{37,39} What accounts for such low fertility rates in two populations residing in very different foraging niches? Researchers have highlighted the high rate of sexually transmitted infections (STIs) across Africa, resulting in pathologically low levels of fertility.^{127,128} The Efe have also been found to have a primary sterility rate of 28%,¹²⁶ perhaps resulting in their significantly lower TFR as compared to neighboring Pygmy populations (Aka = 5.5, Mbuti = 5). While STIs are important predictors of fertility, so are other mechanisms, which modulate females' reproductive effort. Humans have evolved a reproductive system, which is highly responsive to environmental condition, maintained by metabolic and endocrine feedback systems.¹²⁹ Maternal energetics are particularly important predictors of fertility, as multiple elements of the reproductive system respond to breastfeeding (via lactational amenorrhoea,^{130,131} the effects of which are also energetically dependent^{131,132}), dietary,⁵⁹ and activity factors.¹³³ For instance, the Agta have documented TFRs between 6.3 and 7.7 (mean = 6.93) over the last 60 years. While engaging in foraging, the Agta have also historically traded foraged resources for tubers and rice with nearby farmers.¹³⁴ Domesticated grains represent a concentrated source of carbohydrates, which improves nutritional condition and thus reproductive potential.¹³⁵

Beyond inter-population variability, equal attention should be paid to *intra-population* variability. This variability is structured

according to specific behavioral traits that allow for the systematic exploration of the relationship between fertility and subsistence. The HBE framework highlights how individuals rapidly adapt to ecological change by assessing individuals' allocation decisions based on the fitness costs and benefits in a given environment.¹³⁶ To quantitatively test adaptive hypotheses, HBE explore variation in, for instance, fertility between populations as well as between people within these populations. As a framework, it expects and leverages on diversity to better understand why such diversity emerges. By doing so it allows us to systematically explore, which traits (e.g., foraging vs. farming) are predictive of low or high, fertility. The usefulness of this approach is illustrated below with data from the Palanan Agta from the Philippines (see Reference 121 for full analysis and methodology. Further ethnographic information is also available in References 6,1 37, and 138). The use of the Agta case study is not intended to imply this is the “best” data—such a statement would be the antithesis of this paper. Instead, it presents a methodological approach, which leverages on diversity.

The TFR of the Palanan Agta from 2013 to 2014 was 7.7 ($n = 117$). Figure 2 presents the number of reported live births based on the age of the mother ($n = 117$). While the mean number of live births was 5.08 ($SD = 3.44$), there was extreme variation within the population, as women aged 46–55 years had between 4 and 14 live births. This variability was structured by both engagement in cultivation and degree of mobility. Mothers who spent more than 75% of their production activities foraging (compared to cultivation and wage labor) had 1.4 lower age-controlled fertility. However, “farming” does not exist in a vacuum from other traits; farming is closely tied with reductions in mobility and increases in household wealth.¹²¹ Overall, the Agta are a mobile population, moving on average once every 10 days. However, while some households moved more often than this, some never moved residential camps. Settled mothers (defined as those who never moved camp during 2 years of fieldwork) reported

significantly more live births than “mobile” women who moved camp at least once (a mean increase of almost two live births; Figure 3). This relationship appears mediated by maternal energetics as settlement was a significant predictor of maternal body mass index (BMI), which positively predicted fertility.¹²¹ These results highlight that food production is correlated with a number of different traits within the population, such as wealth and mobility. A focus on broad categories such as “hunter-gatherers” as compared to “farmers” risks overlooking the relative importance of these interwoven variables. This approach presents a different way of thinking about fertility and offers a new direction that leverages diversity, which may be particularly useful for modeling demographic trends.

6.2 | Lessons for reconstructing demography in prehistory

Absolute estimates of demographic variables take two main forms in prehistoric contexts: (a) as descriptive values of multiple hunter-gatherer demographic parameters (as in the group size examples discussed in Pitfall four) and; (b) as input values for calculations, equations, or computational models. Modeling approaches are used to gauge trends in population growth and decline, as well as inter-species interactions¹⁰³ and cultural transmission.¹³⁹ While a balance needs to be struck between reality and simplicity in the creation of any model, selecting appropriate input values is of central importance in creating a useful model of population dynamics. Above, we argued that taking “hunter-gatherer” mean or median values are not ideal since (a) hunter-gatherers lack a clear definition, (b) hunter-gatherers are a highly diverse range of populations, and (c) the extensive variability means the average is not an accurate reflection of demographic trends. So, if we cannot use the hunter-gatherer average, what else can we do?

One approach is to take ethnographically relevant comparisons.²⁹ Our knowledge of recent hunter-gatherer demography is heavily skewed toward equatorial, highly mobile, immediate return groups. Therefore, if the prehistoric reference is a large-scale and delayed-returned society then data from groups like the!Kung, Hadza, Ache, or Agta would not be suitable. Instead, comparisons should stem from populations who share these traits, given that mobility and goods accumulation all influence fertility. Such an example is given by Wren and Burke¹³⁹; when modeling the impact of ecological risk on European hunter-gatherer population structure during the last glacial maximum they take the TFR from the Kutchin (4.4) since they resided in comparable sub-arctic conditions in the Canadian Yukon. While this navigates the issues associated with inter-population variability in TFR, it suffers from being reliant on a single data source. As discussed in Pitfall one, ethnographic work is limited by multiple factors, and demographic measures are easily biased by the method and structure of data collection. Therefore, taking the TFR from one population is risky. Furthermore, fertility is reflective of a number of traits, which go beyond geographic location and climate. Ecological similarity cannot be held as proxy for all trends in mobility, subsistence, and goods storage. We argue that we need to go one step further to create more realistic, and thus useful, models of population dynamics.

A improved approach explicitly draws upon the correlations between individual fertility rates and a range of variables—mobility, subsistence, food storage, wealth, and so forth—to provide predictive values applicable to multiple contexts. Regression analyses provide predicted fertility values while controlling for other relationships. Predictive values can be produced for individual variables (i.e., holding other variables constant, what level of fertility is a mobile woman predicted to have?) as well as a cluster of traits (i.e., what is the expected fertility of a foraging woman who is mobile and has little wealth?). Rather than assuming populations are homogenous and overlooking the range of composite traits, which make up a “hunter-gatherer” population, such approaches allow us to establish the relationship between a range of archeologically visible traits and demographic parameters. Such a method provides well-grounded suppositions about how prehistoric hunter-gatherers varied demographically in response to, or as a result of, prevailing socioecological conditions, as well as more relevant input values for computational models.

The Agta is only one population and it would be blinkered to suggest that taking predicted values of a range of traits from a singular population is much better than taking the average TFR. What is required is for anthropologists to systematically improve their understanding of the relationship between subsistence and fertility across a range of populations, from hunter-gatherers, horticulturalist, pastoralists, and agriculturalists. This requires systematically exploring the patterning of human fertility across small-scale societies. By doing so, we can produce a source of data, which goes beyond averages and can be directly used by archeologists in computational modeling as well as interpretation of prehistoric datasets. We hope this piece will stimulate the production of such work, which is sorely required, both for fertility and other demographic processes.

7 | CONCLUSIONS

We have highlighted five key pitfalls faced by researchers seeking to apply demographic data from extant hunter-gatherers to prehistoric contexts. These pitfalls have varying methodological and theoretical implications but share two common elements: (a) they are often caused by poor communication between those studying past and present hunter-gatherers; (b) they mask variation in the demography of hunter-gatherer groups, past and present.

Given the sparse nature of the prehistoric database and the limited range of demographic variables on which it directly informs, data from extant hunter-gatherers will always play a key role in reconstructing prehistoric demography. The specifics of this role will vary depending on the research questions being asked, and whether demography is central or peripheral to these. However, in all cases, it is vital to avoid using demographic data from recent foragers in ways which reproduce a limited view of the present (based on single groups or average values) in the past. Using the example of TFR we have underlined the usefulness of HBE as a framework, which minimizes the risk of using ethnographic data in this way. HBE seeks to

understand the patterning and the reasoning behind human diversity, following the premise that individuals optimize behavioral strategies to particular ecological contexts.^{25,134} Hunter-gatherers worldwide still make allocation decisions based on their mode of subsistence, degree of mobility, and social structures,³⁹ pressures which likely have parallels in prehistory. The recommendation of the use of HBE in prehistoric hunter-gatherer studies is not new,³⁹ but is of clear theoretical benefit,¹³⁵ particularly for research areas such as demography with a fundamentally biological basis. Exploring how hunter-gatherers today respond to different environmental pressures allows us to hypothesize about, and reconstruct elements of, prehistoric demography without relying on assumptions from a few recent foraging populations or on average values, which obscure diversity. Instead, HBE leverages this diversity to understand what predicts it, adding new pathways of investigation, and allowing for a range of possible values to be explored, and their relevance to the prehistoric case assessed. To better understand the demography of hunter-gatherers, past and present, those of us who work with extant hunter-gatherers should aim to improve our datasets by systematically exploring the relationship(s) and patterning of demographic parameters across a range of behavioral variables at the intra- and inter-population level. Concomitantly, archeologists and paleoanthropologists should ensure that they combine an understanding of the limitations and possibilities of demographic data from recent foragers with their expertise on their own paleodemographic methods. We hope that this work presented in this manuscript is a good first step in that direction.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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SUPPORTING INFORMATION

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